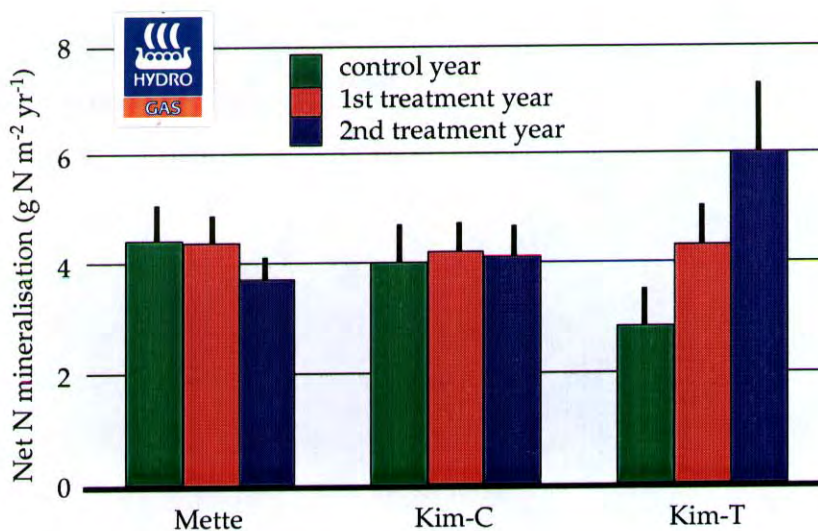


CLIMATE CHANGE RESEARCH

REPORT 9/1997

CLIMEX project: Results from the third year of treatment

May 1996 - December 1996



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Abstract: CLIMEX is an integrated, whole-ecosystem research project studying the response of entire forested catchments to increased CO ₂ and temperature. These whole-catchment manipulation experiments are designed to allow quantification of the links between terrestrial and aquatic ecosystems and provide direct experimental evidence on the effect of climate change on natural forests, terrestrial ecosystems and water resources. The site is located at Risdalsheia, southernmost Norway. Treatment began in April 1994. This report describes results obtained during 1996, the third year of treatment. Significant responses in vegetation, soils and waters were measured.

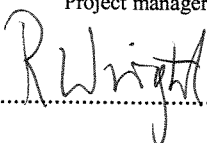
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CLIMEX project:
Report on the third year of treatment
May 1996 - December 1996

Compiled and edited by
A Jenkins
Project Co-ordinator

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Executive Summary

CLIMEX is an integrated, whole-ecosystem research project studying the response of entire forested catchments to increased CO₂ and temperature. This whole-catchment manipulation experiment is designed to allow quantification of the links between terrestrial and aquatic ecosystems and provide direct experimental evidence on the effect of climate change on natural forests, terrestrial ecosystems and water resources.

Changes in ecosystem function observed after 2 years of treatment have largely been consistent with the expected “cascade” of responses. Increased water use efficiency, increased biomass in the shrubs, increased mineralisation of soil organic matter, increased NO₃, NH₄ and TOC concentrations in runoff and increased whole-system respiration all indicate that the N-cycle has speeded up in response to the climate change treatment. In effect, the plants grow more vigorously in response to increased CO₂ and temperature and bacterial decomposition in the soils is increased in response to higher temperatures. The released nitrogen is apparently sufficient to both sustain the increased plant growth and to promote increased nitrogen leakage in surface waters and as gas emissions.

Ideally a further 2 years of treatment would be required to document statistically significant changes in vegetation and soils with respect to N and C. It is unlikely that changes in H₂O fluxes, other than evapotranspiration, will be detected at the level of observation employed. The key questions are now: is the ecosystem a net source or sink of C?; and are the observed responses transient, permanent or the start of an increasing trend?; will the increased N release continue such that increased plant growth can be sustained or is the observed change merely the decomposition of a small labile soil pool of organic matter?

Acknowledgements

The CLIMEX II project is maintained with funding from the Commission of the European Communities (under contract No. ENV4-CT95-0185), Norwegian Ministry of the Environment, the Norwegian Research Council (NFR-NTNF), Hydrogas Norge, the Norwegian Institute for Water Research, the Institute of Hydrology (UK) and the Dutch National Research Programme.

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1. The CLIMEX Project

Alan Jenkins (IH)

CLIMEX (Climate change experiment) is an international, co-operative research project studying the response of entire catchments to increased CO₂ and temperature. The CLIMEX project is located at Risdalsheia, southern-most Norway and involves five catchments and employs multiple treatments and controls (Dise and Jenkins 1995). The objectives of CLIMEX II were:

- * To experimentally enrich with CO₂ and raise the temperature at two entire forested, headwater ecosystems;
- * To investigate the ecosystem response to climate change, in particular the plant-soil-water linkages and processes;
- * To quantify the ecosystem impacts of increased temperature and CO₂, specifically:

Impacts on Vegetation - To determine the effects of increased CO₂ levels and temperature on photosynthesis, growth and nutrition of the dominant species of ground vegetation (*Vaccinium* and *Calluna*) and trees (*Betula* and *Pinus*).

Impacts on Soils - To determine in mineralization of soil organic matter, in soil fauna and biologically-mediated processes in response to increased CO₂ and temperature.

Impacts on Runoff Water - To determine changes in stream water quality and quantity in response to increased temperature and CO₂.

Impacts on Fluxes - To identify whole ecosystem response to increased CO₂ and temperature as reflected in changes in the input-output fluxes of water, nutrients, chemical components and gas flux emissions of N₂O, NO₂ and CH₄ from the manipulated and control catchments.

CLIMEX began in 1993 with installation of the greenhouse facilities. Background (pre-treatment) data were collected during the period April 1993 through March 1994. Treatment began in April 1994 and has continued for a third year.

Boreal ecosystems may be quite sensitive to rising atmospheric CO₂ concentrations and the increased temperatures expected from the associated enhanced greenhouse effect. Of particular importance are the net impacts of such climatic changes on **ecosystem** biogeochemistry. Ecosystem-scale study of biogeochemistry is vital for: (1) Understanding the overall ecosystem functioning in response to global change; and (2) identifying and quantifying the effects on adjacent systems manifest as feedbacks to atmospheric greenhouse gas concentrations and effects on aquatic ecosystems downstream. From numerous plant and pot scale studies of individual ecosystem compartments in laboratories and in field chambers, a plethora of climate change impacts have been identified. Effects on plants often vary with species and the effects of individual processes in ecosystem

biogeochemical fluxes may oppose each other, making it difficult to predict net effects at the ecosystem or landscape scale. Whole-ecosystem manipulation experiments represent the only tool by which ecosystem response can be measured and with which whole-ecosystem models can be tested. Such models are a key to future negotiations on CO₂ emissions control policy and yet they remain invalidated at a scale consistent with their structure.

Increased CO₂ and temperature are expected to affect boreal forest ecosystems at many levels. At the individual plant level, elevated CO₂ is expected to promote increased stomatal closure and decreased stomatal density thereby increasing leaf water use efficiency. This will lead to increased soil moisture manifest in higher water drainage for the same precipitation. Conversely, in some species, elevated CO₂ may increase leaf area so as to nullify the effect of decreased stomatal density on the transpiration loss of the whole plant. Increased temperature may also promote an increase in evapotranspiration to offset the expected increase in drainage water flux.

Increased temperature and longer growing season will tend to increase the volume of standing biomass and annual litter production. We also expect elevated CO₂ to stimulate plant growth even though nutrient availability is low. While nutrient availability may further decrease as a result of increased growth, increased temperature is expected to oppose this effect by stimulating decomposition of litter and mineralization of nutrients, especially of N. These responses should occur rapidly, ie within a few years. While soil and plant respiration will increase, fixation of C in biomass plus litter is expected to exceed total respiration, and making the system a net sink of CO₂-C. Mineralized N will largely be taken up by the increased plant and microbial biomass, so that leaching of inorganic N into drainage water will remain low.

The relatively rapid changes in the biotic compartments are expected to be followed by slower changes in the large, recalcitrant pools of humidified soil organic matter. Several authors provide evidence for production of more recalcitrant plant litter at high CO₂, due to lower N contents and an increase in secondary metabolites capable of slowing down decomposition. Recent reports cast considerable doubt on this scenario, at least in case of unfertilized plants in natural vegetations. But even if plant material formed at elevated CO₂ were more refractory, its slower decomposition would probably be apparent only in the first few years after being added to the pool of soil organic matter. Higher temperatures, on the other hand, would stimulate decomposition of all soil organic matter fractions, litter and older humic material. Therefore, climate treatment is expected to lead to more rapid decomposition of soil organic matter, making the system a net source of CO₂. Because dissolved humic substances and organic acids are decomposed more rapidly at higher temperatures, we also expect a decrease in the flux of dissolved organic material in drainage water.

Only part of the nitrogen released from the shrinking pool of soil organic matter is likely to be accommodated by increased biomass, which is expected to reach a steady state before the SOM pool. This should lead to increased discharge of inorganic N in the drainage water. The more rapid cycling of N may lead to increased soil emissions of N₂O, NO and NO₂. Drainage water nitrate fluxes will also be less if the species composition of the vegetation responds to the increasing nutrient availability.

2. Site Operation

Richard F. Wright and Anke Lükewille (NIVA)

At KIM catchment (CO₂ and heating) the systems generally functioned satisfactorily during 1996. The CO₂ was turned on to the target level of 560 ppmv from 20 April 1996 through 7 November 1996 (Figure 2.1). This level was generally achieved except during summer days when overheating required high rates of ventilation. The 2 “spikes” in June and September were days during which the trace gas team of ITE closed down the CO₂-dosing system to measure trace gas sources/sinks. CO₂ consumption was 70 tons in 1996 (101 tons in 1994; 70 tons in 1995/ the larger sum for 1994 is due to the filling of the tanks at the end of 1994 in preparation for the spring of 1995).

At KIM catchment the air heating system worked satisfactorily during 1996 (Figures 2.2a and 2.2b). The target values were generally met although the increase was somewhat lower than targeted during the coldest periods of the winter, and somewhat higher during mid-summer due to insufficient cooling. These deviations from the targets reflect inherent limitations in the design of the heating and ventilation systems for the greenhouse.

At KIM catchment relative humidity was somewhat higher in the treated section than in the control section (Figure 2.3a and 2.3b); this also was the case in 1994 and 1995. Only two sensors are available; one of these was moved from KIM-T to the outside in April 1996 to allow assessment of the difference in relative humidity KIM-C and OUT. From these data it appears that the relative humidity is somewhat lower in KIM-C relative to OUT (Figure 2.3a and 2.3b).

Measurements of light in 1996 (as in 1994 and 1995) show beneath the roofs that the roof structures block about 50% of the incoming light (Figure 2.4). During summer 1996 problems with the data loggers and sensors made the data unreliable and these are excluded.

At EGIL catchment (soil heating) the heating cables functioned throughout 1996 with the exception of short periods due to power supply failures or where data were lost due to problems with the data loggers (Figure 2.5a and 2.5b). During the late autumn and winter months the systems cannot achieve the target temperature increase completely.

The sprinkling systems for precipitation functioned satisfactorily at both KIM and EGIL catchments during 1996. The lack of snow beneath the roofs was as usual compensated by adding extra water (ion-exchanged with appropriate additions of seasalts and acid) during the spring.

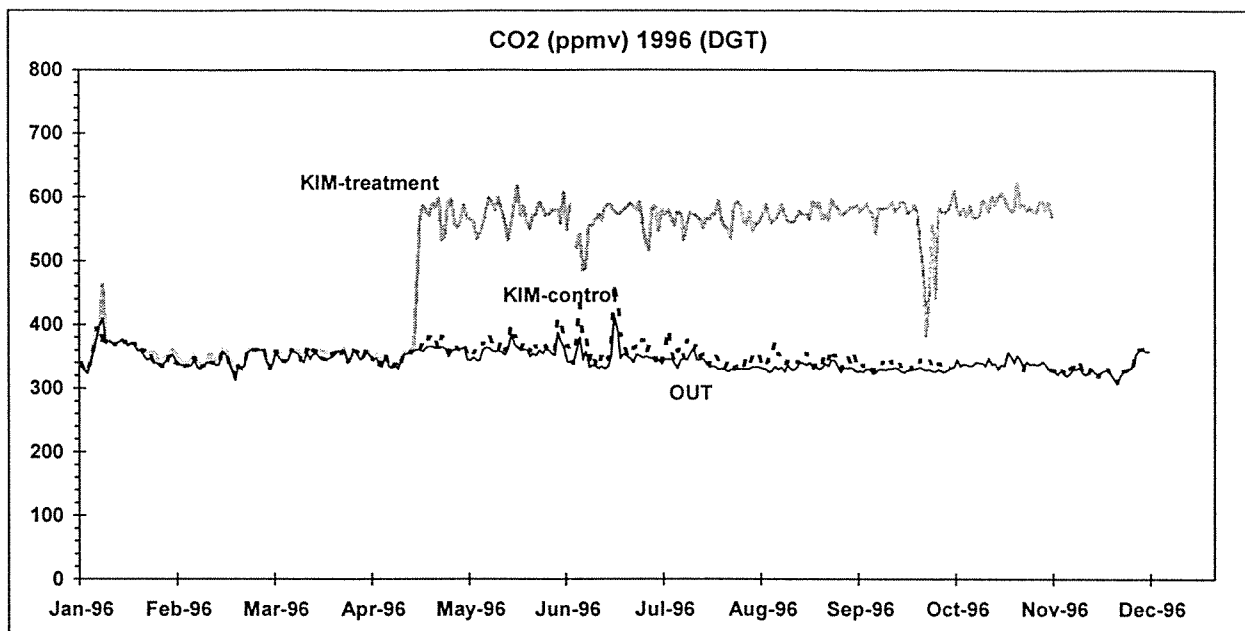


Figure 2.1
CO₂ concentrations (ppmv) in air at KIM treatment, KIM control and outside during 1996, the third year of treatment.

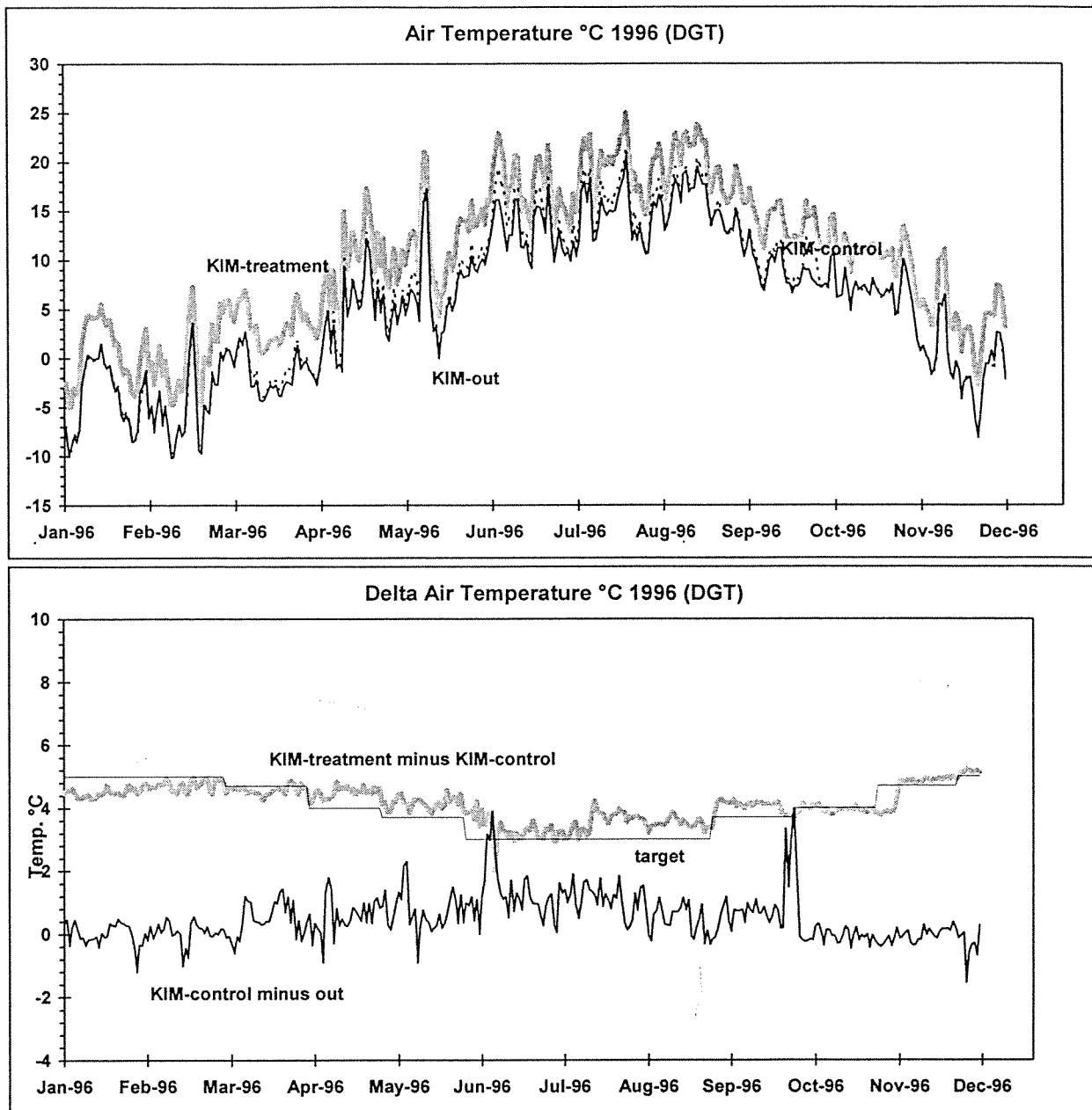


Figure 2.2

Air temperatures ($^{\circ}\text{C}$) at KIM treatment, KIM control and outside during 1996, the third year of treatment. Upper panel: measured temperature. Lower panel: temperature differences and target levels.

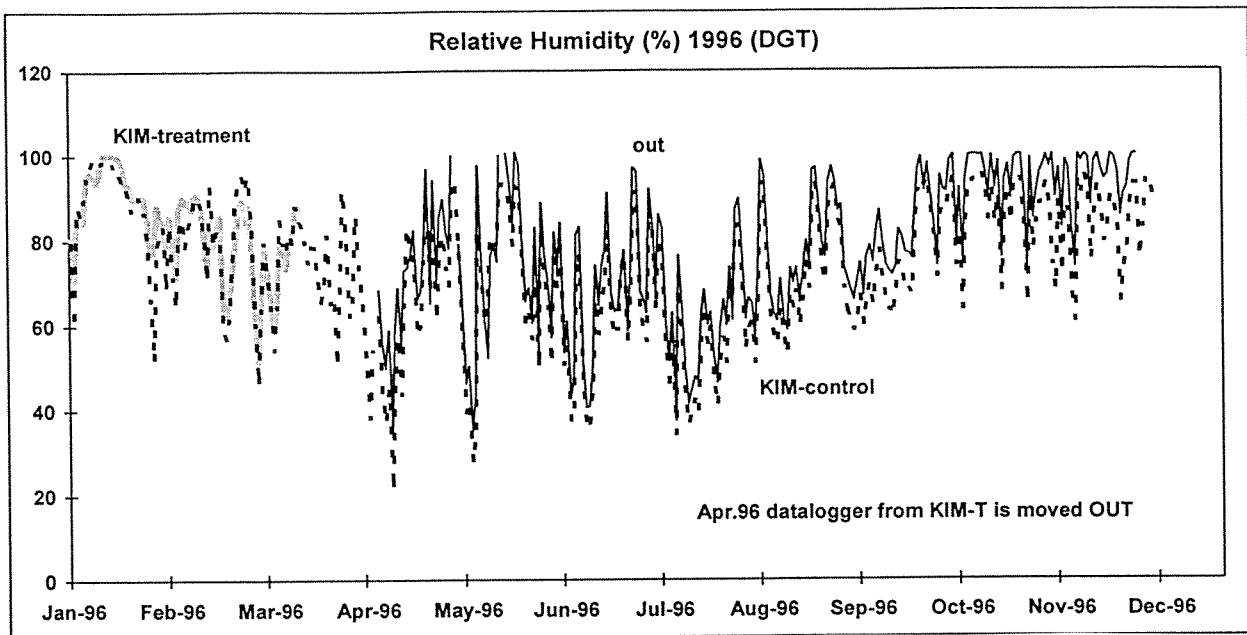


Figure 2.3
 Relative humidity (%) at KIM treatment and KIM control during 1996, the third year of treatment. Only two sensors were operative during 1996. In April the sensor in KIM-T was moved to outside.

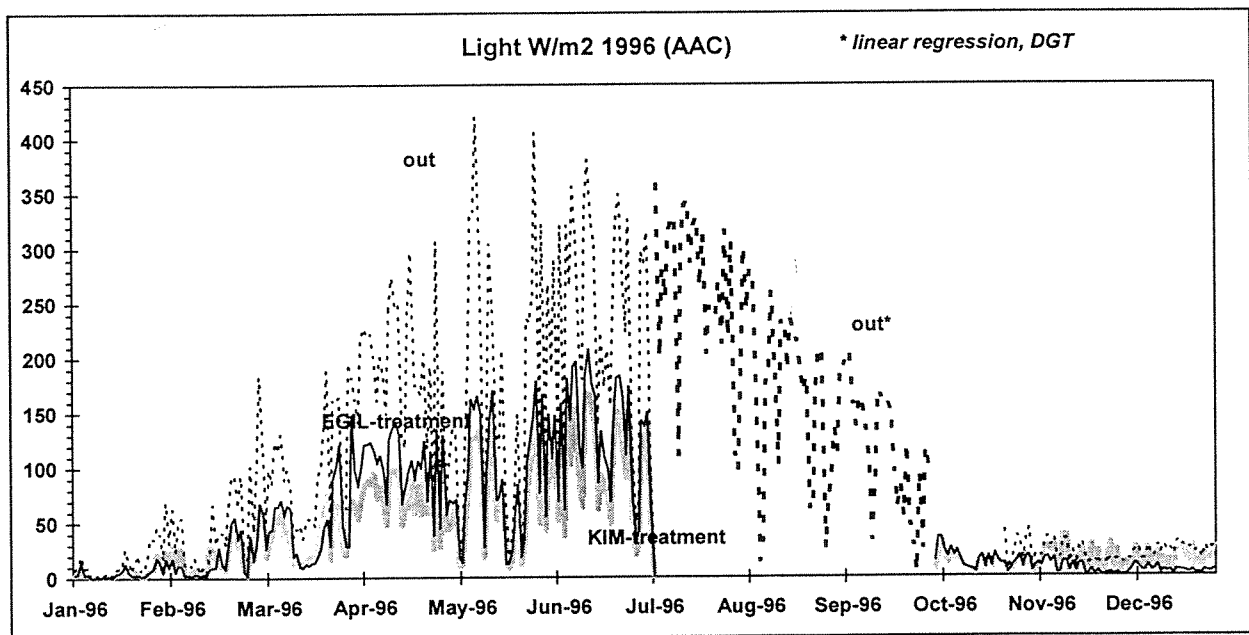


Figure 2.4
 Light (W/w^2) at KIM, EGIL and outside during 1996, the third year of treatment. During the period July to October the datalogger was not functioning. Another datalogger was in operation outside and the data shown here are estimated from linear regression of the data from the two loggers for the first half of 1996.

