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A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming

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Abstract Climate change due to greenhouse gas emissions is predicted to raise the mean global temperature by 1.0–3.5°C in the next 50–100 years. The direct and indirect effects of this potential increase in temperature on terrestrial ecosystems and ecosystem processes are likely to be complex and highly varied in time and space. The Global Change and Terrestrial Ecosystems core project of the International Geosphere-Biosphere Programme has recently launched a Network of Ecosystem Warming Studies, the goals of which are to integrate and foster research on ecosystem-level effects of rising temperature. In this paper, we use meta-analysis to synthesize data on the response of soil respiration, net N mineralization, and aboveground plant productivity to experimental ecosystem warming at 32 research sites representing four broadly defined biomes, including high (latitude or altitude) tundra, low tundra, grassland, and forest. Warming methods included electrical heat-resistance ground cables, greenhouses, vented and unvented field chambers, overhead infrared lamps, and passive night-time warming. Although results from individual sites showed considerable variation in response to warming, results from the meta-analysis showed that, across all sites and years, 2–9 years of experimental warming in

the range 0.3–6.0°C significantly increased soil respiration rates by 20% (with a 95% confidence interval of 18–22%), net N mineralization rates by 46% (with a 95% confidence interval of 30–64%), and plant productivity by 19% (with a 95% confidence interval of 15–23%). The response of soil respiration to warming was generally larger in forested ecosystems compared to low tundra and grassland ecosystems, and the response of plant productivity was generally larger in low tundra ecosystems than in forest and grassland ecosystems. With the exception of aboveground plant productivity, which showed a greater positive response to warming in colder ecosystems, the magnitude of the response of these three processes to experimental warming was not generally significantly related to the geographic, climatic, or environmental variables evaluated in this analysis. This underscores the need to understand the relative importance of specific factors (such as temperature, moisture, site quality, vegetation type, successional status, land-use history, etc.) at different spatial and temporal scales, and suggests that we should be cautious in "scaling up" responses from the plot and site level to the landscape and biome level. Overall, ecosystem-warming experiments are shown to provide valuable insights on the response of terrestrial ecosystems to elevated temperature.

Introduction

Atmospheric concentrations of CO_2, CH_4, and N_2O have increased dramatically since the beginning of the industrial revolution largely due to human activities such as fossil fuel combustion and land-use change [Intergovernmental Panel on Climate Change (IPCC) 1996]. These gases have the capacity to trap heat in the atmosphere by absorbing infrared radiation reflected by the earth's surface. Considerable evidence is now available showing that greenhouse gases have increased the global mean surface temperature by 0.3–0.6°C over the last century (IPCC 1996; Rind 1999; Karl et al. 2000). Current predictions based on general circulation models indicate that the mean global temperature will increase by an additional 1–3.5°C in the next 50–100 years, with greater warming occurring at higher latitudes (IPCC 1996).

Temperature is a key factor that regulates many terrestrial biogeochemical processes, such as soil respiration (Raich and Schlesinger 1992), litter decomposition (Meentemeyer 1978; Jansson and Berg 1985; Hobbie 1996), N mineralization and nitrification (MacDonald et al. 1995), denitrification (Malhi et al. 1990), CH_4 emission (Crill et al. 1988; Crill 1991; Johnson et al. 1996), fine root dynamics (Boone et al. 1998; Pregitzer et al. 2000; Gill and Jackson 2000), plant productivity (Warren-Wilson 1957), and plant nutrient uptake (BassiriRad et al. 2000). Despite the relatively robust literature on the response of individual ecological processes to changing

temperature, a comprehensive understanding of whole ecosystem response to global warming remains elusive. For example, it is not clear which processes will be most affected by warming. How will the relative sensitivity of ecosystem respiration and photosynthesis affect net ecosystem C balance? What will control or limit the magnitude of these responses? Will the response remain constant over time? What types of ecosystems will be most affected? Will higher latitude or higher altitude ecosystems be affected more than equatorial or lower altitude ecosystems? Is the response linear with increasing temperature, curvilinear, humped, or is it a step function?

Recently, Shaver et al. (2000) proposed a conceptual model of ecosystem response to global warming. A key element of this model is that, on a global scale, ecosystem response to elevated temperature will be more varied in time and space than the response to elevated CO_2. This is because of the greater spatial and temporal variations in the projected temperature increase compared to the relatively uniform and continued increase in atmospheric CO_2, the multitude of interacting direct and indirect physical, biological, and chemical processes that will potentially be affected by temperature, and the variable time scale of response to temperature of different ecosystem components. Shaver et al. (2000) also postulated that ecosystem response would be strongly affected by initial conditions, such as stocks and initial turnover rates of labile soil C and N, the relative size of the plant and soil C pools, the dominant form of available N in the soil, the soil water and precipitation regimes, the chemical composition and turnover rates of plant residues, and the longevity of individuals and population turnover rates of dominant species. More research on ecosystem response to elevated temperature is clearly needed to validate and refine this conceptual model of ecosystem response to global warming.

