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Soil N dynamics in a natural calcareous grassland under a changing climate

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Abstract This paper reports the results from a medium-term field scale investigation into the effects of simulated climate change on soil N mineralisation in a semi-natural calcareous grassland in southern England. The experiment utilised soil warming cables, automatic rainshelters and a watering system to examine two climate change scenarios: warmer winters with summer drought and warmer winters with enhanced summer rainfall. Gross N mineralisation rates in treated plots were determined, using ^{15}N pool dilution techniques, at 6-weekly intervals over a 3-year period. Results from control plots showed a strong seasonality of mineralisation with highest rates in autumn and winter and lowest rates in summer. They suggest that water availability is the main constraint on microbial processes and plant growth. Unexpectedly, additional summer rainfall had no direct effect on N mineralisation at the time of application (summer). The treatment did, however, significantly ($<0.05\%$) reduce rates in subsequent autumn and winter months. In contrast, summer drought significantly increased N mineralisation rates in autumn and winter. Winter warming similarly had no direct effect on N mineralisation in winter but decreased rates in spring. We hypothesise that the observed treatment effects result from changes in organic C and N input, in plant litter, resulting from the direct impact of climatic manipulation on perennial plant growth, death and senescence. This paper compares and contrasts the response to climate manipulation in the grassland system with results from other ecosystem types such as northern forests.

Key words Climate change · Nitrogen mineralisation · ^{15}N pool dilution · Calcareous grasslands · Soil warming

Introduction

Current models of climate change predict a global increase in mean air temperatures of between 1.5 and 4.5 °C for doubling CO_2 concentration, with the largest change expected in high latitudes. Precipitation changes are less certain. Several high resolution models predict increases of 10–20%, though increased frequency of drought events may reduce soil moisture by 17–23% (Houghton et al. 1990).

Historical records suggest that changes in climate could have profound effects on ecosystem structure and function. Short-term responses to climate change may include changes in rates of processes (e.g. decomposition) and species interactions, which in the long term could lead to changes in community structure with feedback effects on climate change and community structure. The complexity of terrestrial ecosystems has made it inevitable that large-scale simulation models become a major tool in assessing the impact of various climate change scenarios (e.g. McGill et al. 1981; Schimel et al. 1990; Parton et al. 1994). However, these models are only as reliable as the mechanisms and relationships they encode, most of which are derived from the response of isolated parts of a system such as soil and plants. Large-scale field experiments provide an opportunity to measure the response of ecosystems to perturbation and test the reliability of global models.

Modifying and controlling individual climatic factors (e.g. temperature and rainfall) in the field, with no disruption of other environmental factors (e.g. wind-speed), is difficult. A number of technologies have developed from a range of disciplines over the years to tackle this problem. Automatic rainshelters of various individual design, which move across a plot when rain starts and off when rain stops, have been developed, tested and used to study drought in agricultural research (Legg et al. 1978; Day et al. 1981; Lawlor et al. 1981). Soil and air temperatures have been manipulated using either soil warming cables (Peterjohn et al.

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1993; Melillo et al. 1995; Lukewille and Wright 1997) or open top polythene tents (Robinson et al. 1997), in a number of field experiments studying climate change in temperate/boreal forest and tundra sites. Soil warming cables have the advantage that they cause minimal disruption of other climatic variables, and tight temperature control can be maintained through the soil profile over time.

Grassland ecosystems cover about 37% of the 82 million km² of land surface occupied by rangelands and store about 14% of terrestrial carbon (Tate and Ross 1997). Above-ground production in grasslands is frequently limited by rainfall and the availability of nutrients, particularly N and P. The potential impact of climate change on these systems could be substantial, mediated by direct effects of changes in temperature and precipitation on plants and indirect effects arising from changes in nutrient availability. While a number of models have been developed to examine climate change in grasslands (Schimel et al. 1990; Parton et al. 1994), no field scale experiments, comparable to those performed in other systems, have been done to validate the impacts of climate manipulation. This paper describes a field experiment, on a semi-natural calcareous grassland site in southern England. The experiment was designed to examine the effect of manipulating local climate (temperature and moisture) using automatic rainshelters, soil heating cables and a watering system. The experiment involved a multi-disciplinary team, comprising soil scientists, plant ecologists and entomologists. Results presented here relate to the effects of climate treatments on soil processes and focus on N transformations.