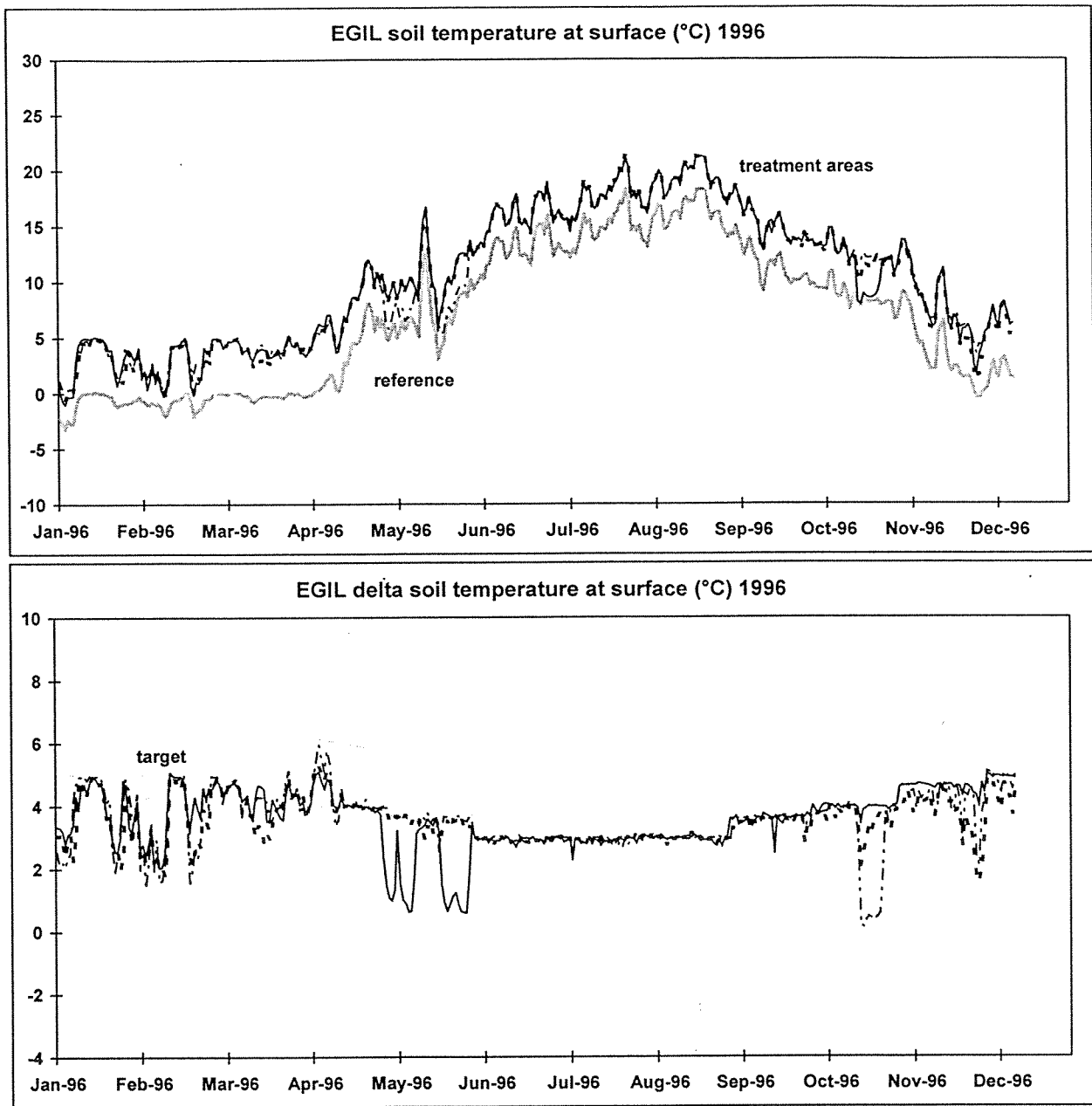


Figure 2.5
 Soil temperatures ($^{\circ}\text{C}$) at the soil surface at EGIL treatment and EGIL control during 1996, the third year of treatment. Upper panel: measured treatment. Lower panel: temperature differences and target levels.

3. Water Chemistry

Richard F. Wright and Anke Lükewille (NIVA)

Runoff samples from the five CLIMEX catchments were taken weekly during 1996 and water was analysed for H^+ , Na^+ , K^+ , Ca^{2+} , Mg^{2+} , Al, NH_4^+ , NO_3^- , Cl^- , SO_4^{2-} , TOC (total organic carbon), SiO_2 , tot-N (total nitrogen) and tot-P (total phosphorous). Sampling and analysis methods are described by Wright and Lükewille (1996).

Nitrate and Ammonium Concentrations

The general patterns measured during 1994 and 1995, the first two years of treatment, continued during 1996, the third year of treatment (Wright and Lükewille, 1996). At the reference catchments CECILIE, METTE and ROLF the concentrations of NO_3 and NH_4 were very similar and showed a strong seasonality (Figures 3.1 and 3.2). Concentrations were higher during the winter, spring and autumn and somewhat lower during the summer growing season. High rainfall in the autumn appears to dilute NO_3 in runoff.

The winter of 1995-96 was “normal” in that ambient air temperature was often below zero. Temperatures were below zero during periods in January also inside KIM-T. During 1996 NO_3 concentrations at KIM-T were again systematically higher than KIM-C. The concentrations at KIM-T also showed the seasonality with generally lower concentrations during the summer, with the exception of the first runoff following dry periods (Figure 3.1). NH_4 concentrations showed the same patterns (Figure 3.2).

At EGIL the NO_3 concentrations generally followed those of the three reference catchments, but at a higher level (Figure 3.1). Concentrations generally followed the same pattern as ROLF, but at high levels. NH_4 concentrations at EGIL were higher during the second half of the year compared to the reference catchment ROLF (Figure 3.2).

Organic Nitrogen and Total Carbon Concentrations

In 1996 as in previous years, organic N as well as total C concentrations at the control catchments followed the air (and soil) temperature curves (Figures 3.3 and 3.4). They increased with rising temperatures in spring and decreased during autumn and winter. During the winter months organic-N and TOC concentrations are higher at KIM-T than at KIM-C (and the reference catchments).

Randomised Intervention Analysis

To test the significance of changes in concentrations of major elements and compounds measured in runoff, Randomised Intervention Analysis (RIA) was used (Carpenter *et al.*, 1989). RIA compared paired, chronologically-ordered samples for pre- and post-manipulation periods from treated (EGIL) and untreated (ROLF) catchments. The changes in mean inter-catchment differences of major parameters were computed for each of 1000 random assignments. The actual mean difference between pre- and post-treatment periods

was compared to the frequency distribution of mean differences obtained from the 1000 randomly ordered assignments.

The technique is not appropriate for KIM catchment, because the clean rain treatment has resulted in major differences in runoff chemistry prior to onset of CLIMEX at KIM relative to all the other catchments. Unfortunately there are no pre-CLIMEX data from KIM-C.

Pre-treatment samples analysed within the RAIN project were paired for the period June 1991 to July 1994 (n = up to 60). 1991 was chosen because at that time a new equilibrium between clean rain input and output was established, ie no trends in SO₄, NO₃, ANC concentrations were observed. The post-treatment period was end of July 1994 to December 1996.

RIA analysis indicates that after 2½ years of treatment soil warming at EGIL catchment caused a significant increase in NO₃, NH₄, TOC, SO₄ and SBC (sum base cations) concentrations in runoff relative to ROLF (Figures 3.5 and 3.6).

Total N input was reduced by about 90% in 1984 when the clean precipitation treatment at KIM started (RAIN project). The catchment thus went from N-saturated (about 30% of input N was lost in runoff prior to 1994) to N-limited in 1994 when the CLIMEX manipulation began. At all other experimental catchments at Risdalsheia a significant fraction of the N input is lost in runoff at NO₃ and NH₄.

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NO₃

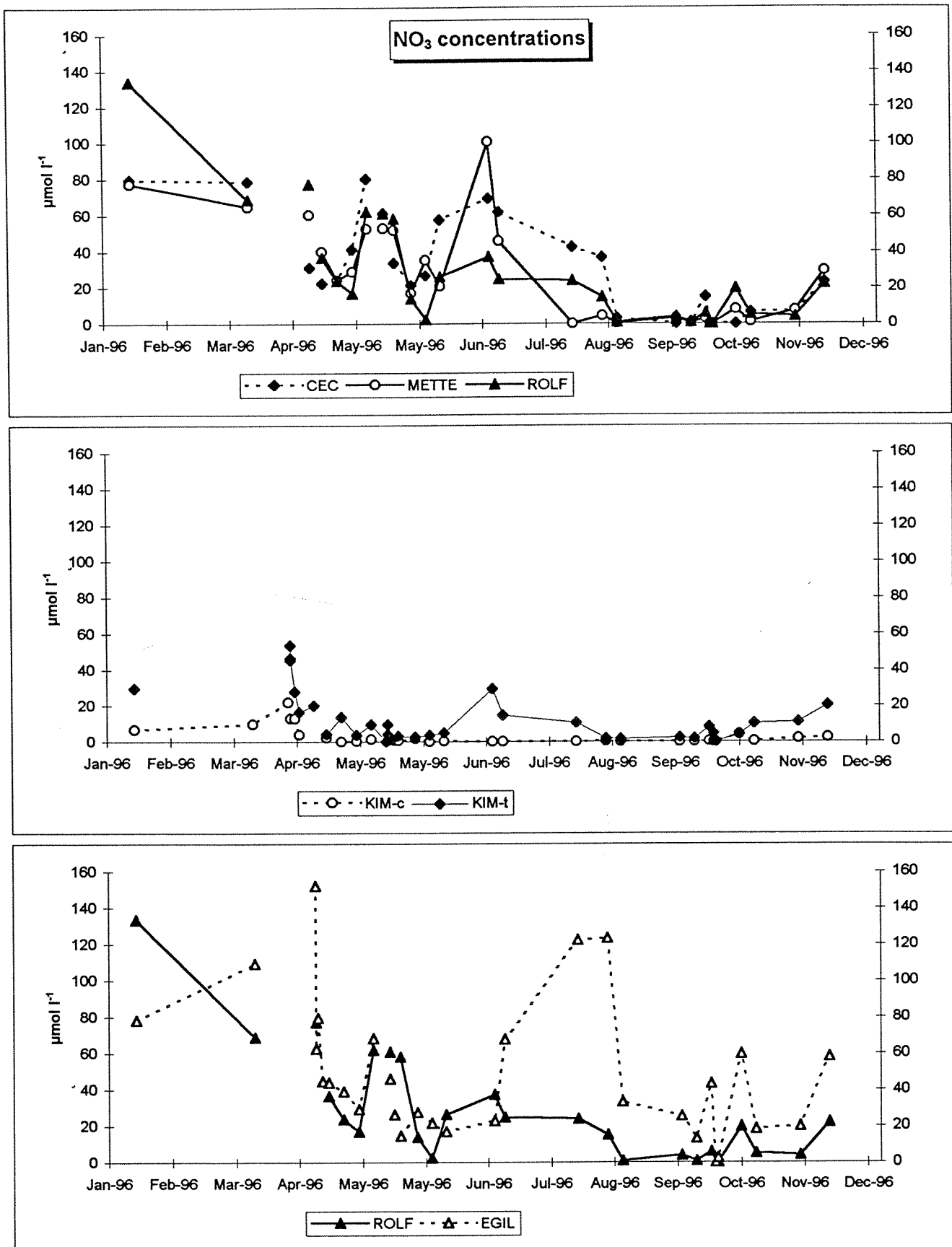


Figure 3.1
Nitrate concentrations at control and treated catchments in 1996.

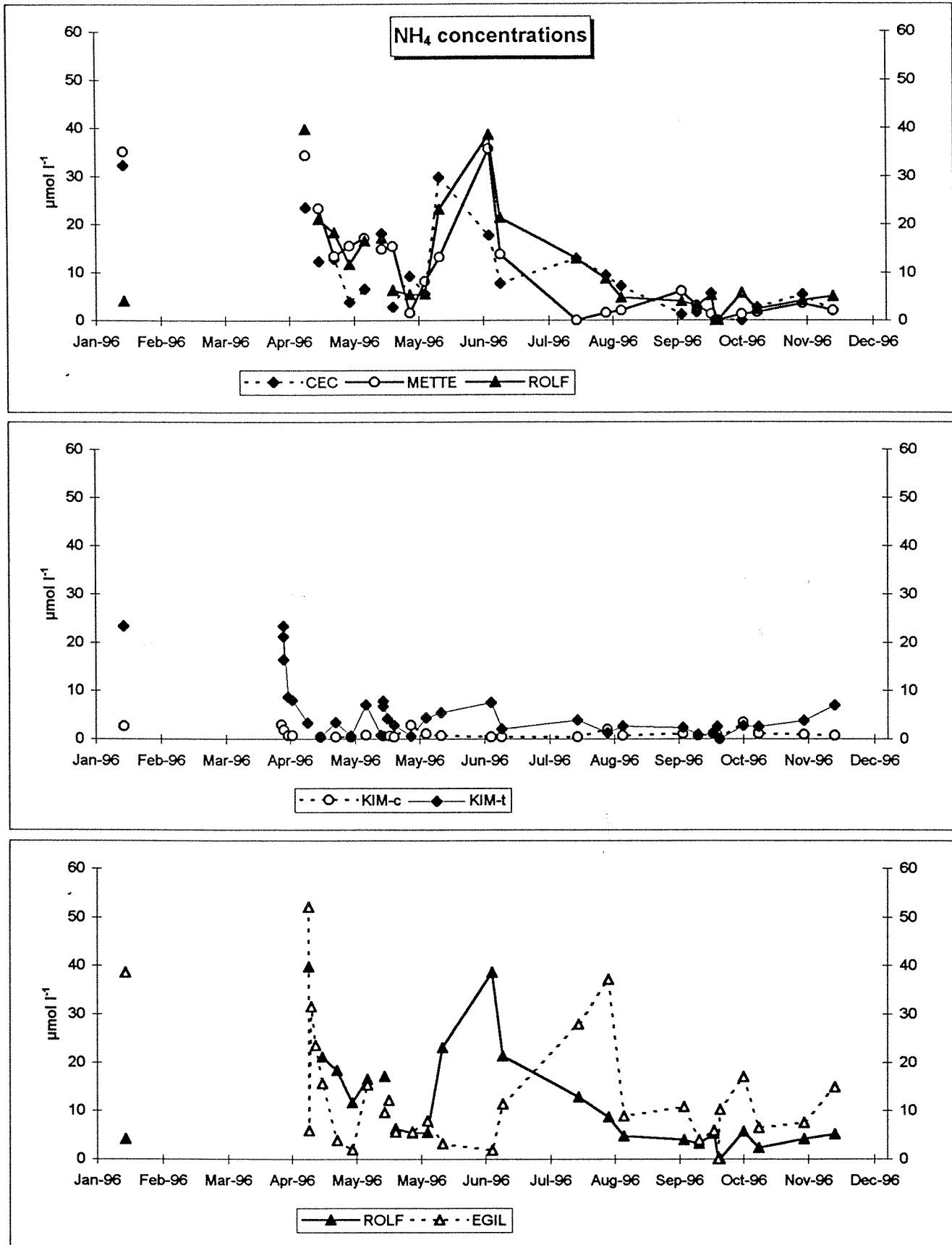


Figure 3.2
Ammonium concentrations at control and treated catchments in 1996.

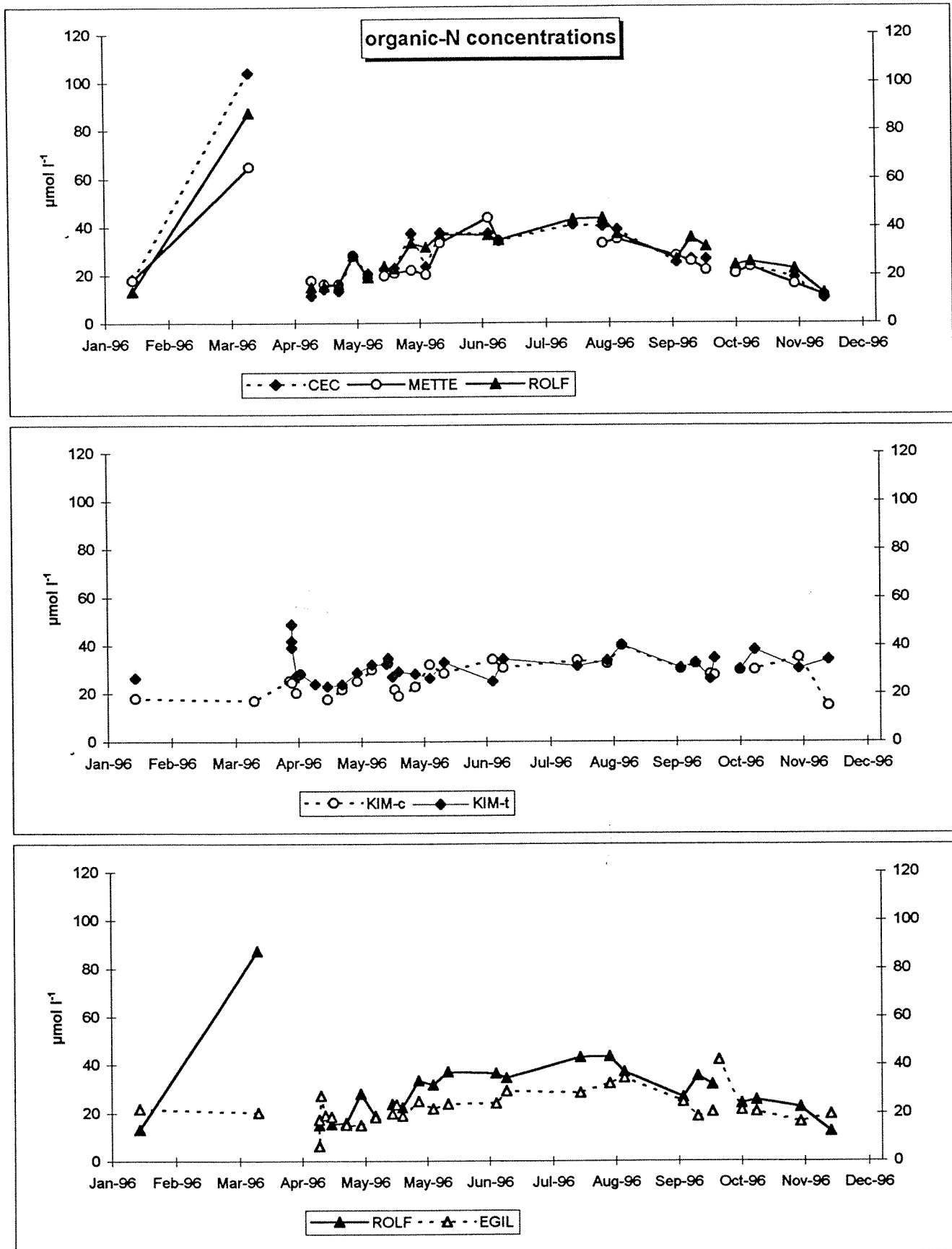


Figure 3.3
Organic nitrogen concentrations at control and treated catchments in 1996.