Over the last 5–10 years, as predictions of global warming have become more widely recognized and accepted, the need for information on the response of ecosystems to changing temperature has been addressed by a growing number of temperature-manipulation experiments initiated around the world. These experiments have shown that rates of soil respiration generally increase with warmer temperatures (Peterjohn et al. 1993, 1994; McHale et al. 1998; Rustad and Fernandez 1998a), but the response to warming of other ecosystem processes has been more variable, and general response patterns have been difficult to identify. For example, litter decomposition, CH_4 production and oxidation, N cycling rates and losses, net C flux, and plant productivity have all been shown to increase, decrease, or remain unchanged by warming (Van Cleve et al. 1990; Joslin and Wolfe 1993; Peterjohn et al. 1993, 1994; Harte and Shaw 1995; Hantschel et al. 1995; Robinson et al. 1995; Hobbie 1996; Lukewille and Wright 1997; Ineson et al. 1998; Jamieson et al. 1998; Jones et al. 1998; McHale et al. 1998; Rustad and Fernandez 1998b; Olszyk et al. 1998; Shaver et al. 1998; Arft et al. 1999; Hartley et al. 1999; Verburg et al. 1999; Welker et al. 1999; Johnson et al. 2000; Rustad et al. 2000; Thompson et al. 2000; Welker et al. 2000).

Fig. 1 The Global Change and Terrestrial Ecosystems Network of Ecosystem Warming Studies sites
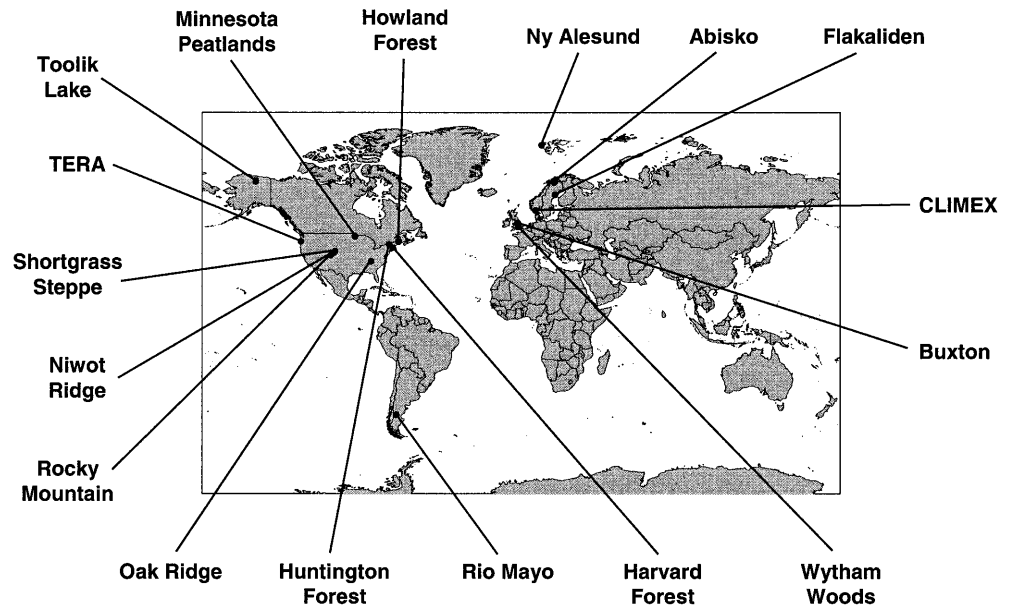
As some of these experiments are nearing completion, and others are being planned, there is a clear need to synthesize the existing data on ecosystem response to experimental warming in order to understand differences in response to date, to develop and refine current conceptual and quantitative frameworks for evaluating the response of ecosystems to elevated temperature, and to provide direction for future work in this relatively new field. Meta-analysis is a technique developed specifically for the statistical synthesis of independent experiments (e.g., Cooper and Hedges 1994; Gurevitch and Hedges 1999). Although meta-analysis has generally been applied to the analysis of data gathered from published literature, it is also well suited for combining the results of experiments carried out by individual researchers (e.g., Hechtel and Juliano 1997) or by networks of research groups (e.g., Arft et al. 1999; Gurevitch et al. 2000). Formal meta-analysis statistical techniques have numerous advantages over older approaches to quantitative data synthesis, such as "vote counting", and have increasingly been used in the ecological literature (e.g., Hedges and Olkin 1985; Gurevitch et al. 1992; Arnqvist and Wooster 1995; Gurevitch et al. 2000). Arft et al. (1999), for example, recently used meta-analysis to synthesize data from 13 circumpolar ecosystem warming research sites associated with the International Tundra Experiment (ITEX). All these sites used a common design of an open top chamber (Marion et al. 1997) and common protocols (Molou and Mølgaard 1996). Results from the ITEX synthesis showed a significant positive aboveground plant growth response to warming (Arft et al. 1999).