The impact of environmental factors on nutrient availability in grasslands cannot be determined by simple spot measurements of nutrients such as NH₄ and NO₃, since processes which consume nutrients, e.g. plant uptake, will also be affected, masking any changes in soil nutrient levels. Many workers use net N mineralisation rates, determined by incubating contained soil under field conditions, as a measure of N availability (Raison et al. 1987). However, in grasslands the soil/plant system is closely associated, and plants may have a significant effect on N mineralisation. An ideal method for measuring N cycle processes in the field would cause minimal disturbance to the plant/soil system and would isolate the process of interest, e.g. gross N mineralisation. A technique developed by Kirkham and Bartholomew (1954), ¹⁵N pool dilution, allows gross rates of N mineralisation to be determined. The method involves adding a pulse of ¹⁵NH₄ into the soil NH₄ pool, and observing the rate at which the atom % ¹⁵N enrichment of that ammonium pool declines as native inorganic ¹⁴N is mineralised to ¹⁴NH₄. Pool dilution technique was used to measure gross N mineralisation rates at 6-weekly intervals over 3 years of climate manipulation at Wytham.

Materials and methods

Study site

The study site is located on a 10 ha semi-natural calcareous grassland field situated at Wytham estate, Oxfordshire, UK. The site and vegetation has been described in detail by Gibson et al. (1987). The soil, overlying corallian Jurassic limestone, is a shallow (<10 cm) stony rendzina of the Sherbourne series. Selected soil properties for the top 0–5 cm horizon are: organic matter 8.5%, total C 4.9%, total N 0.5%, biomass N 98.6 mg N kg⁻¹, extractable P 8.0 mg P kg⁻¹, pH 7.8. The site has a mean annual rainfall of 600 mm and an annual temperature of 10.1 °C. The experimental site is a 1 ha area within a 2 m high fence which excludes the main grazing animals, sheep and deer.

Experimental design and treatments

An experiment was designed in which various climate manipulations were factorially combined to test two possible climate change scenarios: warmer winters with increased summer rainfall and warmer winters with summer drought. In 1993, five replicate 12 m × 12 m grids were positioned within the 1 ha site. Each grid was divided into nine 3 m × 3 m plots with 1.5 m walkways. Six climate treatments were randomly assigned to plots in each grid to achieve a fully randomised block design. The treatments were: (1) control (ambient conditions), code C; (2) winter warming by 3 °C above ambient, code WW; (3) summer drought, code SD; (4) enhanced summer rainfall, code ER; (5) winter warming with summer drought, code WWSD and (6) winter warming with enhanced summer rainfall, code WWER.

A brief summary of the various climate manipulations is presented here. Full details of the technology involved will be published elsewhere. Winter warming to 3 °C above ambient from 1 November to 30 April each year was achieved using soil warming cables pinned zigzag fashion to the soil surface. Soil temperatures were measured using thermistor temperature probes linked to a Campbell data logger, which maintained a 3 °C temperature difference between heated and control plots by switching the power on and off via a relay. Summer drought through July and August was imposed using mobile perspex rainshelters mounted on an aluminum frame. Shelters automatically moved across the plot when rain was detected by a rain sensor. Summer rainfall was supplemented, from 1 June to 30 September, to 20% above the 10 year weekly average for the site through weekly additions of deionised water.

Sampling regime

Field plots were first sampled in December 1993 following installation of heating cables but prior to switch on, which first occurred in January 1994. Plots were subsequently sampled at approximately 6-weekly intervals through 1994, 1995 and 1996; a less frequent, strategic sampling was adopted in 1997. At each sample date, gross N mineralisation rates in each of the treated plots were determined by ¹⁵N pool dilution technique (Kirkham and Bartholomew 1954; Barraclough et al. 1985). Gravimetric soil water contents were determined at the same time. In addition to the routine sampling, a number of other soil parameters were determined for the various treatments at strategic sampling times. These included biomass N and organic C and N. Biomass N determinations were performed in May 1994, using the direct extraction method of Brookes et al. (1985). Organic C and N concentrations were measured in September 1995. Organic C was determined on ground (<1 mm) air-dried samples by wet oxidation and titration (Tinsley 1950). Total N was determined for the same samples using a VG Micromass 622 mass spectrometer linked to a Europa Roboprep combustion analyser.