TOC

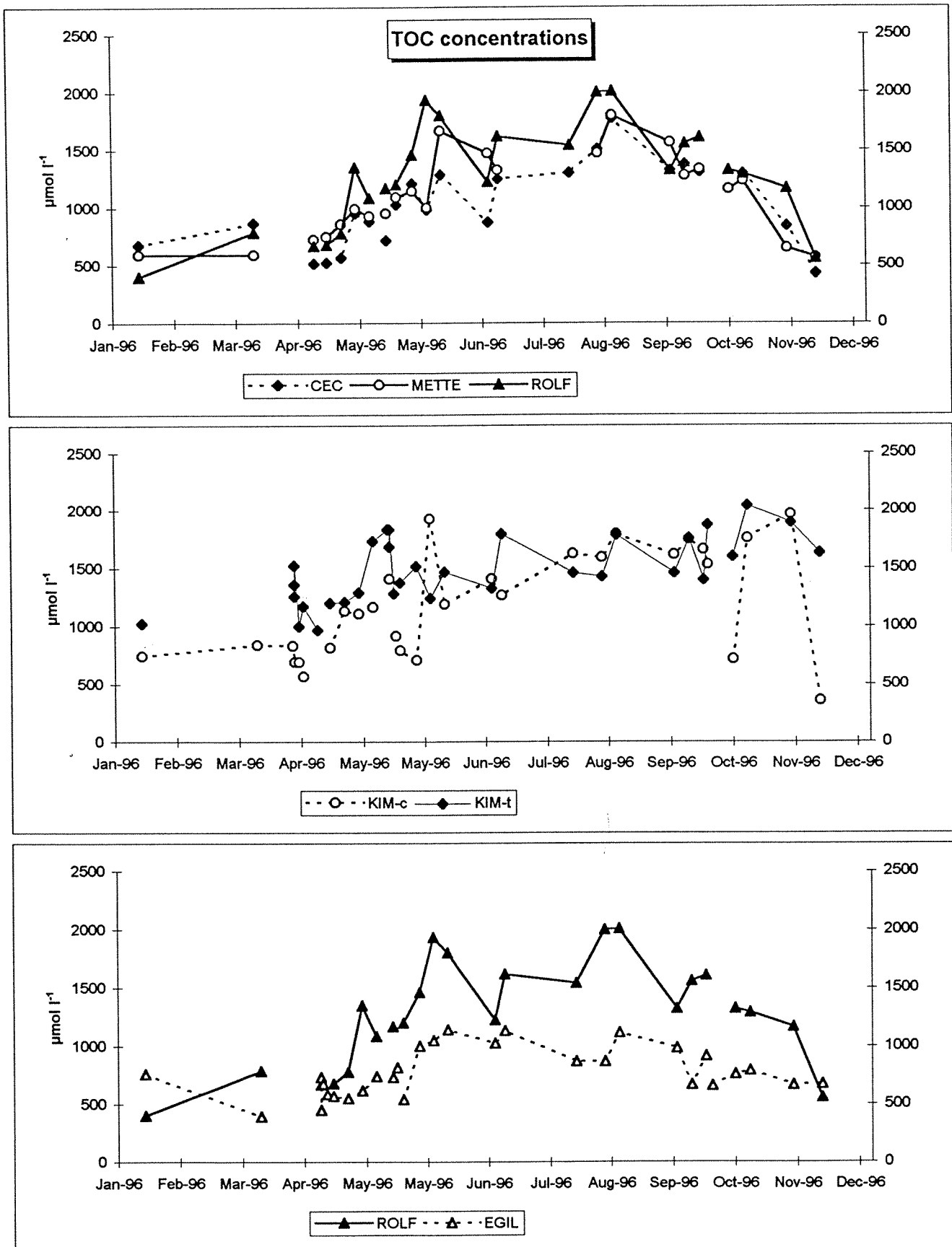


Figure 3.4
Total carbon concentrations at control and treated catchments in 1996.

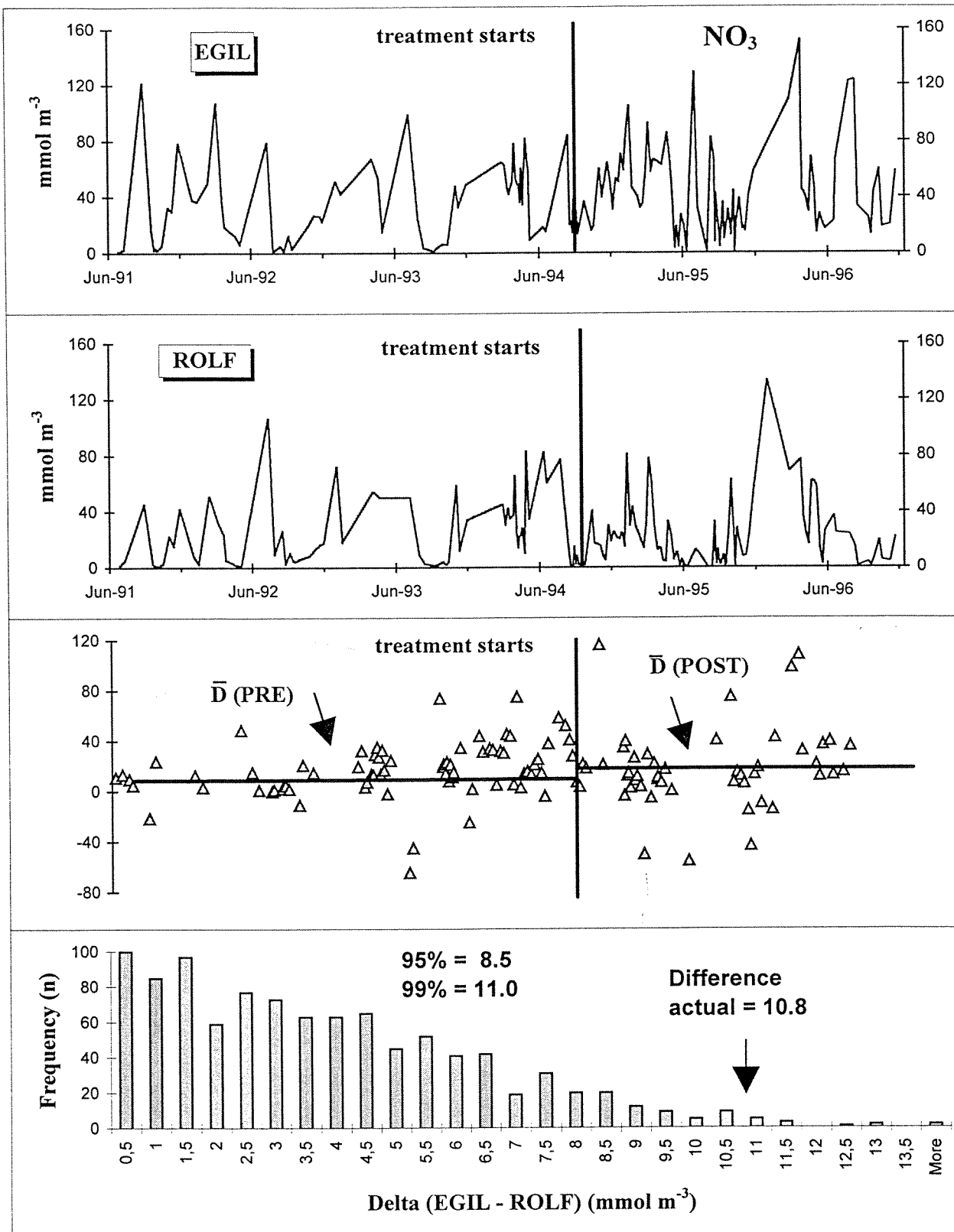


Figure 3.5
Randomised intervention analysis of nitrate concentrations in paired samples of runoff from EGIL (soil warming) and ROLF (reference) catchments for the pre-treatment period June 1991 - June 1994 and the first 2½ years of treatment June 1994 - December 1996.

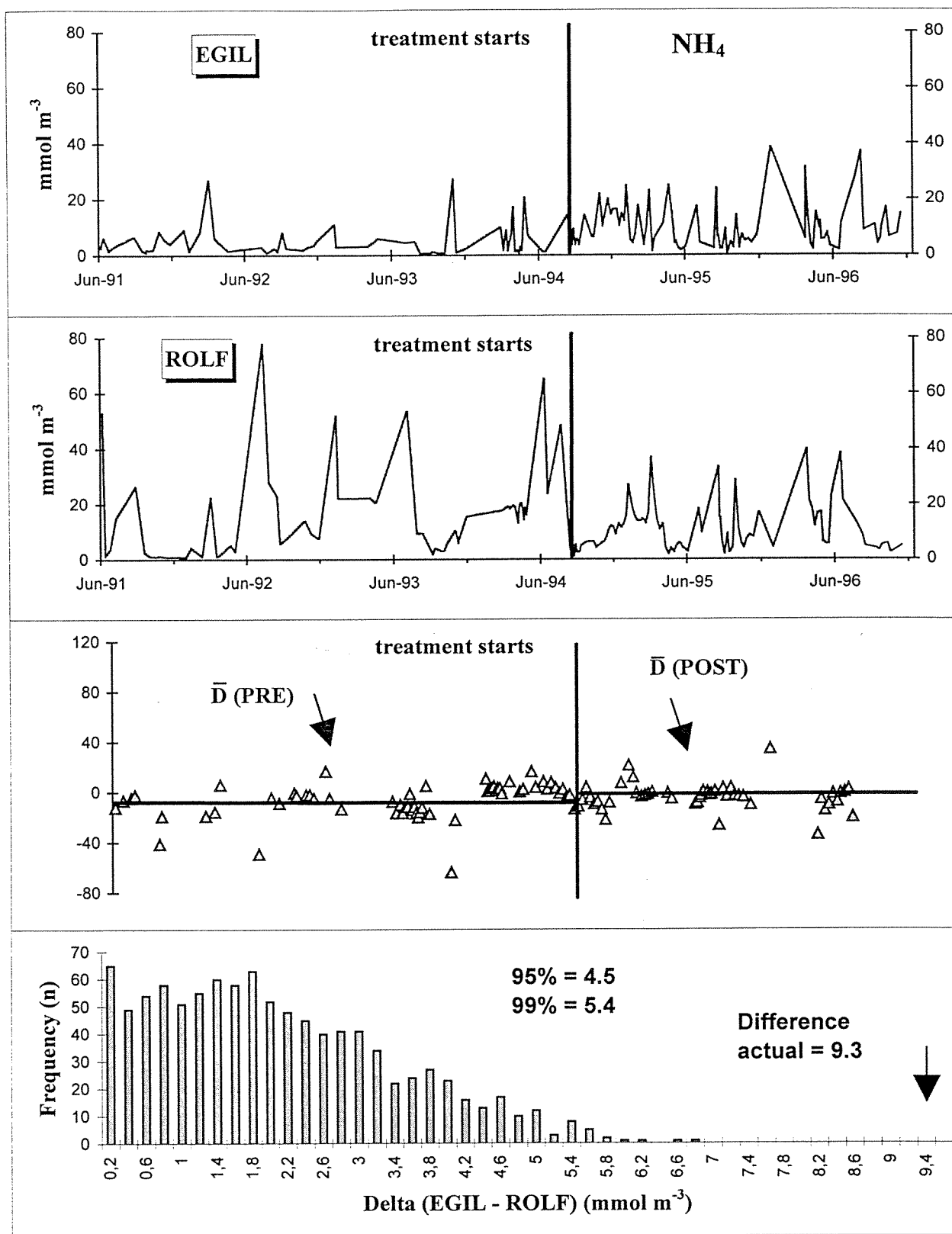


Figure 3.6
 Randomised intervention analysis of nitrate concentrations in paired samples of runoff from EGIL (soil warming) and ROLF (reference) catchments for the pre-treatment period June 1991 - June 1994 and the first 2½ years of treatment June 1994 - December 1996.

4. Soil Moisture Responses

R. Collins and A. Jenkins (IH)

KIM Catchment Soil Moisture Content

The soil moisture time series data for the control and treatment areas of KIM from May to August in both 1995 and 1996 are illustrated in Figure 1. The area under each time series response represents the cumulative daily soil moisture for each month and this is summarised in Table 1. The time series reflect the response of two 35 cm tdr probes installed vertically in the soil which best represent the average change in soil moisture content in the control and treatment areas, respectively. The soil in the control section is generally significantly drier than in the treatment, the fast drainage and rapid hydrological response reflecting its topographical position at the top of the catchment.

A relatively high soil moisture content (c. $0.5 \text{ m}^3/\text{m}^3$) was maintained in the treatment area throughout May and June in both 1995 and 1996 but this was followed by a steady drying of the catchment during July in both years. In the absence of significant rainfall in July 1995, loss through evapotranspiration decreased the soil moisture content from 0.4 to $0.1 \text{ m}^3/\text{m}^3$, the catchment continued to dry until mid August with soil moisture content falling to below $0.05 \text{ m}^3/\text{m}^3$. The response of tdr probes located in deep soil pockets and pressure transducer time series data indicate that during this period remaining moisture was located at the soil rock interface and held at very high tension within the soil pores. Consequently, it was likely to be unavailable for root uptake, accentuating plant stress. In contrast, rainfall during late July and early August 1996 maintained higher moisture levels in the catchment, reflected by a cumulative daily soil moisture content of 11.89 m^3 during August in the treatment area, contrasting with 5.3 m^3 in 1995. Twelve hours of rainfall were required to initiate runoff following the extremely dry period in August 1995, flushing out high concentrations of nitrate. The antecedent soil moisture status is, therefore, clearly a fundamental control upon the hydrochemical response of the catchment.

During late August catchment soil moisture levels return to those of June reflecting increased rainfall and decreased evapotranspiration losses.

	Control '95	Treatment '95	Control '96	Treatment '96
May	8.04	11.34	8.08	11.27
June	10.12	14.38	7.29	13.10
July	6.17	8.87	5.02	11.38
August	7.94	5.30	5.70	11.89

Table 1

Cumulative daily soil moisture content m^3/m^3) KIM Catchment.

Modelling the Effect of Change in Organic Matter Content

Enhanced rates of soil organic matter decomposition caused by the higher temperature in KIM treatment may exceed the increase in net primary productivity. This conjecture is tentatively supported by the initial gas flux measurements in KIM which indicate that the catchment is a net source of C, potentially, therefore, a long term loss of soil organic matter could result caused soil structure to be diminished. A loss of structure will cause a shift in the soil moisture characteristic curve such that, for a given tension, less moisture will be held by the soil. Consequently, porosity and saturated hydraulic conductivity (K_{sat}) will increase, resulting in a hydrologically more responsive soil. Conversely if the catchment is shown to be a net sink for C, soil organic matter may increase, promoting moisture retention down the profile. Figure 2 illustrates an attempt to model the effect of soil organic matter depletion upon runoff at EGIL catchment. In scenario 2, K_{sat} and porosity are increased and the characteristic curve shifted to the left (alpha parameter) in the mineral layer relative to present day, scenario 1. However, the net result is a negligible change in runoff since the increase in hydrological response in the mineral layer is counterbalanced by a physical loss of 2 cm of the organic rich surface layers which provide a rapid flow pathway. In the absence of data describing the loss or gain of organic matter over time, such estimation of the alteration of soil structure is likely to introduce considerable error into the modelling scenarios.

	Scenario 1	Scenario 1	Scenario 2	Scenario 2
	organic layer	mineral layer	organic layer	mineral layer
K_{sat}	0.2 m/hr	0.04	0.2	0.1
Porosity	0.75	0.55	0.75	0.7
Alpha	-0.23	-0.185	-0.23	-0.23
Depth	6 cm	variable	4 cm	variable

*Table 2
Model parameters used under each scenario.*

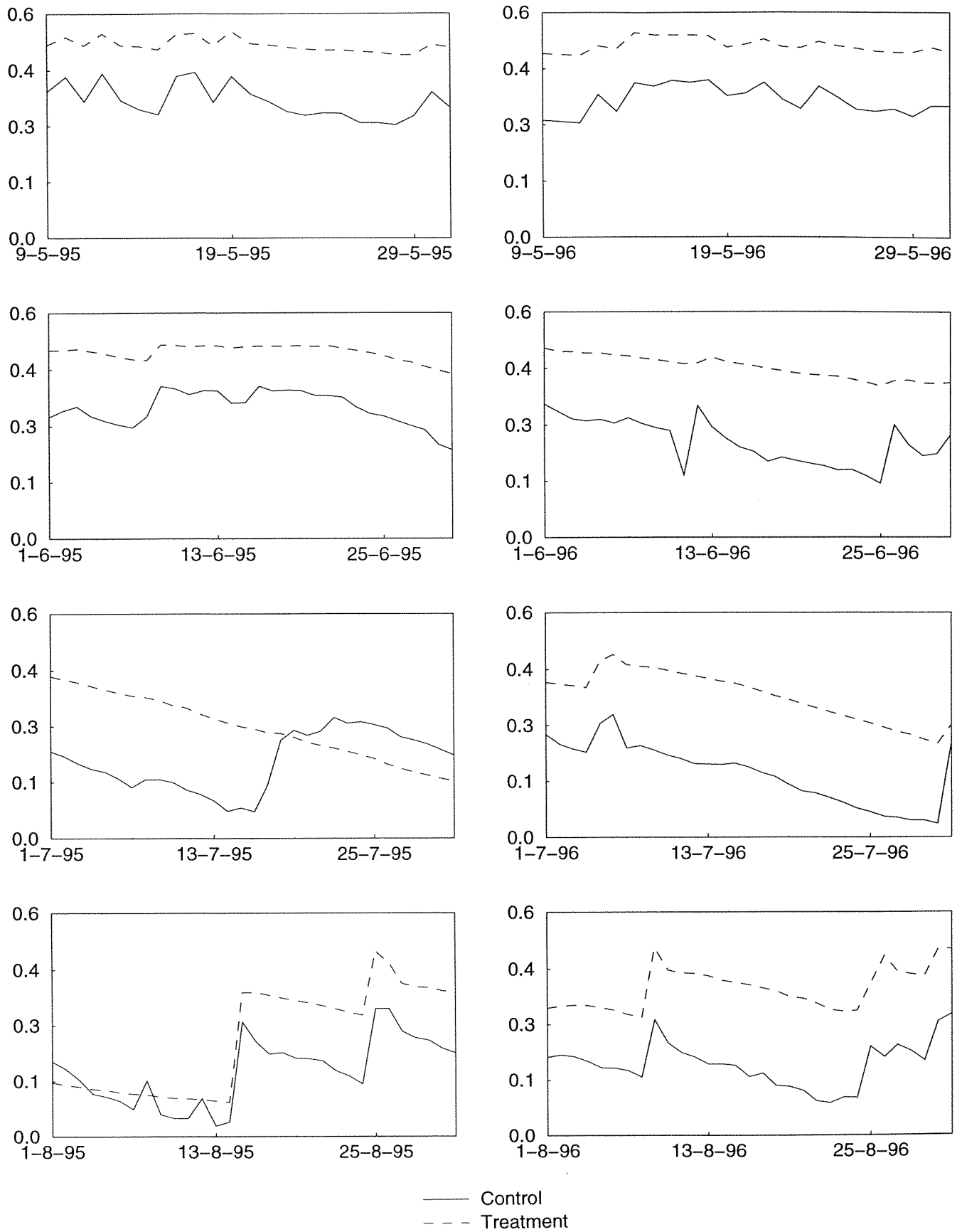


Figure 1
 Soil moisture content (m^3/m^3) - KIM catchment.

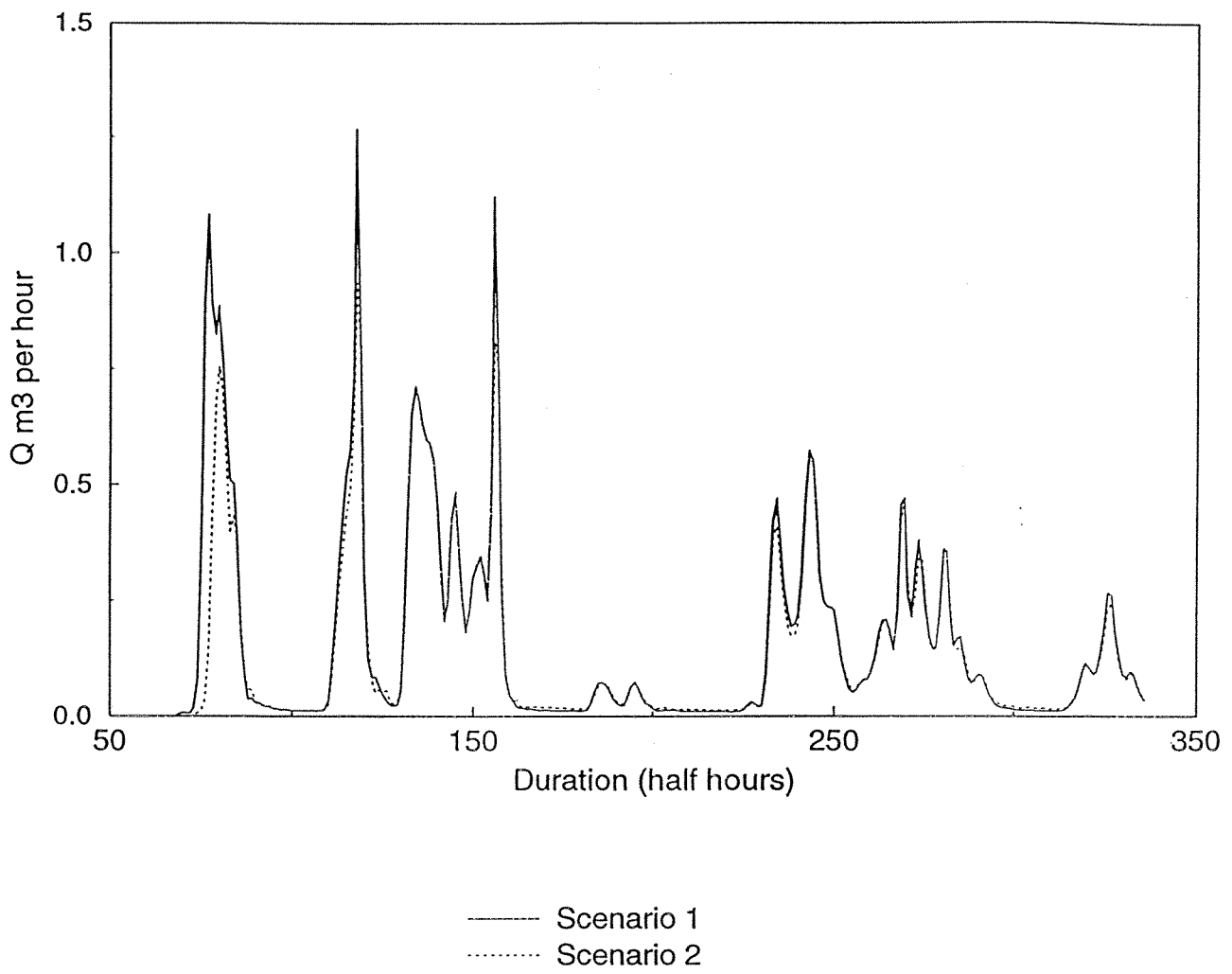


Figure 2
Runoff - EGIL January 1995.

5. Decomposition of Soil Organic Matter

Paul Verburg and Nico van Breemen (WAU-SSG)

Nitrogen mineralisation

Nitrogen mineralisation was measured under field conditions by incubation of undisturbed soil cores. Measurements were carried out in KIM, EGIL and METTE in plots dominated by either *Calluna vulgaris* or *Vaccinium myrtillus*. In the first year of treatment, in both EGIL-T and KIM-T a (non-significant) increase in annual mineralisation was found. In the second treatment year however, a significant increase in mineralisation especially in *Calluna* plots in KIM-T was observed. No change in N mineralisation was observed in the control areas EGIL-C, KIM-C and METTE (Figure 1). The treatment effect was particularly strong in winter.