In the present paper, we use meta-analysis to synthesize data on the response of three critical ecosystem processes – soil respiration, net N mineralization, and aboveground plant productivity – to experimental ecosystem warming at 32 research sites representing four broadly defined biomes, including high (latitude or altitude) tundra, low tundra, grassland, and forest. Warming was accomplished using electrical heat-resistance ground cables, greenhouses, vented and unvented field chambers, overhead infrared lamps, and night-time warming. Due to logistical, scientific, and financial constraints, and because the goals and study designs differed among investigations, all three processes were not measured in each experiment. Meta-analysis, however, provides us with a tool to evaluate data from a range of sites, and ask questions relative to the effects of increasing temperature on nutrient cycling and C uptake and release. These questions had been addressed previously in part by the ITEX synthesis. However, this analysis differs from the ITEX synthesis by the inclusion of belowground ecosystem processes, and the evaluation of ecosystem response in a wider range of biomes over longer time periods, using a variety of experimental methods.

In evaluating the data in this synthesis, we hypothesized that increasing air and/or soil temperature in the range of ~1–5.0°C would increase rates of soil organic matter decomposition (as reflected by increased rates of soil respiration) and net N mineralization, resulting in greater nutrient availability, and consequently more rapid plant growth and greater net primary productivity (NPP). We also hypothesized that ecosystems would be more sensitive to warming at higher latitudes, because higher latitude ecosystems are typically strongly limited by both temperature and nutrients (Bliss et al. 1981; Chapin 1983; Chapin and Shaver 1985).

Methods

Experimental sites

The data for this analysis came from 32 ecosystem warming experiments located from ~35–79°N latitude, with an additional site at 45°S latitude (Fig. 1). Experiments ranged in duration from

2 to 9 years (many are ongoing). Mean annual air temperatures ranged from –9 to 14°C; mean annual precipitation ranged from 150 to 1400 mm, and length of the growing season ranged from 71 to 365 days. Additional site characteristics are given in Appendix 1. Although initiated independently and in various stages of completion, all sites are part of the Global Change in Terrestrial Ecosystem (GCTE) Network of Experimental Warming Experiments (NEWS), a new initiative designed to integrate and foster research on ecosystem-level effects of rising temperature.

Each site was classified as either high (latitude or altitude) tundra ($n=3$), low tundra ($n=14$), forest ($n=9$), or grassland ($n=6$) based on latitude, mean annual temperature, mean annual precipitation, and dominant vegetation. A North American temperate peat bog was classified as low tundra because of similarities in vegetation and soil to other low tundra sites. Vegetation at each site was also classified more generally as *predominately* woody ($n=16$) or non-woody ($n=16$). Heating was accomplished using electrical heat-resistance ground cables ($n=10$), vented and unvented field chambers ($n=13$), greenhouses ($n=3$), overhead infrared lamps ($n=5$), and night-time warming ($n=1$). Heating occurred either all year ($n=9$), during the snow-free months only ($n=21$), or during the winter months only ($n=2$).

Data collection

For each site, data were available on a variety of parameters designed to describe the general geography, climate, and environment. Not all data were available from all sites. Geographic parameters included latitude and longitude; climatic data included long-term mean annual and growing season temperature, mean annual and growing season precipitation, and average length of the growing season; environmental data included dominant vegetation type, stand age, successional status, soil classification, soil texture, upper organic and mineral soil C, N, pH, and bulk density, upper organic soil horizon thickness, and foliar N of one or more species. In addition, several climatic indices were calculated for temperature, precipitation, and combined temperature and precipitation as follows:

Tindex=1/1+exp(1.315–0.119×mean annual air temperature)
Pindex=1-exp(-0.000664×mean annual precipitation)
PTindex1=min(Tindex, Pindex)
PTindex2=Tindex×Pindex

The Tindex and Pindex are based on the Miami model of relationships between NPP and climate (Lieth 1975). Tindex1 and PTindex2 are two approaches to combining the influences of temperature and precipitation. The first, which chooses the minimum of Tindex and Pindex, assumes that NPP is controlled by the more limiting factor, whereas PTindex2 assumes an interactive influence of precipitation and temperature.