Determination of gross N mineralisation rates

One quarter of each plot was assigned to destructive soil sampling. This quarter was divided at 10-cm intervals to form a grid containing 196 cells. On each sample date, three pairs of cells were randomly selected and marked in the centre with a coloured flag. Soil corers, with a 7.5 cm diameter and a 5 cm depth, were chosen to sample each cell following injection of 20 at% $^{15}\text{N}(\text{NH}_4)_2\text{SO}_4$ at an application rate of $15 \mu\text{g N g}^{-1}$ soil. A plastic ring was used to mark the outer perimeter of the corer during injection. A single hypodermic needle with four outlet holes was used to apply 0.5 ml of ^{15}N solution at six points and three depths down to 5 cm within the sampling ring. This method of multiple single injections was chosen to maximise ^{15}N distribution through the stony soil (Monaghan 1995). Half of the injected cores were sampled after 1 day, while the remaining cores were sampled 3 days later. On each sample day, soil cores were immediately taken to the laboratory and thoroughly mixed. Seventy-five grams of each soil sample was then extracted in 300 ml of 1 M KCl by shaking for 1 h, then filtering through GF/A glass-fibre filter paper.

KCl extracts were prepared for isotope ratio analysis of the ammonium pool by diffusion with MgO onto an acidified GF/D glass fibre paper disc for 1 week (Brookes et al. 1989). After drying over anhydrous calcium sulphate, discs were analysed on a VG Micromass 622 mass spectrometer linked to a Europa Roboprep combustion analyser, referenced against IAEA standard 305B. Available NH_4 and NO_3 were analysed by flow injection (Tecator 5010).

Gross N mineralisation rates were determined by a zero order pool dilution equation (Barraclough et al. 1985):

$$A_t^* = A_0^* / (1 + \theta t/A_0)^{m/\theta} \quad (1)$$

where A is the ammonium pool size, t is time and m is the rate of mineralisation. Subscripts t and 0 represent the time intervals for soil sampling following ^{15}N injection, and superscript * indicates atom % excess. θ is the rate of change of the soil ammonium pool size over the sampling period, and is calculated as

$$\theta = (A_t - A_0)/t \quad (2)$$

Plant biomass

Plant biomass measurements were made in a complementary experiment carried out by M. Unkovich in 1995. This work examined the response of the biomass to water and nutrient additions over a 6-week period beginning on 9 May 1995. Above-ground plant material was harvested from 1 m² plots, replicated 5 times, oven dried (80°C) and weighed. Root biomass was estimated from two 75 mm × 50 mm cores taken from each plot. Roots were separated from bulk soil by hand, shaken to remove adhering soil then oven dried (80°C) and weighed. Tissue N concentrations were measured on sub-samples of finely ground plant material by combustion in a Roboprep automatic N analyser (Europa Scientific). Results from control plots were used to estimate above- and below-ground partitioning of biomass (Table 1).

Statistical analysis

Three-way analysis of variance was used to analyse the data, using a randomised block design with two levels of warming and three levels of watering.

Results

Partitioning of C and N

The distribution of C and N in the plant/soil system at Wytham is shown in Table 1. Of the 20,324 kg C ha⁻¹

Table 1 C and N pool size distribution at Wytham

	Biomass (kg ha ⁻¹)	C (kg C ha ⁻¹)	N (kg N ha ⁻¹)
Plant	—		
Above-ground biomass	1000	400	12
Below-ground root biomass (5 cm depth)	12570	5028	126
^a Soil (5 cm depth)		14896	1520
^b Microbial biomass		150	29
KCl extractable N			2
Total	13570	20324	1658

^a Soil C and N calculated for a soil volume of 5 cm depth and a bulk density of 0.608 g dry cm⁻³ soil

^b Biomass C calculated from biomass N assuming a C:N ratio of 5:1

stored in the whole system, 73% was soil organic C, and 27% was in plant biomass. Below-ground root biomass was approximately 12 times greater than above-ground biomass and contained >90% of plant C and N. Root biomass estimates should be treated with some caution as no distinction was made between live and dead roots during analysis. The data do however indicate a substantial investment in root versus shoot production at this site. The microbial biomass pool contained just 1% of the soil organic C.

Climate manipulation and N dynamics

Figure 1 shows soil temperatures recorded every 30 min, in the heated and control plots over a 1-week period of soil warming during November 1994. Fluctuations in temperature in control plots were closely tracked in the heated plots, resulting in a temperature difference of $3^\circ\text{C} \pm 0.3^\circ\text{C}$ over the time period. Hence, the soil warming system used at this site was capable of maintaining tight temperature control over the winter period, which effectively simulated winter warming.