Decomposition of litter

The influence of temperature and substrate quality on decomposition of fresh litter under field conditions was assessed using litterbags. Litter of birch trees grown at 350 and 700 ppm CO₂ was incubated in all catchments. Litterbags (mesh size of 1.5 mm) were retrieved every 6 months. Analysis of variance on the percentage weight remaining showed that the high-CO₂ litter decomposed significantly faster than the low-CO₂ litter. In addition, decomposition was higher in the control than in the treatment sections. This effect was strongest in EGIL, and may be due to desiccation of the litter by the heating cables. In KIM, at several sampling times, the litter also appeared to be drier in the treatment sections which may depress decomposition rates. However, we do not have evidence that this difference in moisture content is sustained throughout the year.

Gross N fluxes in organic surface horizons.

We incubated soil material from two organic surface horizons (LF and H) in the lab at 5 and 15°C to determine the effects of elevated temperature on C and N mineralisation. The combination of a ¹⁵N addition and modelling allowed for calculation of gross N fluxes. Data on extractable NH₄⁺ and NO₃⁻, microbial C and N, respiration were used for calibration of the model. The incubations lasted 2 weeks. The simulations showed that in the LF layer both gross mineralisation as well as immobilisation increased at elevated temperature. However, net mineralisation did not increase. In the H layer, neither gross and net mineralisation nor immobilisation increased at elevated temperature. Based on C/N ratio of the microbial biomes we concluded that the microbial population in the litter layer was dominated by fungi whereas bacteria were dominant in the fermentation layer. The absence of a clear temperature response in the H layer could be due to direct uptake of organic N by bacteria since the ¹⁵N signal only allows for quantification of gross inorganic N fluxes.

Below ground C inputs

In a greenhouse experiment we quantified the change in belowground C inputs for heather as a function of CO₂ and N. Seedlings of *Calluna vulgaris* were grown at 380 and 580 ppm

CO₂. In each CO₂ treatment, two N levels were maintained. After two months, plants were pulse labelled by exposing them to ¹⁴C-CO₂ for one day. Three weeks later, the plants were harvested and ¹⁴C contents of plant, soil and soil/root respiration were measured. Total dry weight of the plants was not affected by the CO₂ treatment but almost doubled at elevated N. Root growth did not increase at elevated CO₂. Relative distribution of ¹⁴C was not affected by CO₂ suggesting that at elevated CO₂, more C is added to the soil only when the total biomass increases. At elevated N more ¹⁴C is allocated to the shoots (Table 1). Consequently, more C will be added to the soil as root deposits if the increase in biomass offsets the shift in C allocation to shoots. After the harvest, the labelled soil was incubated separately. Respiration of labelled root deposits was initially stimulated by CO₂ and N. However, respiration rates correlated well with ¹⁴C microbial biomass and ¹⁴C in roots. Therefore, the respiration rate reflects a direct effect of roots on size of microbial biomass rather than differences in substrate quality of rhizodeposits.

Discussion

The increase in N mineralisation fits well with the observed increase in biomass as well as increased N in runoff. However, the litterbag study suggests that the increased N mineralisation is not due to increased litter decomposition but may be due to decomposition of 'old' organic matter deeper in the soil. In addition, the ¹⁵N addition experiment suggests that on the short term, an increase in temperature does not automatically result in increased net N mineralisation. However, on the longer term N mineralisation has to occur since continuous immobilisation would imply accumulation of microbial N. We expect that microbial growth will ultimately be restricted either by predation by soil mesofauna or by C limitation of the substrate. The ¹⁴C labelling experiment suggests that only more C will be deposited in the soil below ground if total biomass increases. However, also N availability increases due to increased mineralisation at elevated temperature. Consequently relatively more C will be allocated to the shoots. The response of the vegetation in terms of biomass production will determine whether more C will be added to the soil as rhizodeposits.

	L-N ¹	L+N	H-N	H+N	CO ₂	N	CO ₂ *N
Shoot	46.1	66.6	49.3	68.0	ns ²	***	ns
Root	17.3	10.2	17.3	9.3	ns	***	ns
Soil residue	11.1	6.1	8.9	6.2	ns	***	ns
SMF ³	0.4	0.4	0.4	0.4	ns	ns	ns
Respiration	25.2	16.8	24.2	16.2	ns	***	ns

¹ L-N = ambient CO₂, low N; L+N = ambient CO₂, high N; H-N = elevated CO₂, low N; H+N = elevated CO₂, high N.

² * p < 0.1; ** p < 0.05; *** p < 0.001; ns = not significant.

³ SMF = Soil microbial flush after fumigation

Table 1
Relative distribution (%) of ¹⁴C in plant and soil

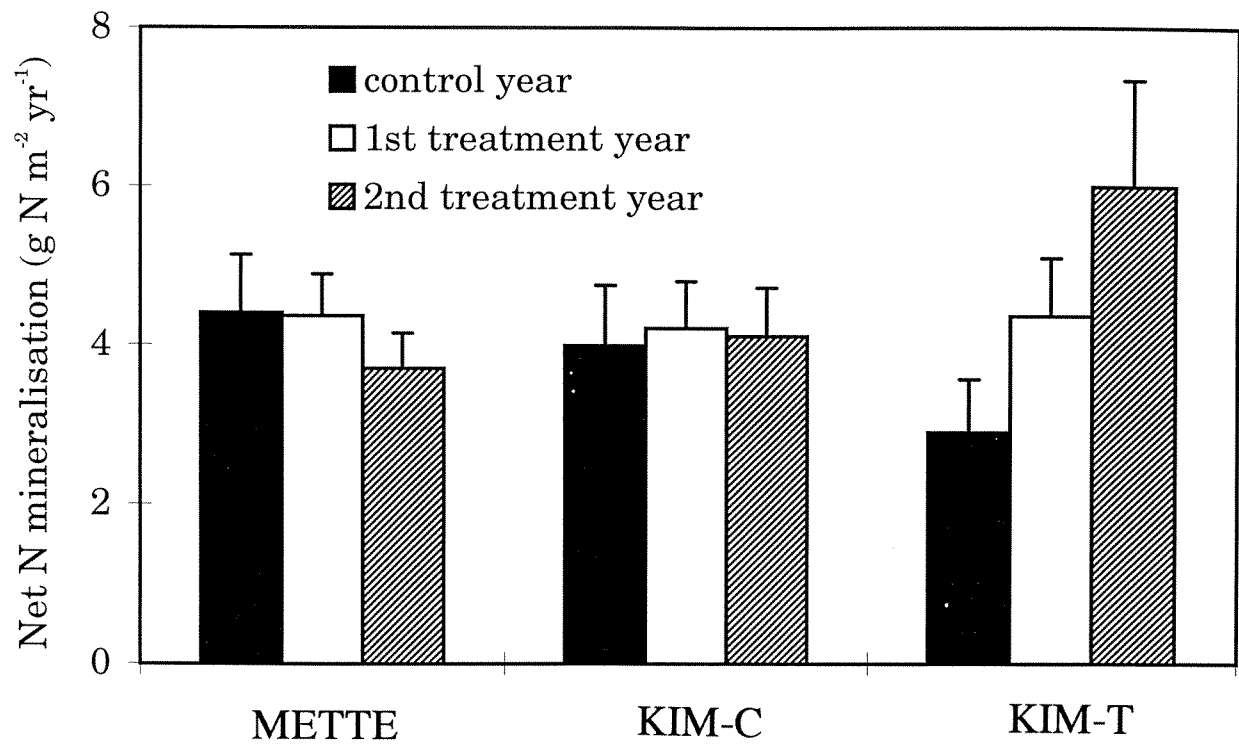


Figure 1
Annual net N mineralisation in control and treatment areas under Calluna vegetation.

6. Effects on the dwarf shrub vegetation

Wim Arp and Frank Berendse (WAU-TENC)

Growth of dwarf shrubs

In the CLIMEX experiment destructive sampling had to be kept at a minimum to prevent disturbance of the system. Effects of the treatments on biomass could therefore not be measured directly. A limited number of shoots which were harvested showed a good correlation between stem diameter and the biomass above this point of measurement. Stem diameter was therefore measured *in situ* to determine effects of climate change on growth of *Calluna* and *Vaccinium*.

From 1993 to 1996, we measured the stem diameter of 25 plants per treatment of both species, four times each growing season. For each plant, the stem diameter of differently aged stem sections was measured. In 1993 the stem diameter was measured on 1, 2, 3 and 4 year old stems. In the following years measurement of these same labelled stem sections continued and new shoots segments were added to the measurements. The average lifetime of these shrubs is about five years. To replace dead marked plants, new plants were labelled during the experimental period and of these new plants only stems up to four years old were measured. Because of this turnover of measured plants no stems older than five years were measured in 1996.

Stem diameter data of each stem section of each plant were compared and outlying datapoints were removed or corrected because: at the first measurement in spring many dead plants were replaced and markers on existing plants replaced, growth measurements over the winter period are less reliable; the measurement error is fairly large and growth is small between two consecutive measurement points, the growth data presented show the overall increase in stem diameter from early May to the end of September. Growth was calculated for each separate stem segment. The diameter of the fragile young shoots could not be measured during the first two measurements of the season, so no data are available for the youngest stems segments.

Calluna

The effects of treatments on *Calluna* growth is shown in Figure 1 (the exact values and significant differences of *Calluna* and *Vaccinium* growth are summarised in Table 1). In most years, but not all, the absolute increase in diameter of the older stems of *Calluna* was larger than for the younger stem segments. The age of the stem segment was therefore included in the statistical analyses.

The results show a large year to year variation in stem diameter increase. This could be caused by differences in weather, especially periods of drought. In most years growth is less in the outside control area (METTE) compared to the control section of the greenhouse

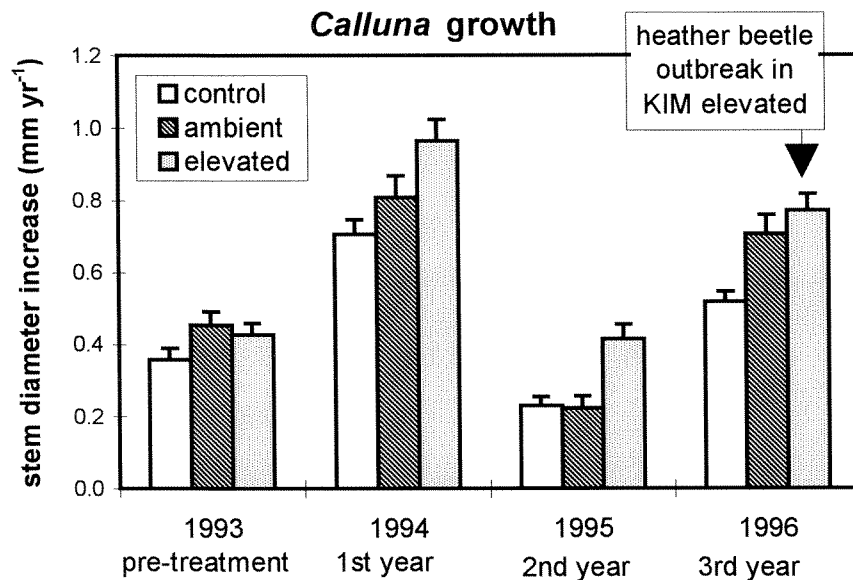


Figure 1

Average increase in stem diameter of *Calluna* between early May and late September for the three treatments for four years. Error bars represent standard error.

(KIM ambient). This chamber effect is statistically significant in 1993 and 1996. In the pre-treatment year 1993, no difference in growth rate was found between the two sections of KIM. In 1994 growth was higher in KIM elevated, but this was not yet significant. The growth rate was low in all areas in 1995, but significantly higher in KIM elevated. During the course of the experiment the treatment effect appears to increase, but in 1996 this effect was absent. There is a clear explanation for this change in 1996. In the treated section of KIM the majority of *Calluna* plants was infected by the heather beetle (*Lochmea suturalis*) in 1996. While these insects were also present in the control section of KIM and outside, it did not turn into a plague as in KIM elevated. Of the measured plants in KIM elevated 80% was infected, in KIM ambient only one plant (4%) and outside no plants. The heather beetle outbreak in KIM elevated appears to be a direct effect of the treatment, specifically the increase in temperature.

Vaccinium growth

Effects of the climate treatment and of the greenhouse structure on growth of *Vaccinium* were determined using the same methods as were used for *Calluna*. Growth of *Vaccinium* differs from *Calluna* in that the yearly stem diameter growth of *Vaccinium* is much less than the difference in diameter between two consecutive stem segments. This means that the diameter of newly formed branches of *Vaccinium* plants are thinner than the previous years' young shoots. Eventually growth stops and the plant dies. This growth strategy is possible because *Vaccinium* is a clonal plant. New plants emerge from the rhizome and start off with a fairly large stem diameter which during the lifetime of the plant increases little. *Calluna*, on the other hand, grows from seedlings and the yearly stem diameter increase is therefore more or less equal the difference in stem diameter between the age classes.

Because of this growth pattern of *Vaccinium* the stem diameter increase is not so much correlated with stem age, but more with stem branching order (new shoots emerging from the rhizome have a branching order of one, the branches of these shoots have order two, etc.) Statistical analyses of the stem diameter growth data therefore use branching order as a covariant.

Results of the *Vaccinium* growth measurements are presented in Figure 2 and Table 1. The year-to-year variation in stem diameter increase is even larger than for *Calluna*, with almost no growth in the first three years, and a significant increase in 1996. Although the small increases and the large variation make it difficult to pick up treatment and chamber effects, there was a higher growth rate in the treated part of KIM in all treatment years, which was highly significant in 1996.

A chamber effect is visible in 1993, with growth in the outside control lower than in KIM, and in 1996 where growth is higher outside than in the ambient section of KIM. Factors which could stimulate growth in the greenhouse are protection from wind and snow, while increased shading and reduced mineral input are likely to have a negative impact on growth of *Vaccinium*. These last two factors have become more important since closure of the greenhouse in 1994.

Other observed differences between the treated and the control section of KIM are a longer growing season in KIM elevated, with new leaves emerging about 2-3 weeks prior to leaves in KIM ambient. In 1995 a significant fraction of *Vaccinium* plants in KIM elevated had a

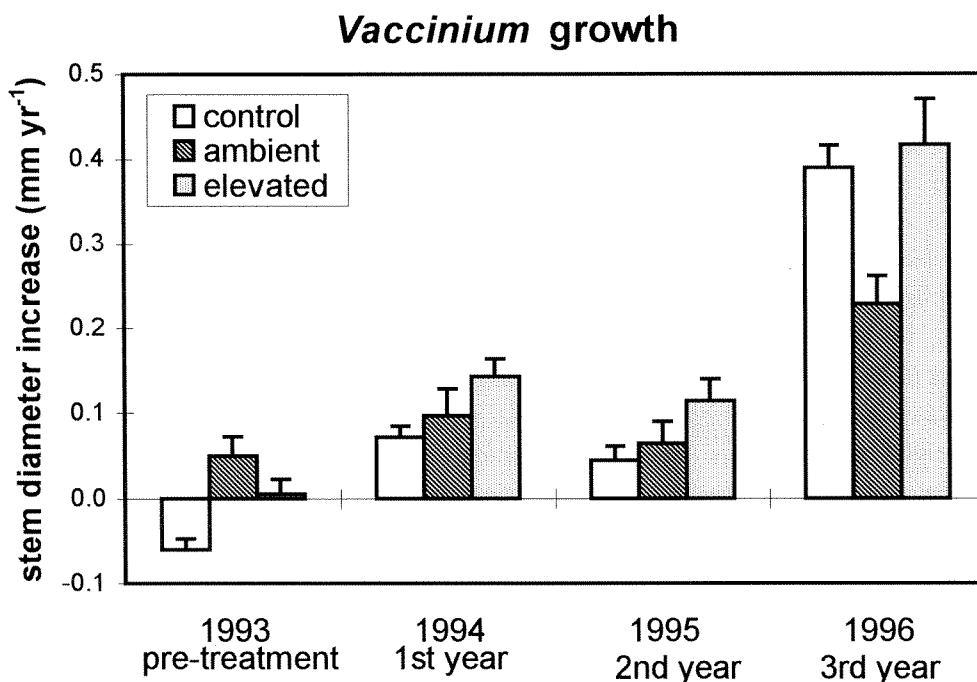


Figure 2
Average increase in stem diameter of *Vaccinium* between early May and late September for the three treatments for four years. Error bars represent standard error.

new growth flush in late summer, something which was only rarely seen in the other treatment areas.

Vaccinium leaves

In addition to stem diameter measurements, the number of leaves on new *Vaccinium* shoots were counted. The results are shown in Table 2. In 1993 there was no difference between the two sections of KIM. In 1994 plants in KIM ambient had the most leaves, but since the number of leaves on a shoot is determined during bud formation in the previous year, data for 1994 on the number of leaves reflect the pre-treatment conditions. In 1995 and 1996 plants in KIM elevated had more leaves.

A significant pre-treatment (1993 and 1994) chamber effect was found with plants in KIM ambient having more leaves than plants in the control area. No chamber effect was present in 1995 and 1996.

Because the number of leaves per new branch is negatively correlated with the branching order of the plant, the branching order is used as a covariant in the statistical analysis.

Vaccinium myrtillus leaves start to senesce early in the season. In some years, less than half of the green leaf area is still present in August, when the leaves are about 3 months old. The rate of senescence shows a large year-to-year variation, with a rapid senescence during the first two years and plants staying green until late in the season in the last two years. A treatment effect is seen in 1995 and 1996, where leaves in KIM elevated start to senesce earlier in the season. This is likely caused by the 2-3 weeks earlier appearance of the leaves in spring of these years.

Nutrient content

Leaf and stem material of *Calluna* and *Vaccinium* was harvested four times per growing season, in all four years of the experiment. Carbon and nitrogen analyses have been made on material from three harvests in 1993 and four harvests in 1996 (to study seasonal changes) and from the June harvest of all four years (as an indicator for year-to-year variation and long-term changes).

<i>number of leaves</i>	1993 <i>pre-treatment</i>	1994 <i>1st year</i>	1995 <i>2nd year</i>	1996 <i>3rd year</i>
METTE control	5.74	3.90	5.44	6.41
<i>chamber effect</i>	<i>0.019</i>	<i><0.001</i>		
KIM ambient	6.64	5.58	5.00	6.09
<i>treatment effect</i>		<i>0.018</i>	<i>0.009</i>	<i>0.080</i>
KIM elevated	6.84	4.74	7.16	6.92

Table 2

Average number of leaves per new branch for each treatment and year. Significance of chamber and treatment effects are indicated by p-values (only where $p < 0.1$).

For two harvests (June 1993 and June 1996) leaf material was also analysed for other nutrients (P, K, Ca, Mg) to test the effect of three years of treatment on uptake of the other nutrients and changes in nutrient ratios.

Calluna

In both 1993 and 1996 nitrogen content declined through the season from 1.2% to 1.0%. The ash content of *Calluna* leaves has only been measured for two harvests in 1993 and 1996, but tends to show an increase during the season. No seasonal effects on carbon content were found.

In 1993 no differences in N content of *Calluna* leaves were found between the treatments (Figure 3). *Calluna* in METTE appeared to have the highest N content over the entire period, which may reflect the lower N input in KIM. No effects of climate change on N, ash or C content were found for *Calluna* leaves. Also no treatment effects or trends were found for the composition of the woody *Calluna* stems.

In Table 3 the data are given for 5 elements and for the N/P ratio. As a reference, the normal range of mineral content for land plants is also given (Larcher, 1983). In 1993 the content of all nutrients was slightly lower in plants in KIM elevated, but this effect was not significant. In 1996 this difference had increased for P and Mg, resulting in a significant treatment effect. While in the other areas the N/P ratio had declined, it had increased in the treated area.

For all nutrients measured, the content in *Calluna* leaves is at or below the lowest value of the range found in land plants (Larcher, 1983). The P content is well below this level and appears to decrease even further as a result of the climate treatment.

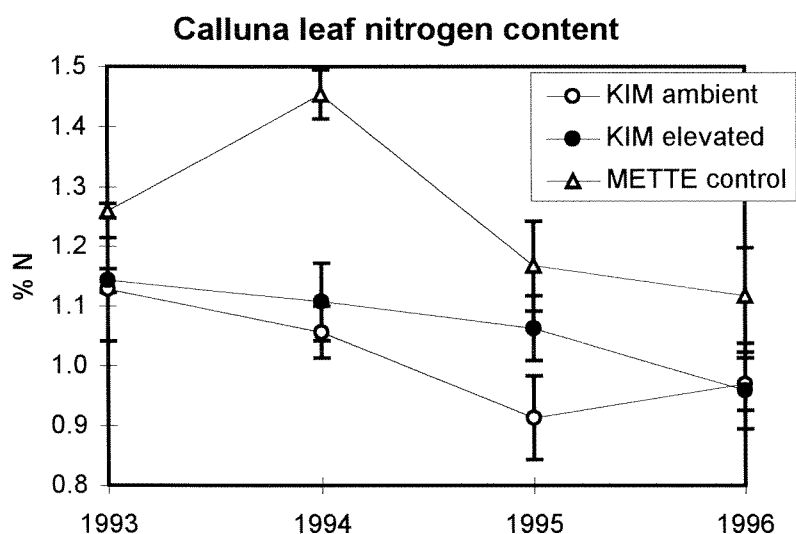


Figure 3
Nitrogen content of *Calluna* leaves harvested in June, for all four years. Average and standard error of five replicates are shown.

leaf nutrient content (mg g ⁻¹)	N		P		K		Mg		Ca		N/P	
	93	96	93	96	93	96	93	96	93	96	93	96
Calluna												
METTE control	11.6	12.0	0.58	0.67	5.47	6.03	1.29	1.34	4.13	4.03	21.9	18.0
chamber effect		.016								.084	.049	
KIM ambient	10.5	9.8	0.62	0.59	5.27	5.01	1.16	1.32	4.93	4.45	17.0	16.7
treatment effect				.005				.005				.033
KIM elevated	9.6	9.4	0.55	0.49	4.74	5.29	0.99	1.04	4.06	4.39	17.4	19.1
Vaccinium												
METTE control	17.1	21.0	0.75	0.91	7.57	7.74	1.29	1.55	5.49	5.81	22.9	23.6
chamber effect	.040		.005				.021			.013	.009	
KIM ambient	18.5	19.6	1.06	0.92	7.26	8.82	1.78	1.59	6.36	7.33	16.1	21.4
treatment effect		.023	.072	.001							.069	.054
KIM elevated	17.2	16.1	0.84	0.63	8.77	7.67	1.72	1.31	6.60	6.94	20.9	26.2
reference range	10 - 50		1 - 8		5 - 50		1 - 10		5 - 50			

Table 3

Mineral content of *Calluna* and *Vaccinium* leaves collected in June 1993 and June 1996. Data are average values of 5 replicates. Chamber and treatment effect are given as *p*-values (only where *p* < 0.1). The bottom line shows reference value ranges for the different nutrients (Larcher, 1983).

Vaccinium

Vaccinium leaf N content shows a large decline from the beginning to the end of the growing season (Figure 4). In early May the N content of the emerging leaves is about 3%, by the end of June this has been reduced to approximately 1.7%. During senescence of the leaves this is further reduced to the N content of leaf litter, about 1.5% N. The ash content of *Vaccinium* leaves shows the opposite trend: it increases from about 3.4% in early May to 5% in October, while the leaf litter contained about 4.2%.

These data suggest that in the buds and young leaves, nitrogen is present in a very high concentration, while other nutrients are almost absent. During the growing season nitrogen content is reduced, while other nutrients are increasing. The availability of nitrogen early in the season suggests that this is recycled N which has been relocated to storage organs during senescence the previous season. The other nutrients are not stored during the winter and are taken up during the growing season, after which they are lost again in the leaf litter. The ash and N content of *Vaccinium* stems fluctuate less throughout the season, although here also the N content is highest in early spring and lowest at the end of the season.

At most harvests, N content of *Vaccinium* leaves appears to be slightly lower in KIM elevated, but this pattern was already visible in 1993 and has not changed due to the treatments. A clear treatment effect is visible early in the season, when the N content of

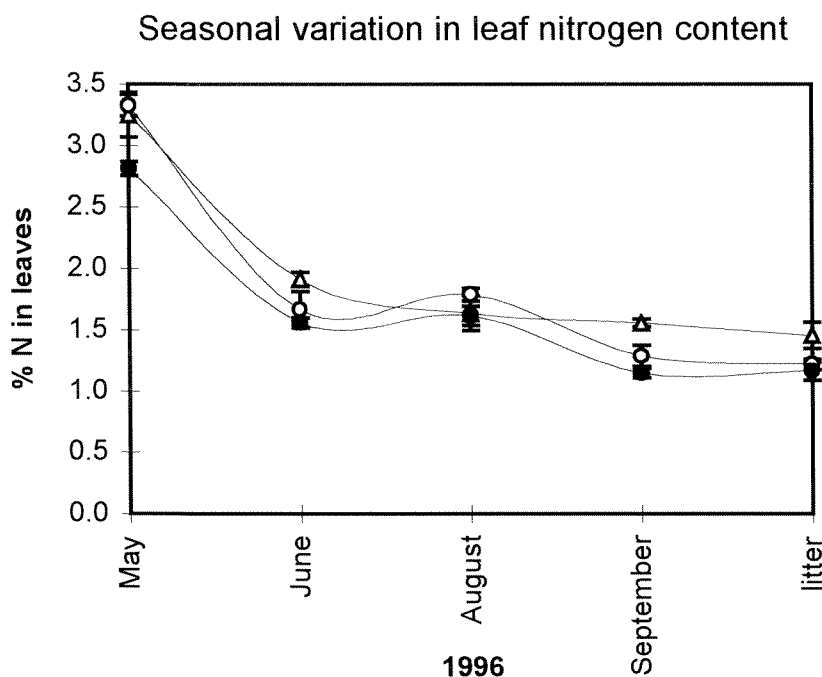


Figure 4
Seasonal variation in N content of *Vaccinium* leaves in 1996. Shown are average and standard error of five replicates.

Vaccinium leaves in KIM elevated is lower than in the other treatments. This effect is probably due to the earlier emergence of leaves in KIM elevated (about 3 weeks), diluting the initial pool of N over a larger amount of biomass. This effect is mostly gone when growth of the new shoots has stopped in all areas.

In Table 3 the data are given for five elements and for the N/P ratio. In 1993 the content of N, P and Mg was lowest in the plants of the control catchment, followed by plants in KIM elevated. In 1996 the chamber effect had disappeared except for Ca, but a treatment effect was apparent with a significantly lower N and P content in KIM elevated. The lower N content agrees with the results from the C/N analysis described above and is most likely an effect of a difference in phenological development. For both areas in KIM the P content decreased more than the N content during this three year period, resulting in a higher N/P ratio. The very low P content of plants in KIM elevated and the high N/P ratio suggest that phosphorus is becoming more limiting to growth than nitrogen in this system.

Conclusions

Increasing the temperature and CO₂ concentration does not significantly change the nitrogen content of the dwarf shrubs. The lower N content of *Vaccinium* in the treated area appears to be the result of an earlier start of the growing season and therefore advanced development of *Vaccinium*. In *Calluna*, which shows less seasonal variation, this effect is nearly absent. The nitrogen content of the litter produced by both species is not affected by

the treatment. Of the other nutrients phosphorus content shows a significant decline as a result of climate change, which leads to an increased N/P ratio.

These data, and the data on growth show that while elevated temperature and CO₂ increase growth, the plants are able to take up enough nitrogen to maintain a constant nitrogen content. In this environment which is nitrogen limited, this means that the availability of nitrogen has increased, probably through an enhanced mineralisation. The reduction in phosphorus content indicates that mineralisation of P is not increased to the same extent and suggests a dilution of the available phosphorus over an increased biomass. Given the reduction of the already very low P content of these species, a phosphorus limitation appears imminent. A continued higher availability of nitrogen could then result in an increased N content and eventually in a loss of N from the system.

It is likely that the increase in growth is not only due to direct effects of increasing temperature and CO₂, but is at least partly the result of the larger supply of nitrogen. Greenhouse studies show that the effect of CO₂ on growth depends on the availability of nitrogen, and since nitrogen is severely limiting in this system no direct CO₂ effect is expected. In addition to the positive interaction between CO₂ and nitrogen, a positive interaction between CO₂ and temperature has been found in other studies (Idso et al., 1987). The conclusion of this study is that the combination of factors which make up 'climate change' significantly affect the ecosystem processes in the system, for a large part by affecting the interaction between plant and soil. The complex interactions between the environmental factors emphasise the importance to study the effects of climate change on natural ecosystems.

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7. Tree responses

Claus Beier and Lennart Rasmussen (RISO)

During 1995 and 1996 several measurements have been performed to assess the tree response to the treatments at Risdalsheia. These have been concentrated within the areas:

- Pool measurements/estimates
- Tree growth
- Nutrient content in needles
- Throughfall measurements
- Litterfall

Pool measurements and estimates

The biomass pools for the trees have been estimated based on cutting of six pine trees and six birch trees in the Risdalsheia area outside the experimental plots. The principle has been to separate the trees into different sub-pools (stem wood, bark, big branches, small branches, needles and roots) and to measure each of these pools in order to create biomass-relationships between tree size expressed by the diameter of the tree at breast height (DBH) and the different pools. Subsequently the pools and the growth in the experimental plots can be calculated based on these relationships. In order to use this procedure it is assumed that the treatments did not change the relationships which is probably valid for climatic treatments but not for N-treatments.

Measurements:

The measurements were done in the field by cutting six pine and six birch trees representing different size classes in an area adjacent to the KIM and METTE plots. For each tree the following measurements were performed.

- Total height of each stem
- Diameter (crossed) per 0.5 metre of each stem + breast height (1.3 metre)
- Bark thickness at bottom, middle and top
- Total weight of all branches including needles (branches separated into big, medium and small branches)
- Root-system from one tree was excavated and weighed

Samples were taken to the lab to perform drying and weight measurements:

- Wood sample - density and dry weight measurements
- Bark-sample - density and dry weight measurements
- Branches - dry weight and needle fraction measurements

Results

Based on the measurements relationships between DBH and the weight of the different pools were established. These were subsequently checked by comparison to the standard equations given by Marklund (1988).

Stem and Bark biomass

The stem volume was calculated by assuming the stem consisted of 0.5 m cylinders of which the diameters were measured in the field. The total weight of the stem was then calculated from the wood/bark density measurements and the bark and wood fractions were finally separated from bark:wood ratios measured in the lab.

The total stem-volume could be expressed as (Figure 1):

$$\text{Pine: Stem volume} = \exp(1.742 + 0.146 \cdot \text{DBH}) \quad (r^2 = 0.93)$$

$$\text{Birch: Stem volume} = \exp(0.125 + 0.324 \cdot \text{DBH}) \quad (r^2 = 0.95)$$

which were subsequently separated into wood and bark weights by multiplication with the measured stem density (605 kg/m^3) and the wood fraction (73%) or bark fraction (27%) respectively.

The calculated wood and bark-weight relationships for the pine trees were finally compared to the relationships given by Marklund (1988) (Figure 2):

$$\text{Wood: Wood-weight} = \exp(11.4219 \cdot ((\text{DBH}/10)/(\text{DBH}/10) + 14)) - 2.2184$$

$$\text{Bark: Bark-weight} = \exp(10.3876 \cdot ((\text{DBH}/10)/(\text{DBH}/10) + 14)) - 3.2518$$

The measured relationships for volume as well as weight are generally quite good. It is seen that the use of the equations by Marklund (1988) would overestimate the wood and bark weights.

Branch and needle biomass

The total canopy weight measured was related to the DBH. For pine the fractions of branches, twigs and needles were calculated from measurements in the lab. For birch the

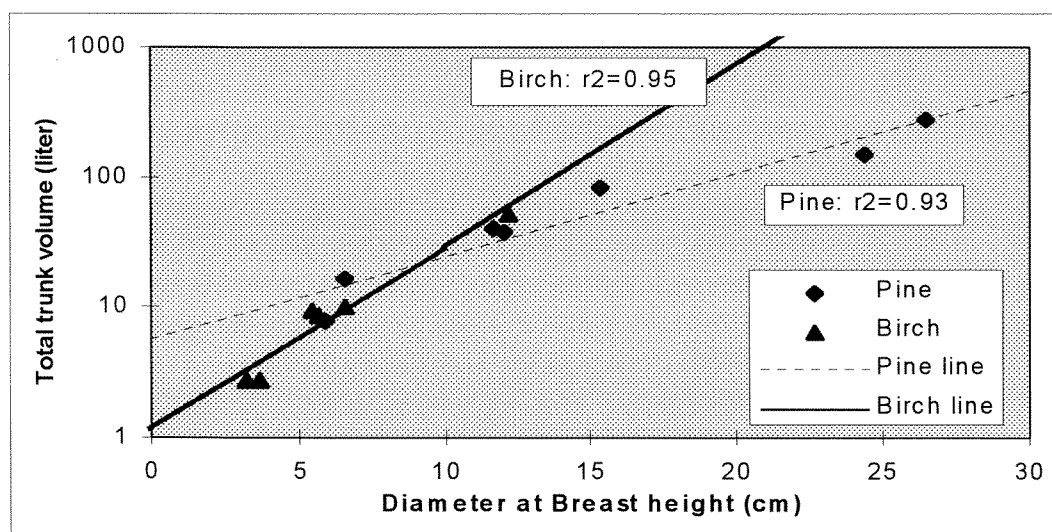


Figure 1

Stem volume: DBH relationships for pine and birch measured at Risdalsheia.

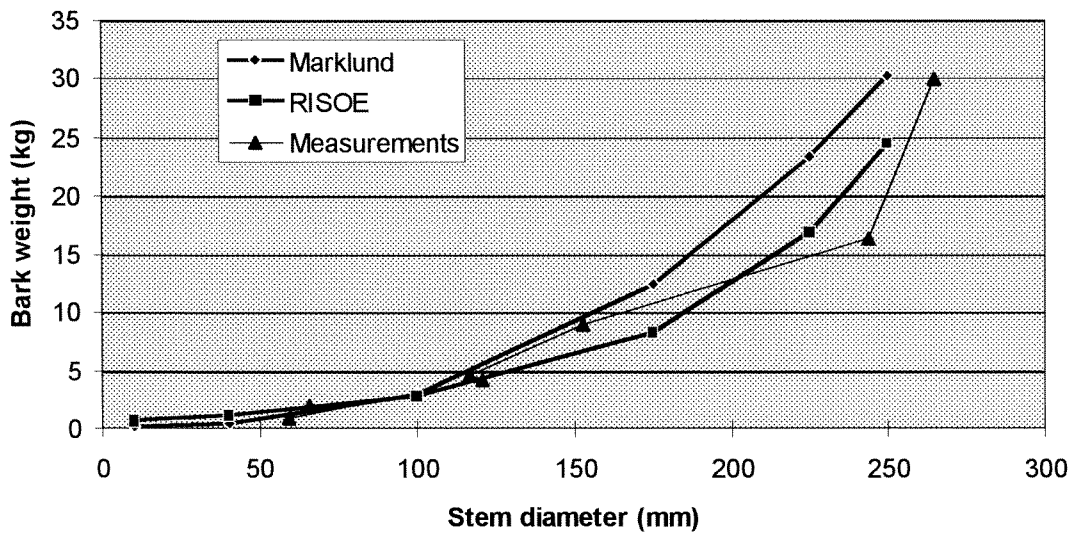
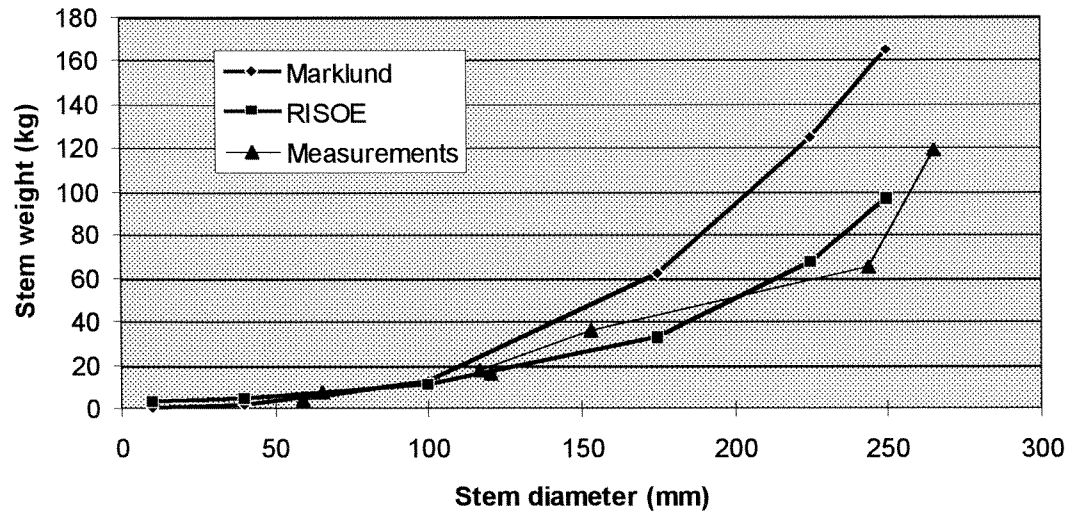


Figure 2
 Wood weight: DBH and bark weight: DBH relationships for pine measured at Risdalsheia and compared to relationships given by Marklund (1988)

branches were not separated into sub-pools, which means that the pools for birch did not include leaves.

The total canopy weight could be expressed by the equations (Figure 3):

Pine: Canopy weight = $\exp(0.736 + 0.131 \cdot \text{DBH})$ ($r^2 = 0.96$)
 Birch: Canopy weight = $\exp(-1.1438 + 0.2356 \cdot \text{DBH})$ ($r^2 = 0.91$)

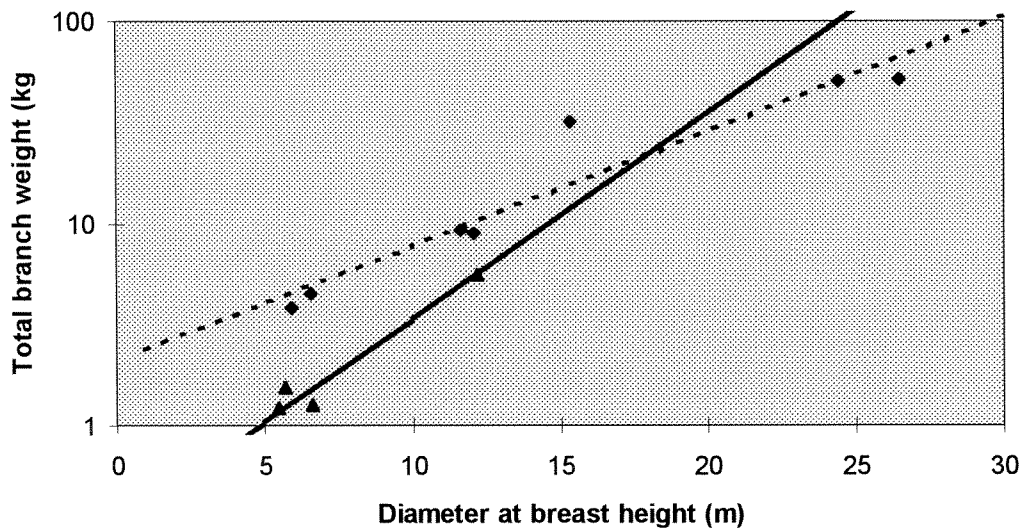


Figure 3
Total canopy dry weight : DBH relationships for birch and pine trees at Risdalsheia.

Comparison to the expression given by Marklund (1988) (Figure 4) shows almost identical relationships for the smaller trees (<17 cm) but the Marklund estimates would underestimate the canopy weight for the bigger trees. It has to be mentioned however, that the canopies are very irregular (Figure 4).

The total canopy dry weight for the pine trees were finally separated into fractions of branches (68%), twigs (5.8%) and needles (26.2%) according to measurements. There are differences in this separation depending on the branch size (small branches have a larger fraction needles). Attempts were therefore made to do the separation to take into account the size of the branches but because of the irregularity of the canopies it was not possible to

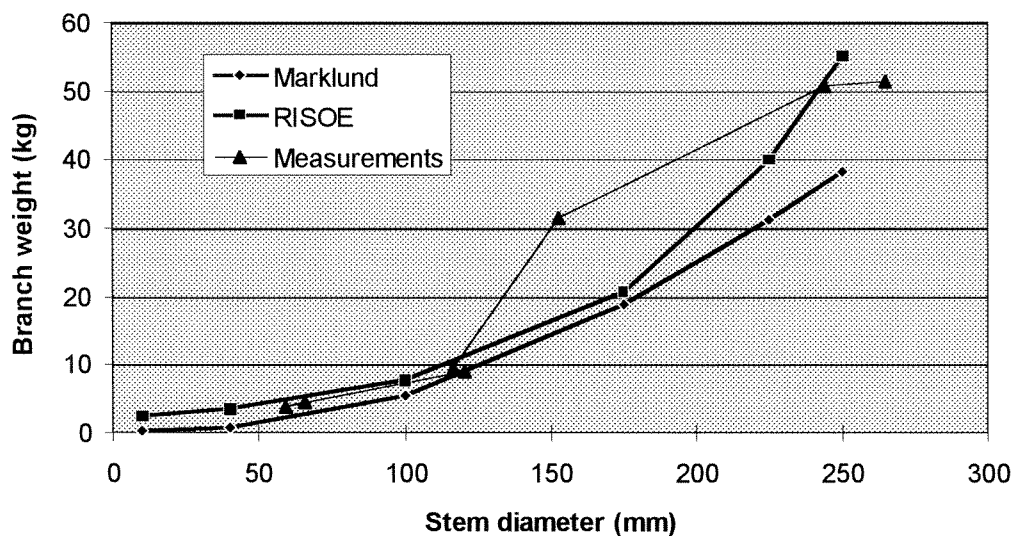


Figure 4
Comparison of the canopy dry weight : DBH relationships measured at Risdalsheia and given by Marklund (1988).

obtain a relationship between the tree size and the branch sizes and a simple arithmetic mean was used.

Root-biomass

The root-system of the trees at Risdalsheia is mixed up with the ground-vegetation, and a detailed excavation of the whole root system is in practice not possible. However, the root system of one Pine tree was excavated and measured, and the measurement was related to the tree size (DBH). It is obvious that this measurement is not very precise, since it does not include trees of different sizes or species.

Based on the measurements it was calculated that the root system of a pine tree weighs 94.1 g/mm (DBH). By comparison to the Marklund (1988) relationship (Figure 5) it is seen, that there is a large discrepancy for trees larger than DBH=100 mm. However, the one single tree measured was 74 mm at breast height, and at that tree size the correspondence is good. Therefore, and also because all other measurements show a logarithmic relationship between the DBH and the various biomass fractions, it is assumed that the Marklund equations can be used for Risdalsheia. In addition, it should be remembered that the Marklund relationships are based on a large number of measurements.