The effect of winter warming on gross N mineralisation rates, soil moisture contents and soil temperatures, averaged for the spring, summer, autumn and winter periods over the 3 year experimental period is illustrated in Fig. 2. Rates were lowest in summer when mean soil moisture contents were close to the permanent wilting point ($0.23 \text{ g H}_2\text{O g}^{-1}$ dry soil equivalent to approximately 1000 kPa). N mineralisation increased through autumn reaching a maximum of 2 mg N kg^{-1} soil day⁻¹ in winter despite low average soil temperatures (4°C). The increase in N mineralisation appears to be related to the soil moisture content, which was just below field capacity in autumn and winter at approximately $0.4 \text{ g H}_2\text{O g}^{-1}$ dry soil (equivalent to 20 kPa). Soil warming by 3°C had no significant effect on N mineralisation during autumn or winter, but significantly ($<0.05\%$) reduced mineralisation rates in the spring following treatment imposition.

Fig. 1 Soil temperatures (1 cm depth) recorded at 30 min intervals over 1 week in control and heated plots during November 1994. *Lines* show temperature differences between the plots over the same time period

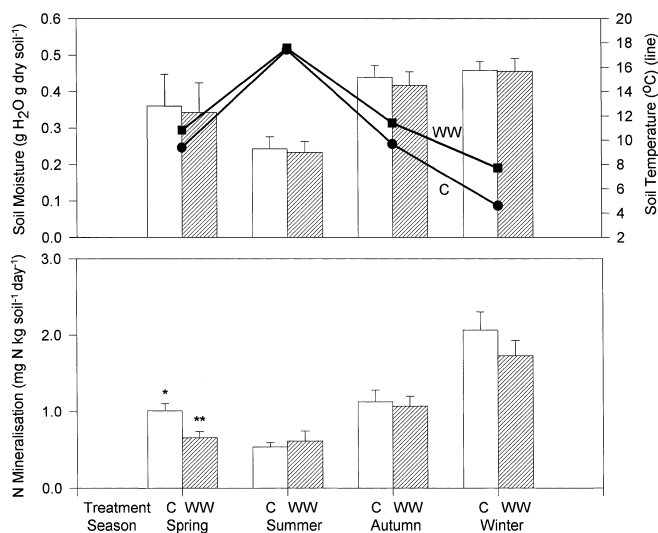
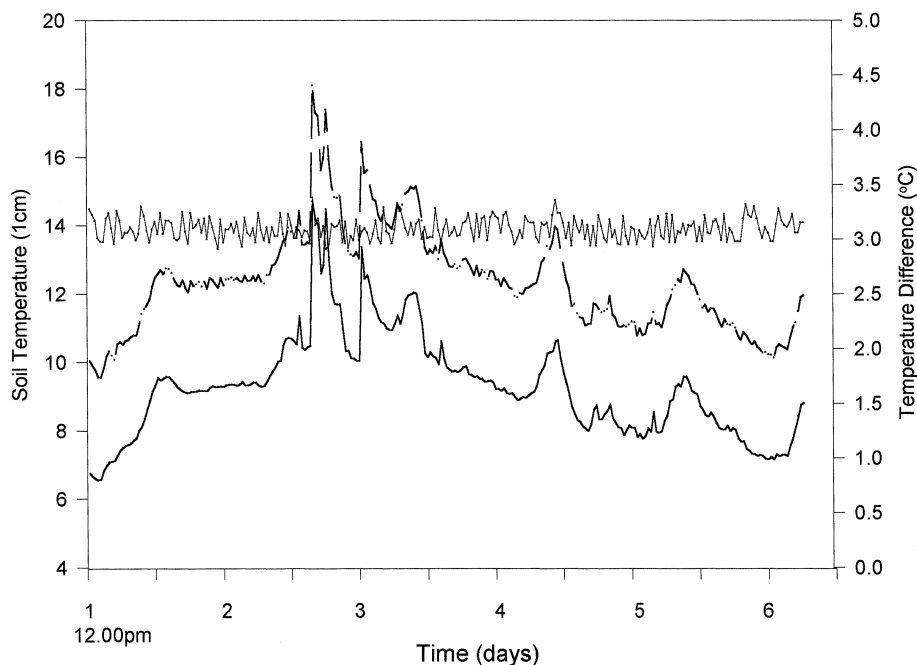