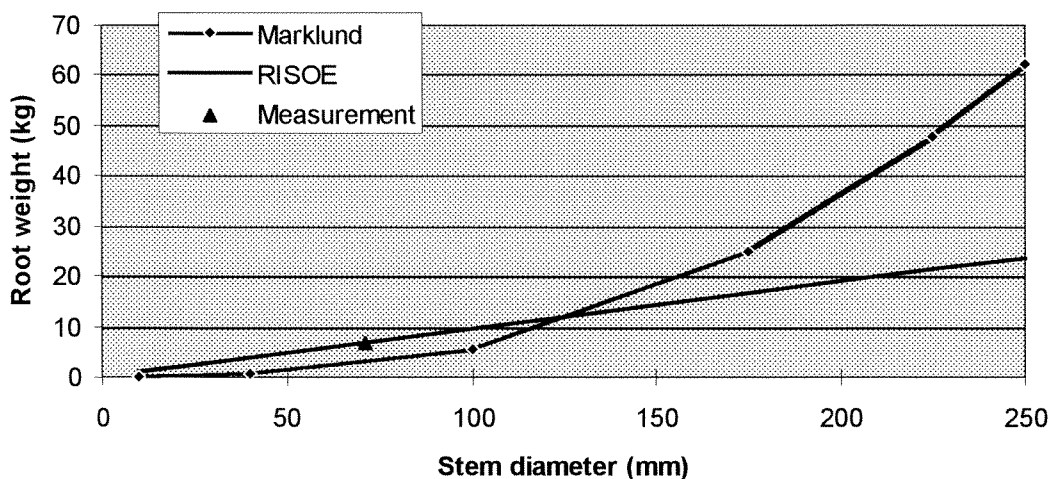


Figure 5

Relationship between root weight and DBH from measurements at Risdalsheia (94.1 gr/mm DBH) and given by Marklund (1988):

$$\text{Stump weight} = \exp(11.0481 * ((DBH/10) / ((DBH/10) + 15)) - 3.9657),$$

$$\text{Big root weight} = \exp(13.2902 * ((DBH/10) / ((DBH/10) + 9)) - 6.3413),$$

$$\text{Small root weight} = \exp(8.8795 * ((DBH/10) / ((DBH/10) + 10)) - 3.8375).$$

Tree growth at Risdalsheia

Tree growth

The size of all trees (height and diameter at breast height, DBH) in METTE, KIM-C and KIM-T was measured in October 1995 and October 1996. Based on these measurements

and the biomass relationships given above the total biomass pools in each of the two years and the biomass increment have been calculated (Table 1).

Plot	Specie	Total biomass (kg)	Above ground increment (kg)	Below ground increment (kg)	Total increment (kg)	Increment - % of total biomass
KIM-C	Pine	1272	3.14	1.25	4.40	0.35
KIM-C	Birch	160	3.60	0.99	4.59	2.88
KIM-T	Pine	2290	11.80	4.08	15.88	0.69
KIM-T	Birch	491	3.67	0.93	4.60	0.94
METTE	Pine	2670	9.51	2.94	12.46	0.47
METTE	Birch	215	1.35	0.36	1.70	0.79

Table 1
Pool sizes at Risdalsheia 1996 and the increment 1995-96.

It is seen that the increment is very small. Taking the large variation within each field and the assumptions made in the calculation procedure into account no differences in growth rate of the trees between the three plots can be seen.

100 needle weight and shoot length

Tree growth measured by diameter at breast height is a very slow responding parameter. The trees at Risdalsheia grow with a DBH increase of c. 1 mm a year, which means that with a calliper accuracy of 1 mm this method is unlikely to reveal a significant change in growth rate already after two years of treatment. Alternatively, a possible change in growth rate was investigated by measurements of "100 needle weights" and shoot lengths. The needle growth and needle weight are indicators of the growth status of the tree and so the 100 needle weight and shoot length from the plots relative to each other may be used as a faster indicator of possible treatment responses.

One branch from five different pine trees in each plot were sampled and the branches were separated into current year shoots (C+0) and one year old shoots (C+1). The lengths of the shoots were measured and the shoots were dried and 10*100 needles were sampled from each shoot and the weight of each 100 needle sample was measured.

The results showed that the 100 needle weights were higher in the KIM-T and KIM-C plots compared to METTE (Table 2). The difference was not significant between METTE and KIM-C for C+1 needles. This indicates that there is an increase in growth in the roof covered plots KIM-C and KIM-T and the effect is a roof effect rather than a temperature and CO₂ effect. This result is confirmed by the shoot lengths of current year shoots (Figure 6).

Nutrient content in the needles

The shoots from the pine trees used for 100 needle weight analyses were also used for

	KIM-C		KIM-T		METTE	
Current year needles	0.886	a	1.006	a	0.621	b
1 year old needles	0.941	cd	0.985	d	0.777	c

Table 2

100 needle weight (gr/100 needles) of C+0 and C+1 needles in KIM-C, KIM-T and METTE plots 1996. Different letters indicate significant differences ($p < 0.05$).

chemical analyses of the needle content of C, N, K, Ca, Mg and Na. This means that the nutrient content was measured on needles from five different trees in each plot and from C+0 and C+1 needles.

The needle content showed two treatment effects (Table 3). Firstly, the content of Na in the needles from the two KIM plots were significantly lower compared to the METTE EGIL plot, and secondly, the content of nitrogen in the needles in the KIM-T and EGIL plot tend to be higher compared to the METTE and KIM-C plots although only the higher N concentration in the C+1 needles in KIM-T compared to KIM-C was significant.

The reason for the difference in the Na content among the roof covered and uncovered plots is that the uncovered METTE and roof covered EGIL plots receive significantly more Na by the sea salt input, which is not the case in the the KIM-C and KIM-T plot. The higher N content in the needles in the KIM-T plot is most likely the results of an increased mineralisation of organic matter and thereby increased availability of nitrogen. This has been observed in the stream output from the EGIL-T plot and recently also, to a minor degree, from the KIM-T plot. This is further supported by correspondingly higher concentrations of N in the needles in the EGIL-T plot, although this can not be tested statistically because of the few trees in the EGIL plot.

Throughfall

In the beginning of 1996 big throughfall collectors were placed in each of the plots METTE, KIM-C and KIM-T, crossing through the whole of the plots and collecting water dripping from the canopies. The collectors were placed to integrate both the area beneath

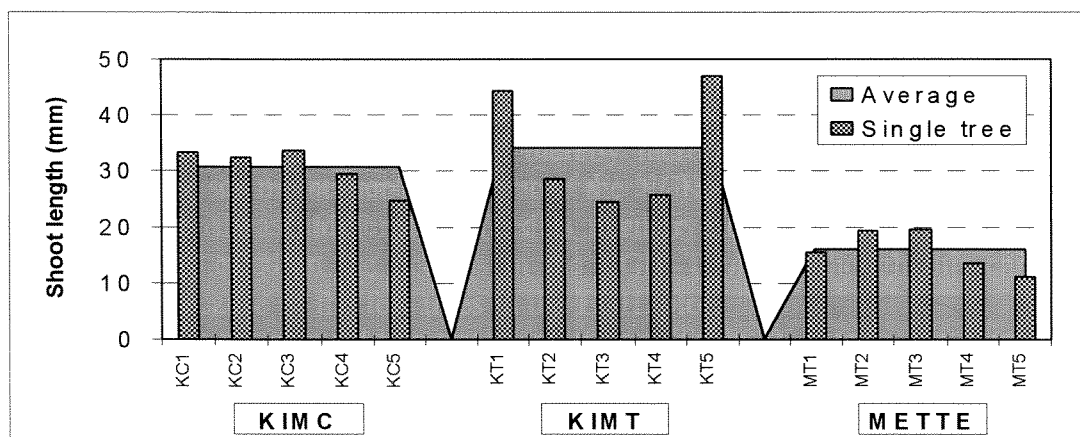


Figure 6

Shoot lengths of current year shoots in METTE, KIM-C and KIM-T plots 1996.

	Current year needles				1 year old needles			
	Mette	KIM-C	KIM-T	EGIL	Mette	KIM-C	KIM-T	EGIL
K average	a143	a141	a,b131	a121	a130	a,b118	a,b118	b96
K std	27	19	37	17	20	22	19	6
Na average	a4.9	b0.8	b1.2	a5.4	a6.2	c2.0	b,c1.7	a9.7
Na std	2.8	0.3	0.4	2.5	2.0	0.1	0.8	5.3
Ca average	a52	a65	b84	a64	a,c64	c,d96	d125	a,c,b89
Ca std	14	15	7	11	25	24	23	24
Mg average	60	75	61	62	50	64	50	50
Mg std	15	20	10	10	7	14	11	11
N average	a,b1.55	a1.48	b1.73	b1.93	d1.97	c1.64	d2.01	d2.32
N std	0.15	0.09	0.18	0.32	0.24	0.14	0.17	0.24
C average	52.8	52.5	51.9	54.8	53.3	53.2	52.4	54.5
C std	0.20	0.15	1.01	0.49	0.25	0.40	1.04	1.30
C/N mean	34.4	35.5	30.3	28.8	27.4	32.7	26.3	23.6

Table 3

Nutrient content in C+0 and C+1 needles in METTE, KIM-C, KIM-T and EGIL-T plots 1996. Units are meq/kg (K, Na, Ca and Mg) and % (N and C). Different letters indicate significant differences ($p < 0.05$).

pine, birch and open air. However, there has been a number of problems connected to the sampling of throughfall:

- the funnels were quite large (1.9 - 2.5 m²), and even with large sampling containers overflow has occurred a number of times. This was also the case in the winter time because of ice in the containers
- the plots are quite variable and the collectors will hardly sample comparable projections of open air and tree species.

Consequently, it is not possible to give a quantitative estimate of the throughfall flux in each plot from these measurements. The samples may rather be used for ion ratio studies to be compared among the plots.

Litterfall

Ten litterfall collectors have been placed in each plot and have been sampled monthly. The litter from each sampler and sampling event was dried and weighed and the litter was pooled within each plot and separated into pine needles, birch leaves and "rest" (dust, pollen etc.).

The measurements showed a highly variable pattern and it is not possible on the basis of these measurements to see any differences due to treatments (Table 4).

	KIM-T				KIM-C				METTE			
	Birch	Pine	Rest	Total	Birch	Pine	Rest	Total	Birch	Pine	Rest	Total
Sum Apr'95- Oct'96 (gr/m ²)	50	19	22	92	21	52	35	109				
Sum Apr'96- Oct'96 (gr/m ²)	26	10	14	50	10	26	19	545	5	18	17	39
Sept'95-Sept'96	30	11	15	56	13	29	24	66				
C (molC/m ²)	1.26	0.47	0.61	2.34	0.53	1.23	1.00	2.76				
N (molN/m ²)	0.04	0.01	0.01	0.06	0.01	0.01	0.02	0.04				
Conc of N(%)	1.74	0.84	1.16		1.35	0.67	0.90		2.06	1.06	0.96	

Table 4

Litterfall fluxes of biomass, C and N in the KIM-C, KIM-T and METTE plots in 1996. Calculations assuming a canopy cover of 33%.

Conclusions

- The nitrogen content in the needles in KIM-T (and EGIL-T) seems to be increased compared to KIM-C and METTE - suggested to be caused by increased mineralisation of organic matter and thereby increased N-availability.
- The tree growth has not been influenced significantly by the treatments. An increased needle weight and shoot length in KIM-T and KIM-C may indicate that there is a roof effect causing increased growth or increased needle size because of increased sheltering.

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8. Gas Exchange Responses

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Introduction

Atmospheric CO₂ enrichment and warmer air temperatures will have direct effects on the biochemical processes of CO₂ fixation. CO₂ enrichment typically leads to increased rates of leaf photosynthesis in the short term because the present CO₂ concentration is insufficient to saturate ribulose-1.5-bisphosphate carboxylase/oxygenase (RuBisCo) and because CO₂ competitively inhibits photorespiration (Stitt, 1991). The degree of photosynthetic stimulation is also temperature dependent (Long, 1991). Increasing temperatures favor oxygenation by decreasing, relative to O₂, both the solubility of CO₂ and the specificity of RuBisCo for CO₂ (Jordan and Ogran, 1984). Therefore, the partial suppression of oxygenation by CO₂ enrichment and the resulting increase in photosynthesis will be greatest at higher temperatures leading to the expectation of higher photosynthetic rates in short term, a feature observed in the first season of treatment (Beerling and Woodward, 1996). However, the long term response of photosynthetic proteins is unclear (Long, 1991). Higher air temperatures, together with CO₂ enrichment, may increase or decrease sink limitation in leaves, depending on plant growth responses (Sage et al., 1989, 1995). Against this background, we report new seasonal measurements of gas exchange and leaf photosynthetic capacity for the dominant tree and shrub species within the CLIMEX greenhouse during the second and third years of growth with elevated CO₂ and temperature. *In situ* instantaneous gas exchange data are complemented by seasonal, time-integrated estimates of the water and carbon balance of leaves for a wide range of species from leaf carbon isotope composition (Farquhar et al., 1982; Farquhar and Richards, 1984) during the second (1995) and third (1996) years of treatment.

Materials and Methods

Gas exchange measurements

Sampling protocols, and gas exchange apparatus were as detailed by Beerling and Woodward (1995a). Gas exchange measurements were made with an open path photosynthesis system (CIRAS-1, PP. Systems, Herts. U.K.) using a 1dm³ leaf cuvette. Measurements were made between 1000 and 1600 h on leaves on clear sunny days (PAR 600-800 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Measurements were conducted at ambient temperatures and at the CO₂ concentration in which the vegetation grew (350 ppmv or 560 ppmv). Gas exchange measurements were made on projected leaf area basis for *B. pubescens*, *P. sylvestris* and *V. myrtillus*. Estimates of instantaneous gas exchange were made at intervals throughout the growing season (June - September) in 1995 and 1996 using fully expanded leaves. Two to three leaves from different mature trees were measured from plants in Gh_C (greenhouse control) and Gh_T (greenhouse treated) These individuals were tagged and subsequent measurements made on the same individuals throughout the seasons. Replication for each species in Gh_C and Gh_T was: (number of individuals given in brackets): *B. pubescens* ($n = 5, 14$), *P. sylvestris* ($n = 5, 14$) and *V. myrtillus* ($n = 10, 10$).

Assimilation, A , versus intercellular CO_2 concentration, c_i , (A/c_i) CO_2 responses curves were measured on several days in July and September 1996 using the automated CIRAS-1 system. Curves were constructed across the CO_2 range 50 - 1500 ppmv for five species (*B. pubescens*, *P. sylvestris*, *Salix cinerea*, *V. myrtillus* and *V. vitis-idaea*) in Gh_T and Gh_C using three leaves per individual and two individuals per treatment under saturating irradiance ($1500 \mu\text{mol m}^{-2}\text{s}^{-1}$). In the case of *P. sylvestris* five pairs of current-year needle classes were used for A/c_i and the other gas exchange measurements. A/c_i curves were fitted using the Farquhar et al. (1980) biochemical model of CO_2 assimilation, following the approach of Wullschlegel (1993), incorporating the temperature correction of McMurtrie and Wang (1993). Stomatal limitation (l) in the growth CO_2 concentration was calculated from the response of A to c_i by the method of Farquhar and Sharkey (1982).

Stable carbon isotope analyses

Newly developed leaves from 5 - 10 individuals of the following tree and shrub species were sampled for measurements of stable carbon isotope composition: *B. pubescens*, *P. sylvestris*, *Salix cinerea*, *V. myrtillus*, *V. vitis-idaea*, *Empetrum nigrum*, *Calluna vulgaris* in July 1995 and July and September 1996 from both Gh_T and Gh_C . Leaves were stored at -5°C for 2 days before being oven dried at 80°C for 24 h, and ground to a homogenized fine powder for isotopic analysis. Isotope determinations were made on a 2-3mg sub-sample for each species collected from each CO_2 concentration using VG-Isogas triple beam stable isotope-ratio mass spectrometer combined with an autoanalysis unit; measurements were reproducible to $\pm 0.05\text{‰}$. The isotopic composition of a sample is calculated as the ratio of a sample to a standard (‰) :

$$\delta^{13}\text{C}_p = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (1)$$

where R_{sample} and R_{standard} are the $^{13}\text{C} : ^{12}\text{C}$ ratios of the sample and the universally accepted PDB standard respectively. As plants have a lower $^{13}\text{C} : ^{12}\text{C}$ ratio than the standard, $\delta^{13}\text{C}_p$ is negative, and carbon isotope discrimination (Δ) calculated as :

$$\Delta = \frac{(\delta^{13}\text{C}_a - \delta^{13}\text{C}_p)}{\left(1 + \frac{\delta^{13}\text{C}_p}{1000} \right)} \quad (2)$$

where $\delta^{13}\text{C}_a$ is the average isotopic composition of the atmospheric CO_2 . In CLIMEX the isotopic composition of the source CO_2 has been recorded biologically using the C_4 species *Zea mays* grown over the same period in Gh_T and Gh_C details of the approach and $\delta^{13}\text{C}_a$ values in each section of the greenhouse since 1991 are given by Beerling (1997).

Leaf Δ values were used to calculate the c_i/c_a ratio, considered as the time-integrated set-point of leaf metabolism (Ehleringer, 1993) from the model of Farquhar et al. (1982) :

$$\Delta = a + (b - a) \times \frac{c_i}{c_a} \quad (3)$$

A relative estimate of leaf water use efficiency was calculated from (Farquhar et al., 1982; Farquhar and Richards, 1984):

$$WUE = \frac{A}{g_s} = \frac{c_a \times \left(1 - \frac{c_i}{c_a}\right)}{1.6} \quad (4)$$

where c_a is the atmospheric CO₂ concentration and c_i/c_a is obtained from carbon isotope discrimination by solving Eq. 3. The factor 1.6 is the ratio of gaseous diffusivities of CO₂ and water vapor in the air.

Results and Discussion

CLIMEX is the longest running experiment exposing an entire boreal ecosystem to increased CO₂ and temperature with all the ecological complexity of such an ecosystem intact. When combined with first year instantaneous gas exchange data (Beerling and Woodward, 1996), periodic measurements made throughout the past two growing seasons (1995 and 1996) provide a long-term (three year) picture of the photosynthetic and stomatal conductance responses of mature trees of *P. sylvestris* and *B. pubescens* and the dominant ground shrub *V. myrtillus* to the past three years of treatment (Figure 1). After three years, leaves of each species grown and measured at elevated CO₂ and temperature had higher photosynthetic rates and lower stomatal conductances compared to the controls (Figure 1a), despite higher rates of non-photorespiratory respiration (Figure 2). The photosynthetic changes are consistent with the predicted short-term effects of CO₂ and temperature on the photosynthetic system (Long, 1991; Beerling and Woodward, 1994; Sage et al., 1995). Long term (three years) CO₂ enrichment experiments with field grown saplings of deciduous trees (Gunderson et al., 1993), and open top chamber experiments lasting for four years exposing young *P. sylvestris* trees to increased CO₂ and climate change (Wang et al., 1995), have shown similar sustained photosynthetic enhancement relative to controls. For vegetation at the CLIMEX site whether the response continues will depend on the annual net mineralisation rates of the skeletal, nutrient poor soils, as in the arctic tundra (Oechel et al., 1994). Measurements of soil nitrogen mineralisation at 0-10 cm suggest increases began to occur during the second year of treatment (Van Breeman et al., in prep).

The substantial drop in photosynthetic rates and stomatal conductance of *P. sylvestris* and *V. myrtillus* between July and September in 1994 (Figure 2) is most likely due to the exceptional weather conditions in July, rather than representing any rapid acclimation by the plants (Beerling and Woodward, 1996). July daytime air temperatures at Risdalsheia, and inside the treated sections of the greenhouse, averaged 27.5°C and 34.0°C respectively and leaf temperatures occasionally exceeded 36°C. At such high air temperatures, and with CO₂ enrichment, stomatal conductance typically increases, in concert with photosynthetic rates, particularly when the growth temperature is lower than the measurement temperature

(Santrucek and Sage, 1996), as at CLIMEX during July. Natural high-temperature events, such as those in July 1994, accentuated species-dependent responses. The expected increased frequency of extreme climatic events (Beerling et al., 1996; Kubiske and Pregitzer, 1996) therefore could play an important role in determining species performance and composition of vegetation.

Over the three year period of the experimental, the stomatal conductance of leaves of *P. sylvestris*, *B. pubescens* and *V. myrtillus* grown and measured with increased CO₂ and temperature was typically lower relative to the controls (Figure 3). There is however some evidence for an increase in the stomatal conductance of *P. sylvestris* and *V. myrtillus* grown with increased CO₂ and temperature since June and August 1995 respectively, suggesting some degree of acclimation by the stomata of these species to prolonged operation under treatment conditions (Figure 1b). Stomatal acclimation to high CO₂ and temperature has been reported for several species from a range of controlled environment (Berryman et al., 1994; Santrucek and Sage, 1996) and open top chamber studies (Hogan et al., 1996). However, the mechanisms of stomatal thermal and CO₂ acclimation occurs remains uncertain (Mansfield et al., 1990; Santrucek and Sage, 1996).

Analysis of the response of leaf CO₂ uptake rates to increases in the intercellular CO₂ concentration (A/c_i curves), showed no overall significant effects of growth at elevated CO₂ and temperature on maximum rates of *in vivo* RuBisCo carboxylation activity (V_{max}) and electron transport (J_{max}) in the majority of species investigated after three year's treatment (Table 1), indicating a lack of down-regulation in the photosynthetic proteins. The absence of changes in RuBisCo amount is supported by leaf nitrogen determinations for each of the species listed in Table 1 which showed no significant differences after three years of growth with elevated CO₂ and temperature relative to the controls (M.A. Wills, unpublished). A similar lack of acclimation has also been reported for other species in field studies where rooting volume of unconstrained (Gunderson et al., 1993; Gunderson and Wullschlegel, 1994; Webber et al., 1994; Ellsworth et al., 1995; Hogan et al., 1996). The reduction in V_{max} and J_{max} of *B. pubescens* in July suggests some degree of acclimation (Table 1) and offers an explanation for the rather small increase in leaf photosynthetic rates compared to the controls (Figure 1a). Light-saturated rates of photosynthesis of leaves grown and measured in elevated CO₂ and temperature were significantly higher than those in the same species under ambient conditions (Table 1). In addition, the control of light-saturated rates of photosynthesis (A_{sat}), calculated from the isotopically-derived c_i concentration and the Farquhar et al. biochemical model of CO₂ assimilation, tended to switch from RuBisCo amount and activity (W_c) to RuBP-regeneration (W_j) as a result of the treatments (Table 1). Therefore, higher photosynthetic rates in the treatment section of the greenhouse were a consequence of leaves operating further along the A/c_i curve at a higher c_i concentration. Long and Drake (1992) suggested from a theoretical standpoint that leaves operating further along the A/c_i curve at elevated CO₂ concentrations, with no change in V_{max} or J_{max} , would have lower stomatal limitation than those operating at 350 ppmv despite lower stomatal conductances. Our analysis of the A/c_i responses for the seven species investigated confirms this prediction with an average reduction across all species of 39.2 % (Table 1).

Discrimination against the heavy isotope of carbon, ^{13}C , decreased in all species of tree and ground shrub in 1995 and 1996 grown with increased CO_2 and temperature, regardless of the time of year and whether they were evergreen or deciduous (Table 2). This response resulted in near-constant c_i/c_a values and sustained increases in leaf water-use efficiency (WUE) (Table 2). *In situ* instantaneous gas exchange data indicate these isotopic responses were driven by higher rates of photosynthesis at a given stomatal conductance (Figure 3), and generally lower stomatal conductances, in accordance with theory (Farquhar et al., 1982). The WUE of all species in Gh_T showed a significant ($P < 0.01$) correlation between July 1995 and July 1996 values (Figure 4) indicating consistently higher WUE in the second and third years of treatment, and strong genetic control over the absolute values (Ehleringer, 1993). Contrary to the interpretation of carbon isotope analyses of historical sequences of tree rings from conifers in Idaho since 1912 (Marshall and Monserud, 1996), all of the species studied here showed an increase in the CO_2 concentration gradient between the atmosphere and the leaf ($c_a - c_i$) (Table 2), suggesting this difference is not homeostatically maintained. These carbon isotope data are unique for such a wide range of tree and shrub species exposed *in situ* to increased CO_2 and temperature and confirm WUE results from other CO_2 enrichment experiments with herb (Beerling and Woodward, 1995b) and tree (Picon et al., 1996; Guehl et al., 1994) species employing stable carbon isotope measurements.

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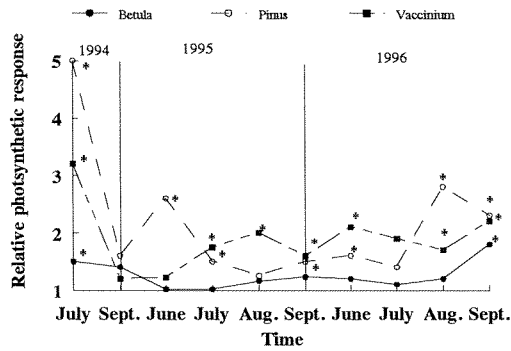
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(a)



(b)

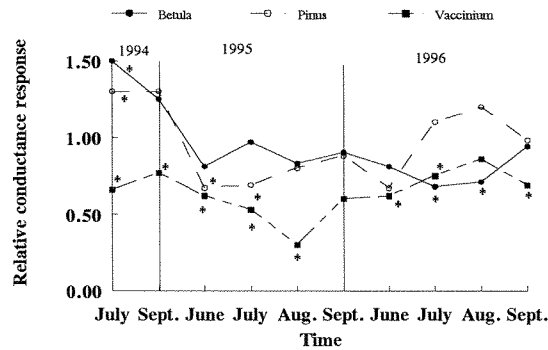


Figure 1

Relative (Gh_T values / Gh_C values) in situ response of (a) net photosynthesis and (b) stomatal conductance of *P. sylvestris* (O, _ _ _ _), *B. pubescens* (●, _____) and *V. myrtillus* (■, _ _ _ _) grown with increased CO_2 and temperature for the past three years. * = significant difference ($p < 0.05$) detected between control and treatment measurements using one-way ANOVA.

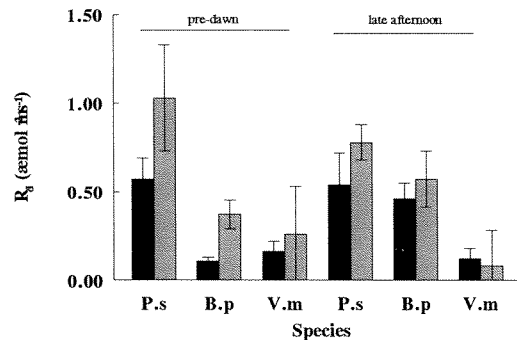


Figure 2

In situ non-photorespiratory respiration rates (R_d) of needles of *P. sylvestris* (P.s), and leaves of *B. pubescens* (B.p) and *V. myrtillus* (V.m) in September 1996 grown with increased CO_2 and temperature (□) and without (■) for the past three years.

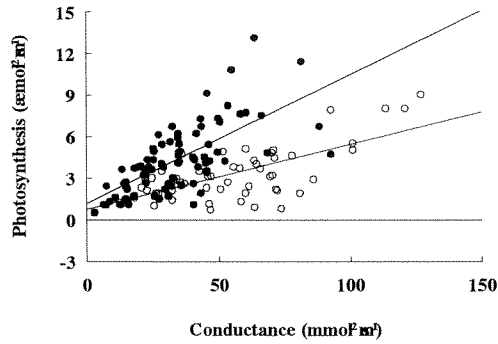


Figure 3

Relationship between leaf photosynthetic rates and control conductance for *P. sylvestris*, *B. pubescens* and *V. myrtillus* in August 1996 growing with increased CO_2 and temperature (Gh_T , ●) and without (Gh_C , ○). Regression details: Gh_C (○) slope = 0.047, intercept = 0.72, $r = 0.68$, $P < 0.01$; Gh_T (●) slope = 0.093, intercept = 1.15, $r = 0.69$, $P < 0.01$.

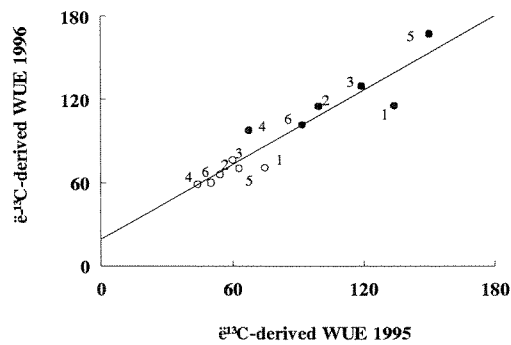


Figure 4

Correlation between $\delta^{13}\text{C}$ -derived water-use efficiency (WUE) of leaves of plants in Gh_C (○) and Gh_T (●) in July 1995 and 1996. Species codes as given in Table 2. Regression details: slope = 0.89, intercept = 18.7, $r = 0.93$, $P < 0.01$.

Species	V_{\max} $\mu\text{mol m}^{-2} \text{s}^{-1}$		Gh _r /Gh _c ratio	J_{\max} $\mu\text{mol m}^{-2} \text{s}^{-1}$	Gh _r	Gh _r /Gh _c ratio	A_{sat} $\mu\text{mol m}^{-2} \text{s}^{-1}$		Gh _r /Gh _c ratio	Stomatal limitation %	
	Gh _c	Gh _r					Gh _c	Gh _r		Gh _c	Gh _r
(a) Trees											
<i>Pinus sylvestris</i>											
July	13.1±5.5	35.1±6.9	2.7	40.9±2.7	61.5±2.5	1.1	2.5(W _c)	6.0(W _r)	2.4	30.1	16.3
Sept.	45.5±6.3	61.0±18.3	1.3	101.8±3.0	107.4±5.5	1.1	5.6(W _c)	12.0(W _r)	2.1	40.6	14.5
<i>Betula pubescens</i>											
July	88.3±20.6	51.7±9.7	0.6	114.9±4.9	67.8±3.8	0.6*	14.7(W _j)	10.1(W _r)	0.7	13.1	10.8
Sept.	44.3±10.5	55.4±30.1	1.3	107.7±2.9	85.6±0.9	0.8*	6.3(W _c)	12.2(W _r)	1.9	32.5	11.5
<i>Salix cinerea</i>											
July	34.0±16.5	48.8±18.7	1.4	76.1±9.1	95.0±6.8	1.2	4.1(W _c)	10.3(W _c)	2.4	34.0	30.0
Sept.	31.1±7.7	39.7±5.8	1.2	75.1±3.6	74.5±7.2	0.9	5.9(W _c)	8.4(W _c)	1.4	27.8	28.2
(b) shrubs											
<i>Vaccinium myrtillus</i>											
July	21.4±5.1	24.4±5.1	1.1	34.5±0.8	35.4±1.0	1.0	3.8(W _c)	5.0(W _r)	1.3	22.8	10.3
Sept.	29.7±5.1	11.3±13.1	0.4	47.7±1.8	29.8±1.4	0.6*	2.7(W _c)	1.7(W _r)	0.6	22.1	31.6
<i>V. vitis-idaea</i>											
July	12.9±1.5	21.4±11.4	1.6	31.7±3.2	31.1±3.4	0.9	2.3(W _c)	4.5(W _r)	1.9	32.8	10.8
Sept.	14.9±7.8	31.2±21.0	2.0	41.0±5.4	28.5±3.4	0.7	2.4(W _c)	3.8(W _r)	1.6	32.2	11.2
Overall means	33.5±7.2	38.0±5.1	n/s	67.1±10.2	61.7±9.2	n/s	5.0±1.1	7.4±1.2	*	28.8±2.4	17.5±2.7**

n/s = no significant differences, * = $p < 0.05$, ** = $p < 0.001$.

TABLE 1. Calculated maximum rates of carboxylation (V_{\max}), electron transport (J_{\max}), light saturated rate of photosynthesis (A_{sat}) and stomatal limitation for plants grown with increased CO_2 and temperature in the treated (Gh_r) and without in the control section (Gh_c) of the CLIMEX greenhouse during the third year of treatment. Values are means \pm s.e. from curves fitted to measurements on each of two leaves per individual, and two individuals per treatment. The limitation on A_{sat} was determined to be either Rubisco amount and activity (W_c) or RuBP regeneration (W_r) according to the Farquhar et al. (1980) biochemical model of CO_2 assimilation. Values are means \pm s.e.

Species and codes	¹³ C discrimination		c _i /c _a		WUE		c _a -c _i	
	Gh _C	Gh _T	Gh _C	Gh _T	Gh _C	Gh _T	Gh _C	Gh _T
(a) Trees								
1. <i>Pinus sylvestris</i>								
July	19.7	19.6	0.68	0.67	70.7	115.3	113.2	184.1
September	19.6	19.5	0.67	0.66	71.5	115.9	114.3	105.5
2. <i>Betula pubescens</i>								
July	20.2	19.6	0.69	0.67	65.9	115.1	105.5	184.1
September	21.2	19.7	0.74	0.68	55.9	113.6	89.6	181.8
3. <i>Salix cinerea</i>								
July	19.7	18.6	0.67	0.63	70.3	129.5	112.5	207.2
September	20.7	19.2	0.72	0.66	61.3	120.5	98.0	192.7
(b) Shrubs								
4. <i>Vaccinium myrtillus</i>								
July	20.9	20.7	0.73	0.72	58.9	97.9	94.3	156.6
September	21.5	20.9	0.75	0.73	52.9	93.5	84.7	149.5
5. <i>V. vitis-idaea</i>								
July	19.1	16.2	0.65	0.52	76.1	167.2	121.8	267.7
September	19.1	20.4	0.65	0.71	76.1	102.8	121.8	164.5
6. <i>Calluna vulgaris</i>								
July	20.8	20.4	0.73	0.71	59.9	101.7	95.8	162.7
September	22.1	22.1	0.78	0.78	47.5	76.2	76.0	121.9
<i>Empetrum nigrum</i>								
July	nd		nd		nd		nd	nd
September	16.6	18.2	0.54	0.61	100.3	135.7	160.5	217.1
Overall means	20.1	19.6	0.69	0.67	66.7	114.2	106.8	176.6
	±0.4	±0.4	±0.01	±0.01	±3.7	±6.2	±5.6	±11.5
significance		n/s	n/s		p < 0.001		p < 0.001	

nd = no data, ns = no significant difference

Table 2

Stable carbon isotope-derived parameters for the dominant tree and ground shrub species sampled in July and September during the third year in situ exposure to CO₂ enrichment and increased temperature in the treated (Gh_T) and control (Gh_C) sections of the CLIMEX greenhouse.

9. Gas Emission Fluxes

D. Fowler and K Hargreaves (ITE)

The objective of the measurements were firstly to demonstrate whether the KIM-T and KIM-C chambers (404 m² and 162 m² soil area respectively) could be used to measure the exchange rates of CO₂ and trace gases which would provide a measure of the processes influenced by the temperature and CO₂ treatments of the whole ecosystems. The second objective was to make measurements of fluxes of a range of trace gases and their response to changing atmospheric or surface conditions (eg temperature and radiation).

The first goal was to measure the effective rates of exchange of air in KIM-T (and C) with the ambient atmosphere with the vents closed. This was achieved using a tracer, in this case CH₄ which could be assumed to behave conservatively. There is a deposition of CH₄ to the soil in both KIM-T and KIM-C which has been measured independently and may be shown to have no significant influence on the ventilation rate measurements. Figure 1 shows the decay CH₄ inside KIM-T following an injection. The decay curve has been measured in both KIM-T and KIM-C under a range of windspeeds and yields fractional ventilation rates of 0.8 h⁻¹ and 1.3 h⁻¹ at a windspeed of 5 m s⁻¹. The form of the relationship between fractional ventilation (F_v) and windspeed (U) is $F_v = 0.0615 U + 0.5$ ($r^2 = 0.97$). Thus the exchange rate of air inside closed KIM-T and KIM-C chambers is well defined.

The chambers were then instrumented to provide continuous measurements of CO₂, CH₄, H₂O, NO, O₃ and SO₂ inside KIM-T, KIM-C and ambient air at a location ~50 m upwind of KIM-T and at a height above ground of approximately 5 m to avoid gradients close to the ground.

CO₂ flux measurements

The measurement of fluxes within KIM-T and KIM-C were made during both night and day in early June, but because of rapid heating in daytime within a closed chamber, the daytime measurements were generally very short (<1 hour). Nocturnal measurements in both KIM-T and KIM-C at ambient CO₂ concentration in Figure 2 show respiration fluxes in the two chambers, expressed per unit soil area, not floor area. The absolute values for respiration which include both soil and vegetation are generally in the range 2 to 15 mmol m⁻² h⁻¹ and show much larger rates of respiration in KIM-T. The values on a range of evenings show a clear temperature response with larger rates at high temperatures, and absolute values of respiration larger in KIM-T than KIM-C by about a factor of 5. These differences are much larger than those measured using small cuvettes and indicate a requirements for larger ventilation rates in KIM-C than those obtained during the test runs. However, the indications of much larger >ecosystem= respiration rates in KIM-T are supported by photosynthesis measurements on several mornings showing much less rapid changes from net respiration to photosynthesis and smaller overall rates for net photosynthesis at the same photon flux density (Figure 3). These effects were seen consistently over a period of three days. In fact with increasing temperature during the short, daytime experiments, KIM-T was generally a net CO₂ source at temperatures in excess of 25°C due to the very large soil respiration fluxes.

Methane

The net methane flux was generally due to oxidation within soils in both KIM-C and KIM-T and was therefore a deposition flux. However, rates of CH₄ deposition were consistently larger in KIM-T than KIM-C by approximately 50%. The average rates of soil oxidation of CH₄ were -5.4 μmol CH₄ m⁻² h⁻¹ in KIM-T and -3.3 μmol CH₄ m⁻² h⁻¹ in KIM-C. The data also provided clear temperature response and, unlike that for total respiration, was consistent from day to day with the form CH₄ oxide = -0.487°C + 5.2, from the data in Figure 4. These large rates of methane oxidation in KIM-T provide an indication of larger soil mineralization rates in KIM-T.

NO emission

A further strong indication of larger soil mineralization rates was provided by measurements of NO and NO₂ exchange in KIM-C and KIM-T. The data in Figure 5 show typical differences between the two chambers, with absolute rates of emission similar to those published for similar ecosystems. The rates of emission of 0.5 to 2 ng N m⁻² s⁻¹ are broadly similar to those published for conifer forests of the relatively unpolluted regions of Europe. However the rapid increase from 0430 to 0500 coincides with a change in ambient NO₂ concentration. The small negative flux results from net NO₂ deposition above a compensation point and emission of NO from the soil which is oxidized within the chamber to NO₂ by ambient O₃ at concentrations. The change from deposition to emission providing an indication of the compensation point, which from these data suggest a value of 0.8 ppb NO₂ and emission rates in KIM-T up to a factor of 5 larger than those in KIM-C.

Conclusions

1. The KIM-T and KIM-C catchment chambers may be used to measure fluxes of a range of gases directly.
2. The gas fluxes measured successfully include CO₂, NO, NO₂, CH₄, H₂O, O₂, SO₂ and N₂O.
3. Uncertainty in differences between treatment fluxes may be resolved by making ventilation rate measurements during each period of flux measurements.
4. The data to date strongly indicate larger rates of soil respiration in the high temperature, high CO₂ treatment when measurements have been made at ambient CO₂ concentrations and the data corrected for temperature differences between treatments.
5. Substantially larger NO fluxes (up to x5) from soil in KIM-T than KIM-C suggest larger soil mineralization rates.
6. Larger CH₄ oxidation rates (by +50%) in KIM-T than KIM-C under ambient and high CO₂ conditions at the same temperature are indicative of larger soil microbial activity in the high CO₂ treatment.

7. Further more detailed measurements using whole chamber and small soil chambers are required to quantify the differences between treatments and identify the underlying cause. There are preliminary data from small chambers which show that accumulations of litter throughout the catchments are very important sources of CO₂ and important sinks for CH₄.

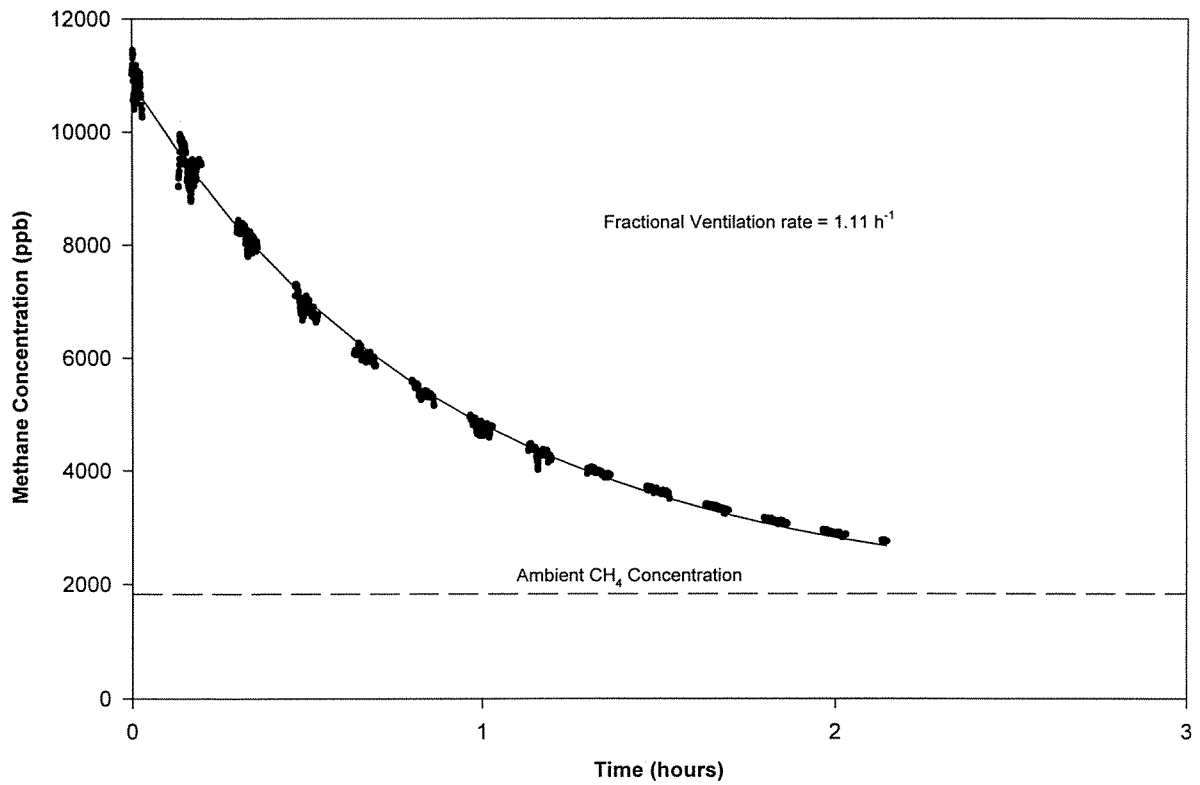


Figure 1
Determination of KIM-T ventilation rate by CH₄ injection.

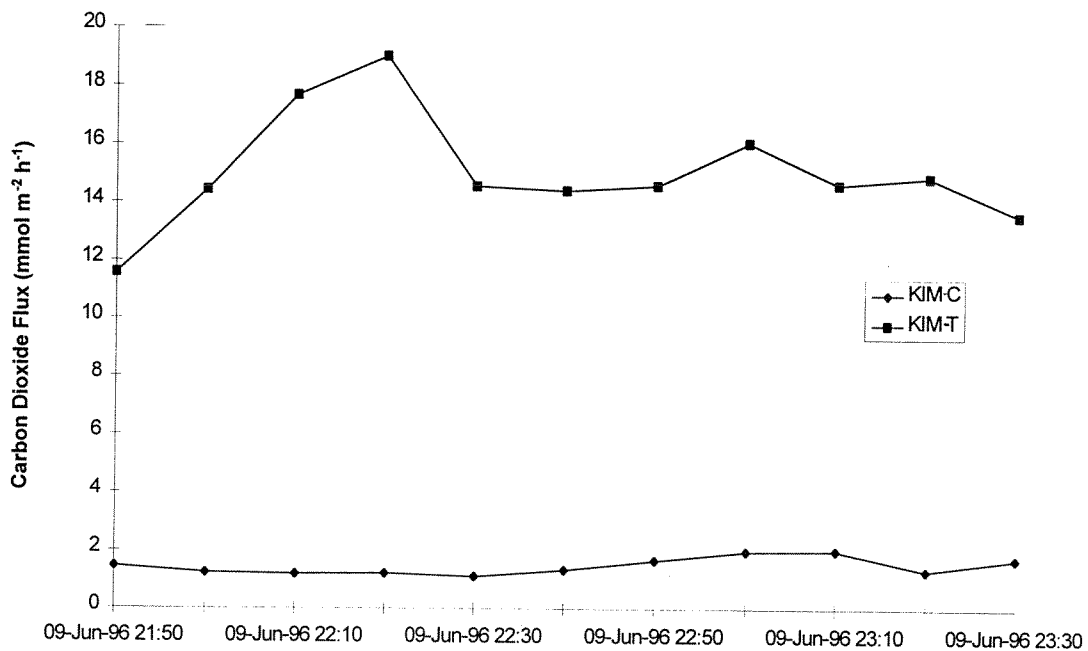


Figure 2
Carbon dioxide fluxes 21:50 9 June 1996 to 23:30 9 June 1996.