Fig. 2 Effect of winter warming (WW) on average spring, summer, autumn and winter, soil moisture contents ($\text{g H}_2\text{O g}^{-1}$ dry soil), soil temperatures ($^{\circ}\text{C}$) and gross N mineralisation rates ($\text{mg N kg soil}^{-1} \text{ day}^{-1}$). Bars on histogram show \pm SE of the mean. Different numbers of asterisks indicate significant differences ($P < 0.05\%$) between treatments

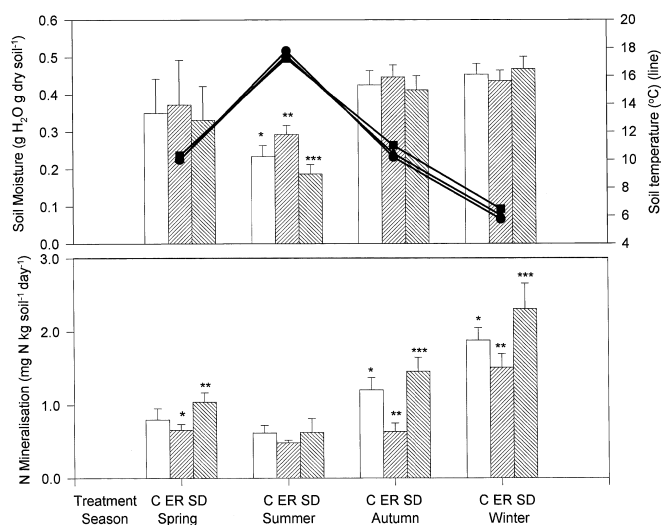


Fig. 3 Effect of summer drought (SD) and enhanced summer rainfall (ER) on average spring, summer, autumn and winter soil moisture contents ($\text{g H}_2\text{O g}^{-1}$ dry soil), soil temperatures ($^{\circ}\text{C}$) and gross N mineralisation rates ($\text{mg N kg soil}^{-1} \text{ day}^{-1}$). Bars on histogram show \pm SE of the mean. Different numbers of asterisks indicate significant differences ($P < 0.05\%$) between treatments

Figure 3 shows the effects of enhanced summer rainfall and summer drought on average gross N mineralisation rates, soil moisture contents and soil temperatures in each season. All treatments followed a similar seasonal pattern of N mineralisation as described for Fig. 2. Neither of the rainfall manipulations had a significant effect on soil temperatures over the experimental period. Enhanced summer rainfall increased average soil moisture contents from 0.23 to $0.30 \text{ g H}_2\text{O g}^{-1}$ dry soil during treatment imposition (i.e. summer). This

increase had no significant effect on gross N mineralisation over the same period. Despite the lack of response to climate manipulation during summer months, significant treatment effects were observed for autumn and winter measurements. Enhanced summer rainfall significantly reduced N mineralisation rates while summer drought increased rates.

The gross N mineralisation measurements from each of the six weekly samples were used to determine cumulative mineralisation for each treatment over the 3-

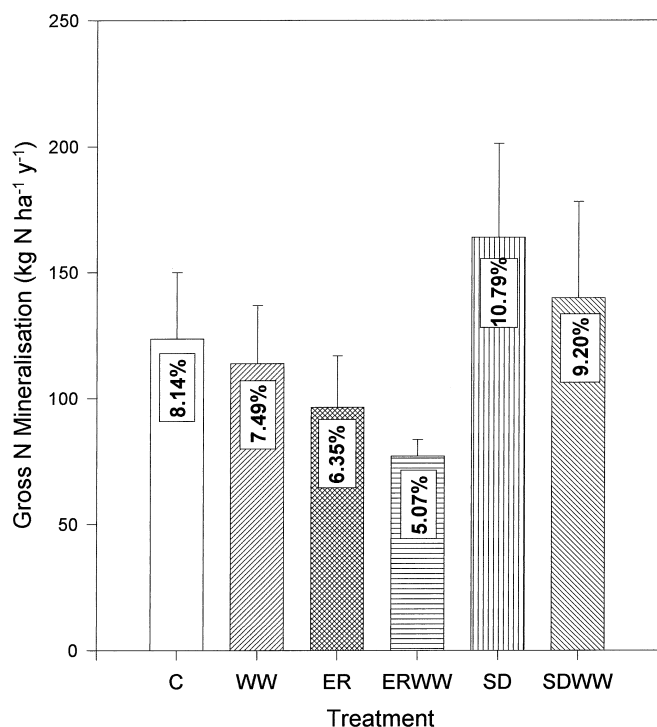


Fig. 4 Yearly gross N mineralisation rates calculated from cumulative N mineralised over 3 years, for a soil depth of 5 cm and bulk density of 0.608 g cm^{-3} soil. Percentages of the total organic N pool mineralised are indicated on each bar

year experimental period. These data were, in turn, used to calculate yearly rates of gross N mineralisation in the grassland system (Fig. 4). Rates ranged from $75 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (equivalent to 5% of the soil total N pool) under winter warming and enhanced summer rainfall to $160 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (11% of the soil total N pool) under summer drought.

Discussion

The major factors limiting plant growth in grassland ecosystems are water and nutrient availability (Parton et al. 1994). Results from the complementary experiment carried out by M. Unkovich (data not shown) showed that above-ground plant biomass responded positively to both water and N (NH_4 and NO_3) additions, but not to P or K. This confirms that the site at Wytham is both water and N limited. Seasonal N mineralisation measurements indicate that microbial activity, and hence N availability, decline during spring and summer when evapotranspiration rates frequently exceed rainfall, and soil water potentials in the shallow stony soils approach the permanent wilting point.

The response of N dynamics to climate manipulation at the ecosystem scale is difficult to predict because of the complexity of plant/soil interactions. Models of ecosystem responses to climate change (e.g. Parton et al. 1994 and Schimel et al. 1990) are largely based on rela-

tionships of microbially mediated soil processes with soil temperature and moisture, established from laboratory incubation of isolated soil samples. Typically, decomposition rates at a constant moisture content increase by factors between 1.5 and 2.5 for each 10°C rise in temperature between 0 and 30°C . Microbial activity is highest at about -0.01 MPa and decreases as soil becomes dry (<-5 to -10 MPa) or saturated (approximately 0 MPa) (Nadelhoffer et al. 1995). From these relationships it is clear that maximum potential N mineralisation rates are unlikely to be achieved in the grassland soil at Wytham, where microbial activity will be limited by low soil moisture potentials in summer and low soil temperatures in winter. Based on our knowledge of the site and the seasonal N mineralisation pattern, we would have predicted a direct positive effect of enhanced summer rainfall and winter warming on N mineralisation rates at this site.

The results of our field measurements over 3 years of climate manipulation contradict these predictions. Enhanced summer rainfall had no direct effect on N mineralisation during treatment imposition but significantly reduced N mineralisation in subsequent autumn and winter months. The lack of a direct effect of water addition may simply reflect the high potential evapotranspiration at the site; indeed, soil moisture contents only increased to approximately $0.3 \text{ g H}_2\text{O g}^{-1}$ dry soil (equivalent to 160 kPa) during summer. Average water additions were 6 mm, equivalent to the daily evapotranspiration. Likewise, summer drought had no direct effect but increased N mineralisation rates in the subsequent autumn and winter. Winter warming similarly had no direct effect on N mineralisation rates during treatment imposition, but it significantly reduced rates in the following spring. There are limited field data sets on ecosystem responses to climate change for comparison. A number of experiments have utilised soil warming cables to manipulate soil temperature in temperate and boreal forest sites (Van Cleve et al. 1990; Peterjohn et al. 1993; Melillo et al. 1995; Lukewille and Wright 1997). In all these studies there is evidence of increased mineralisation of organic N and C. Melillo et al. (1995) observed a doubling of net N mineralisation and increased CO_2 flux in a deciduous forest floor during the first 2 years of warming by 5°C . For a hardwood forest, Peterjohn et al. (1993) found reductions in C and N concentration in the O horizon of 36% and 30% respectively, in heated plots. Other workers have observed increases in available N in forest floor material (Van Cleve et al. 1990) and runoff water (Lukewille and Wright 1997). Laboratory measurements on Wytham soil without plants also showed that gross N mineralisation increased with temperature between 0 and 30°C , albeit with a low Q_{10} of 1.4 (data not shown). The field observations of a reduction in N mineralisation under soil warming at Wytham therefore suggest some other factor must be overriding the small direct temperature effect. Large-scale field experiments on climate change have largely focused on northern forest and

tundra sites. There are a number of models available (Schimel et al. 1990; Parton et al. 1994) to examine the impact of climate change on different ecosystem types such as agroecosystems and grasslands, but there is little experimental evidence to validate the simulated ecosystem responses. Hantschel et al. (1995) employed soil warming cables to heat plots growing winter wheat to 3 °C above ambient. After 3 months of winter warming (January to March), these workers found no change in the soluble N pool, however, N₂O emissions were lower in heated compared to control plots.