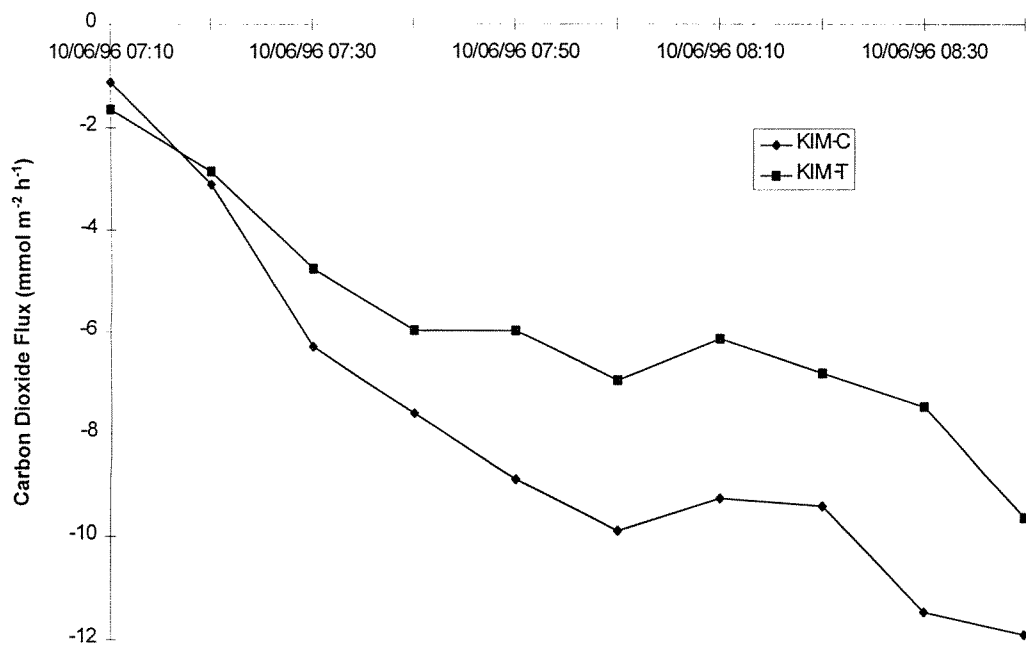


Figure 3
Carbon dioxide fluxes 07:10 10 June 1996 to 08:40 10 June 1996.

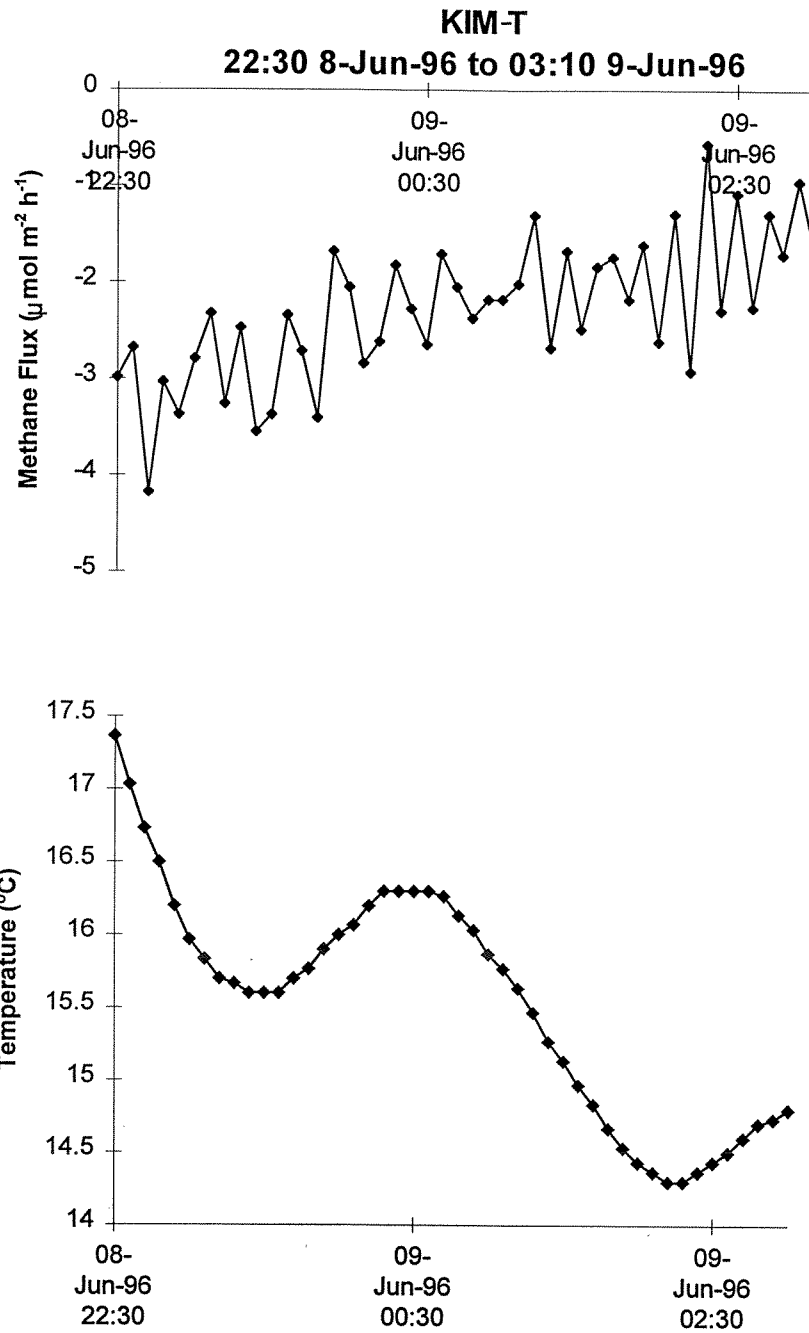


Figure 4
Methane flux and temperature.

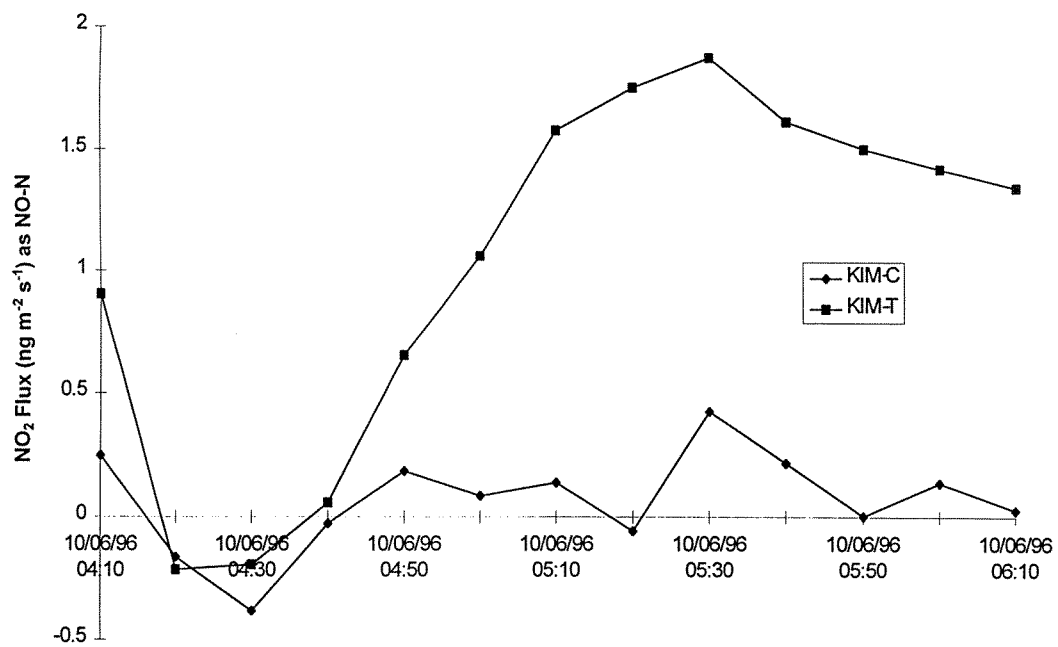


Figure 5
Nitrogen dioxide flux 04:10 10 June 1996 to 06:10 10 June 1996:

10. Soil ecology

Thomas W. Kuyper (WAU-BS)

Mycology

The ability of tree species to respond to increased levels of atmospheric carbon dioxide will be affected by mycorrhizal associations, mycorrhizas being the organs with which tree species take up nutrients. The net benefits that plants derive from the mycorrhizal association would depend on both gross benefits (enhanced uptake of nutrients) and costs (carbon expended to the fungus). Mycorrhizal fungi show interspecific differences both in costs and in benefits.

For these reasons, an experiment was set up at Risdalsheia in which two different ectomycorrhizal fungi of Scots pine (*pinus sylvestris*) were compared, *viz.* *Laccaria bicolor* (nitrogen-tolerant, high carbon demand) and *Suillus bovinus* (nitrophobous, lower carbon demand). A non-mycorrhizal control was also added. Both ectomycorrhizal fungi are of Dutch provenance, whereas seedlings of *Pinus* were of Southern Norwegian provenance. Seedlings were outplanted in both KIM-C and KIM-T. There were 20 replicates. Seedlings were outplanted in June 1996 and initial survival was assessed in September 1996. Final harvesting will take place in 1997.

The assessment in September showed higher survival of mycorrhizal seedlings (51%) compared to nonmycorrhizal seedlings (22%). Seedlings with *Suillus bovinus* were more vital than seedlings with *Laccaria bicolor*. Survival in KIM-T (48%) was higher than survival in KIM-C (35%), possibly as an effect of an increased water use efficiency in KIM-T.

A simultaneous greenhouse experiment with pine seedlings of the same provenance and with the same mycorrhizal treatments was set up under controlled conditions. Plant growth (above and below-ground biomass), mycorrhizal abundance and plant nutrient status will be assessed. Carbon allocation will also be investigated after pulse labelling with ^{14}C . As the chemical analysis of the seedlings is not yet complete, only preliminary data can be given.

Elevated carbon dioxide increased plant biomass of seedlings inoculated with *Suillus bovinus* and *Laccaria bicolor*, whereas non-mycorrhizal plants did not respond to elevated carbon dioxide. Number of ectomycorrhizal root tips and root biomass showed a stronger response than above-ground biomass, suggesting that the additional carbon is largely invested in nutrient-acquiring resources. Response of *Suillus bovinus* to elevated carbon dioxide was much stronger than response of *Laccaria bicolor*.

11. Sulphur Dynamics at Risdalsheia

P Torssander & C M Mörth (Stockholm University)

Sulphur dynamics at Risdalsheia have been investigated by sulphur concentration and sulphur isotope determinations in soil and runoff. The objective of the sulphur isotope study is to:

1. Determine the source of sulphur in runoff.
2. Quantify S net loss or net retention.
3. Determine the effect of sulphur mass balance at increased temperature and elevated CO₂ (g) partial pressure (the CLIMEX objective)

Soil profile samples have been taken from the EGIL, ROLF, METTE, KIM-C and KIM-T catchments. More than 150 samples have been analysed for total and extractable sulphate (extraction with NaHCO₃) and 30 samples have been analysed for their sulphur isotope composition. Of these 10 soil samples have been analysed isotopically for extracted sulphate (the sulphur concentration of extractable sulphate is too low to allow isotopic analyses on the rest). Sulphate in runoff from all the above mentioned catchments have been measured isotopically on three different occasions and compared with bulk deposition $\delta^{34}\text{S}$ values.

Results

The bulk deposition $\delta^{34}\text{S}$ values from Risdalsheia vary between +4‰ and +6‰ (only 4 samples analysed). These data are similar to Lake Gårdsjön $\delta^{34}\text{S}$ values at times when the marine influence there is small or negligible. The $\delta^{34}\text{S}$ values at Lake Gårdsjön, collected during four years, varies between +4 and +15‰ and fall on a mixing line between anthropogenic S ($\delta^{34}\text{S} = +4‰$) and seawater sulphate ($\delta^{34}\text{S} = +21‰$). The Risdalsheia $\delta^{34}\text{S}$ fall on the same mixing line, and the bulk deposition long-term $\delta^{34}\text{S}$ values are probably similar.

The soil profiles have been sampled on two different occasions in 1990 and 1994 at the onset of the CLIMEX project. The soil profiles show very large spatial variation, irrespective of catchment. The total S $\delta^{34}\text{S}$ values in soil profiles are however consistent. The uppermost samples (0-15 cm) vary generally between +5 and 9‰, and remain similar or increasing at intermediate depth (15-30 cm) but decreases largely to $\delta^{34}\text{S}$ values around 0 ‰ at the deepest parts in the investigated catchments (Figure 1). It appears by comparison between KIM samples from 1990 and 1994 that the extractable sulphate concentration has decreased, but as the spatial variation is large no definite conclusion can be drawn.

Runoff data show variation with time and is different between catchments. The $\delta^{34}\text{S}$ increase in summer can be caused by bacterial sulphate reduction (BSR) and the reduction in autumn can be caused by oxidation of BSR reduced sulphide S (Figure 2).

Discussion

Sorption-processes, immobilisation and mineralisation processes fractionate sulphur isotopes little if at all. The only process that can fractionate sulphur isotope ratios to a large extent at Earth surface conditions is bacterial dissimilatory sulphate reduction, the formed H_2S will have a low $\delta^{34}\text{S}$ value and remaining sulphate in solution a high $\delta^{34}\text{S}$ value. The formed sulphide will most commonly precipitate as an iron sulphide or be incorporated as organic S, while the dissolved “heavy” sulphate will form a part of runoff. Reduction-processes causes decrease in sulphate concentration and increase in the sulphur isotope values. During oxidation, the bacteriogenically formed H_2S will oxidise easily with the result that dissolved sulphate concentration in runoff increases and the $\delta^{34}\text{S}$ value decreases or actually become much lower. The soil samples collected at the deepest part of the catchment show low $\delta^{34}\text{S}$ values that is indicative of bacterial sulphate reduction. The $\delta^{34}\text{S}$ variation in runoff are also likely to be caused by bacterial sulphate reduction followed by oxidation-processes, but the time series is too short to make a definite conclusion to what extent the processes affect the runoff from the catchments. The soil samples $\delta^{34}\text{S}$ values at shallow and intermediate depth indicate that the deposition is the sulphur source and that soil sorption-processes and immobilisation-mineralisation-processes are the main sulphur flux mechanisms.

Conclusions

Bacterial sulphate reduction and oxidation of the bacterially formed sulphide S are important processes in all the sub-catchment at Risdalsheia. Processes in the soil and the source control the sulphur isotope distribution.

The spatial variability within and between catchments is large.

A longer time series for runoff is needed to evaluate the sulphur net loss or retention and also calculate the effect from increased temperature and elevated CO_2 partial pressure.

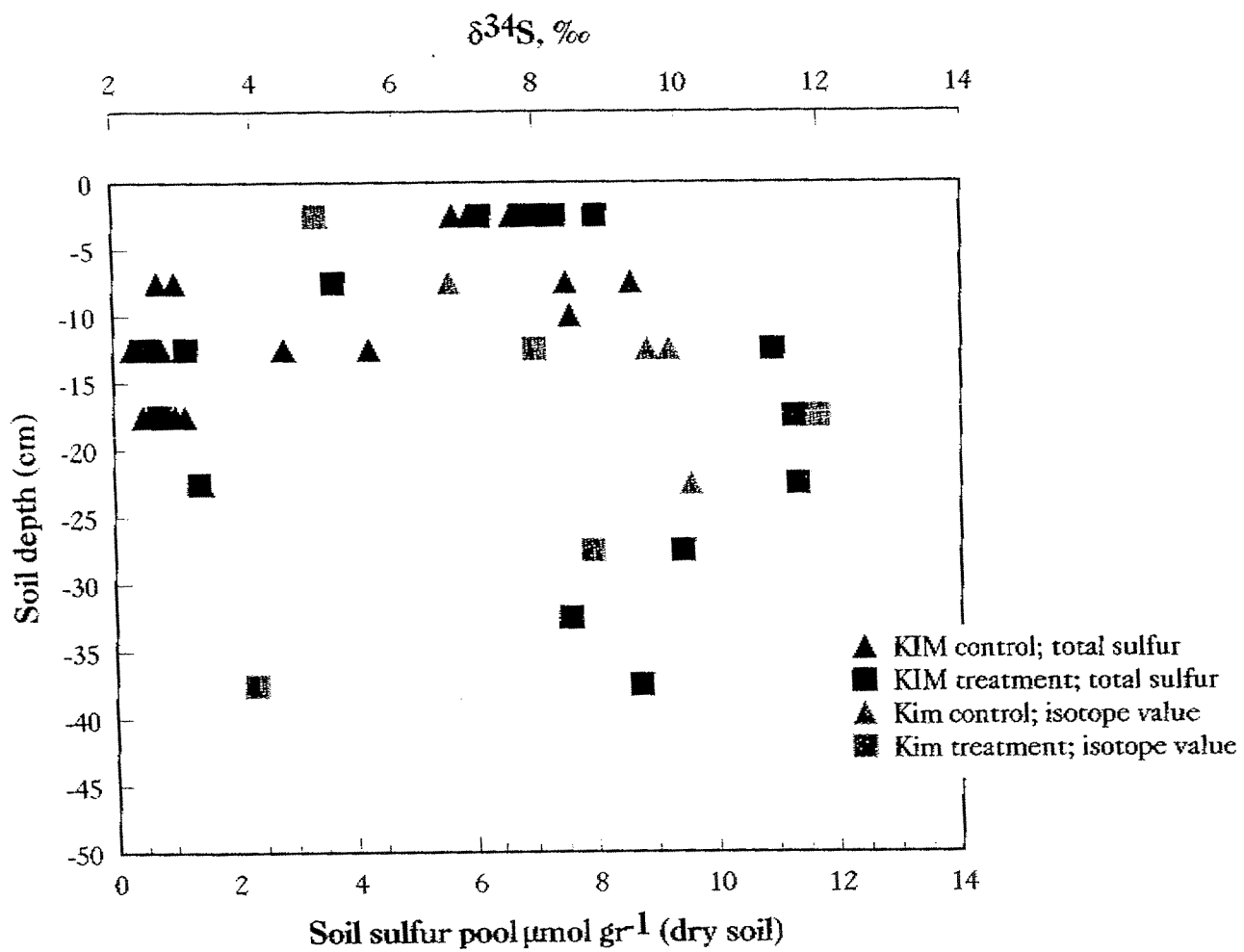


Figure 1
 Sulphur concentration and $\delta^{34}\text{S}$ in soil from KIM-C and KIM-T.

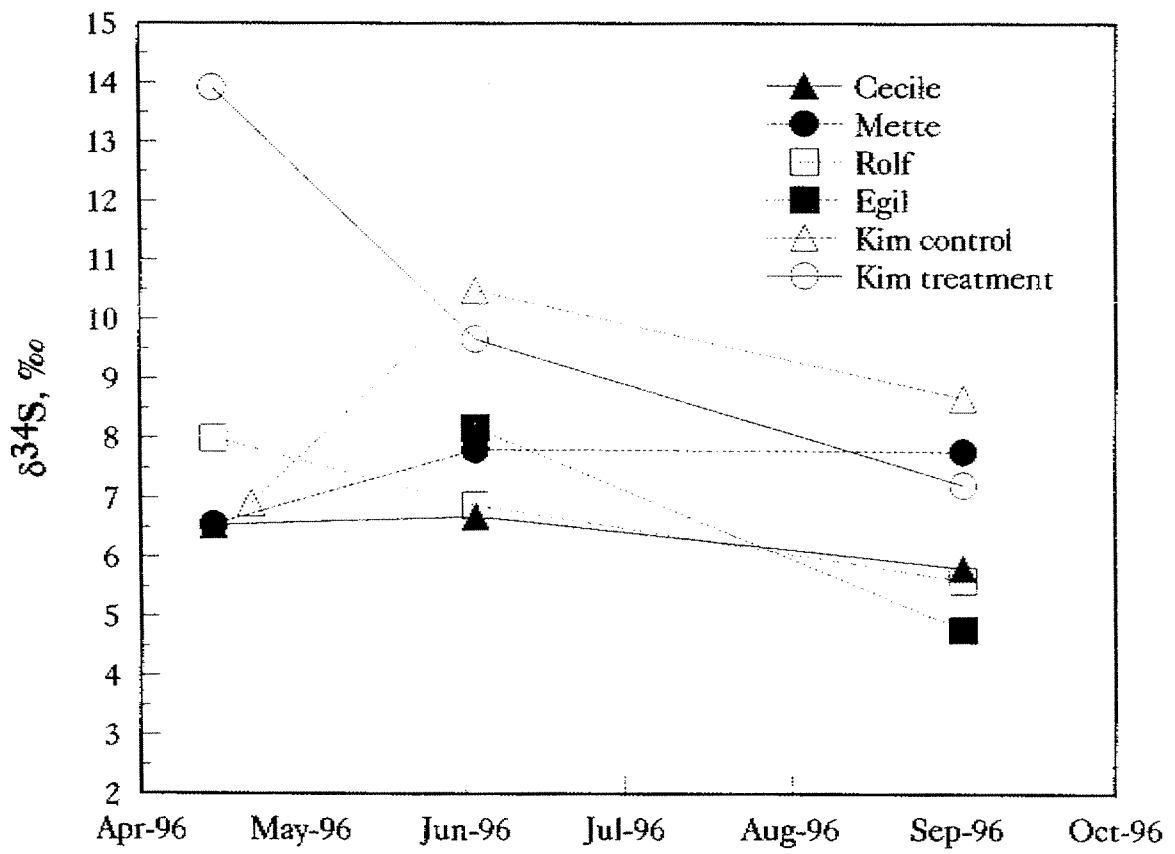


Figure 2
Sulphur isotopes in runoff.

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