The key to understanding the different N mineralisation responses to climate manipulation observed in forest soils compared to the calcareous grassland soil at Wytham may lie in differences in C and N partitioning and cycling between the two systems. In perennial grasslands much of the C and N occurs below ground. Roots are the dominant living plant fraction, with ratios of underground biomass to green shoot biomass ranging from 2 to 13 for temperate regions (Woodmansee et al. 1981; Oades 1995). Root : shoot ratios for forests are thought to be considerably less (Gosz 1981; Melillo 1981). Large woody components with slow turnover times are a major reservoir for organic C and N in forests. Tree foliage generally represents less than 10% of the total biomass, and the leaves of coniferous forests may persist 1–14 years (Gosz 1981). In contrast, a considerable portion of top growth of perennial grasses and forbs dies at least once per annum, due to maturation and senescence, drought, freezing, consumption and disease. The same causes of top death presumably apply to the dominant root biomass, which will produce litter to the decomposer biomass through root death, exudation and root cell sloughing (Woodmansee et al. 1981). The substrate for N mineralisation, organic matter, can be divided into a number of fractions, including: current plant residues, plant residues more than 1 year old, the macroorganic fraction, soil microbial biomass and old organic matter. Evidence suggests that in grasslands the decomposition of current plant residues is an important component of mineralisation in the year they enter the soil. The model of McGill et al. (1981) predicted that the metabolic component of these materials, together with recent microbial debris, supplied 55% of the mineral N processed by micro-organisms. The structural components supplied 39%, while the more resistant components, representing by far the largest pool size for C and N (>90%), supplied just 5%. We hypothesise that at Wytham, where perennial plants are dominant, above- and below-ground plant residues are an important contributor to gross N mineralisation in the year they enter the soil. The climatic treatments imposed are altering N mineralisation rates by increasing or decreasing litter input by their direct impact on plant growth, death and senescence. The main causes of plant top and root death in grasslands are drought and freezing (McGill et al. 1981). By alleviating these stresses, the winter warming and enhanced summer rainfall treatments reduce plant death

and, hence, the input of substrate C and N. This results in reduced N mineralisation rates when the microbial biomass is no longer limited by abiotic factors such as soil moisture stress.

In northern forest systems, particularly coniferous sites, decomposition rates are frequently limited by low temperatures and poor soil moisture status (Gosz 1981). Under these conditions, trees have adapted to conserve nutrients, which results in the production of low quality litter with a high C:N ratio. This low quality litter accumulates on the forest floor over a number of years, creating a large reservoir of organic C and N. In these systems, we expect the contribution of fresh residues to N mineralisation to be considerably lower than in grassland sites. Soil warming will have a direct impact on the decomposition of litter, accumulated over a number of years, resulting in the increased C and N mineralisation as observed in the experiments described previously. We would expect a much slower and less direct effect of soil warming on the vegetation in forest systems, compared to grassland, largely due to the different time scales of growth, death and senescence.

These studies have highlighted the contrasting impacts of climate manipulation on soil processes in different ecosystem types. In a temperate calcareous grassland, the dominant effects of climate change on N mineralisation, even in the short to medium term, appeared to be indirect as a result of the direct impact of climate on vegetation dynamics and litter input. In a number of northern forest sites, climate change was shown to have a direct positive effect on N mineralisation. This, in turn, would have an indirect impact on vegetation by increasing N availability and, hence, N uptake. In the long term, changes in N availability and vegetation chemistry and dynamics could have complex feedback effects in both systems.

From the gross N mineralisation measurements at Wytham, it is estimated that annual N mineralisation in the control plots is equivalent to 8% of the total soil organic N pool. This figure is high compared to estimates based on net N mineralisation measurements which generally suggest a value of 1–2%. Comparable estimates based on gross measurements in different ecosystems are not presently available; however, our results suggest that the soil system is more dynamic and less well buffered against environmental perturbations than previously believed.

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