Experimental response data included mean annual or seasonal air and soil temperature (C), soil moisture (g H_2O g^{-1} dry soil), rates of soil respiration (mg CO_2-C m^{-2} h^{-1}), net N mineralization (g N m^{-2} year^{-1}) and aboveground plant productivity for treatment and control plots for each year of the experiments. The response of soil moisture to the treatments was evaluated to better understand the response of soil respiration, N mineralization, and plant growth to warming. Treatment effects on soil moisture were not interpreted to reflect future climate scenarios as changes in soil moisture will likely be more dependent on future precipitation patterns, which are expected to vary considerably by region (ICPP 1996). A measure of air or soil temperature was available for all sites, and gravimetric soil moisture data were available for 14 of the 32 sites. Soil respiration data were available for 17 of the 32 sites. In all cases, soil respiration was measured as the efflux of CO_2 from the soil surface, and represented the combined respiration of soil micro- and macro-organisms and plant roots. In some cases, respiration of surface vegetation such as mosses was unavoidably included. Soil respiration was measured with static closed chambers (Rochette et al. 1992) at 14 sites, dynamic flow-through chambers (Rochette et al. 1992) at two sites, and soda lime (Edwards 1975) at one site. Net N mineralization data were

available for 12 of the 32 sites for the uppermost organic soil horizon. Because net N mineralization in the mineral soil was only measured at two of the 32 sites, these data were not included in the analysis. All ensuing references to net N mineralization are thus for the upper organic soil horizon only. Net N mineralization was measured at all sites as the change in inorganic N (NO_3+NH_4) over the growing season or year using in situ incubation of soils in buried bags (Eno 1960), with incubation periods ranging from 4 to 12 weeks. N mineralization rates expressed on a per gram of dry soil basis were converted to g N m^{-2} year^{-1} using bulk density measurements from each site. For aboveground plant productivity, we used direct estimates of NPP (annual production of biomass and litter per unit ground area) when data were available. At the Buxton Climate Change Impacts Laboratory and Wytham Woods, productivity was based on leaf area index, which has been shown to scale linearly with aboveground biomass (Hobbie et al. 1999). In expanding woody systems (Oak Ridge National Laboratory and Flakaliden), annual productivity in a given year was strongly influenced by the size of the standing crop and thus by conditions in previous years. These data were converted to relative production by dividing annual production by standing biomass at the beginning of the year. Altogether, indices of aboveground plant productivity were available for 20 of the 32 sites.

Meta-analysis

Meta-analysis was used to analyze the response of soil respiration, net N mineralization, and aboveground plant productivity to experimental warming. Meta-analysis requires the distillation of the results of each experiment in the form of a measure of the magnitude of the effect in that experiment, or the "effect size", expressed on a common scale across studies. Here, the effect size summarizes the magnitude of the response of soil respiration, net N mineralization, and aboveground plant productivity to the warming treatment. There are various choices of effect size indices. We chose to use the "Hedges' d index", or standardized mean difference, which is calculated as:

$$\text{Hedges' } d = \frac{\overline{X}_e - \overline{X}_c}{s} J$$

where $\overline{X}_e$ is the mean of the experimental group, $\overline{X}_c$ is the mean of the control group, s is the pooled standard deviation, and J is a factor that corrects for small sample bias (Hedges and Olkin 1985; Rosenberg et al. 1997). An effect size (d) not significantly different from zero indicates no experimental effect, and effects sizes of 0.2, 0.5, and 0.8 or greater indicate small, medium, and large ds, respectively (Cohen 1969). Values above 0 indicate that the experiment had a positive effect on the variable; values below 0 indicate a negative effect.

The variance around d was calculated with standard methods, and used to determine weighted average effects across studies and the confidence intervals around those effects (Hedges and Olkin 1985; Rosenberg et al. 1997). Temporal response patterns were evaluated by categorizing the data by year. Because the results for different years in a site are not independent of one another, we then calculated a single average value across all years for each site for each of the plant and soil responses to warming. We calculated this average d across years and its variance for each site in the same way as averaging ds across studies, as the weighted average Hedges' d and variance for Hedges' d (e.g., Hedges and Olkin 1985). These average ds across years were then used in all subsequent analyses. We tested for agreement or disparity among categories of studies (e.g., among biomes) using a mixed model and parametric tests of homogeneity (Hedges and Olkin 1985; Rosenberg et al. 1997). Categories of studies had to include two or more sites to be included in the analysis. In some cases, the hypothesized explanatory variables were continuous rather than categorical. For the analysis of continuous data in the meta-analysis, we used weighted regressions and tested whether the slopes differed from zero using a parametric mixed model approach (Rosenberg et al. 1997; Hedges and Olkin 2000). Mean differences in rates of soil respiration, net N mineralization,
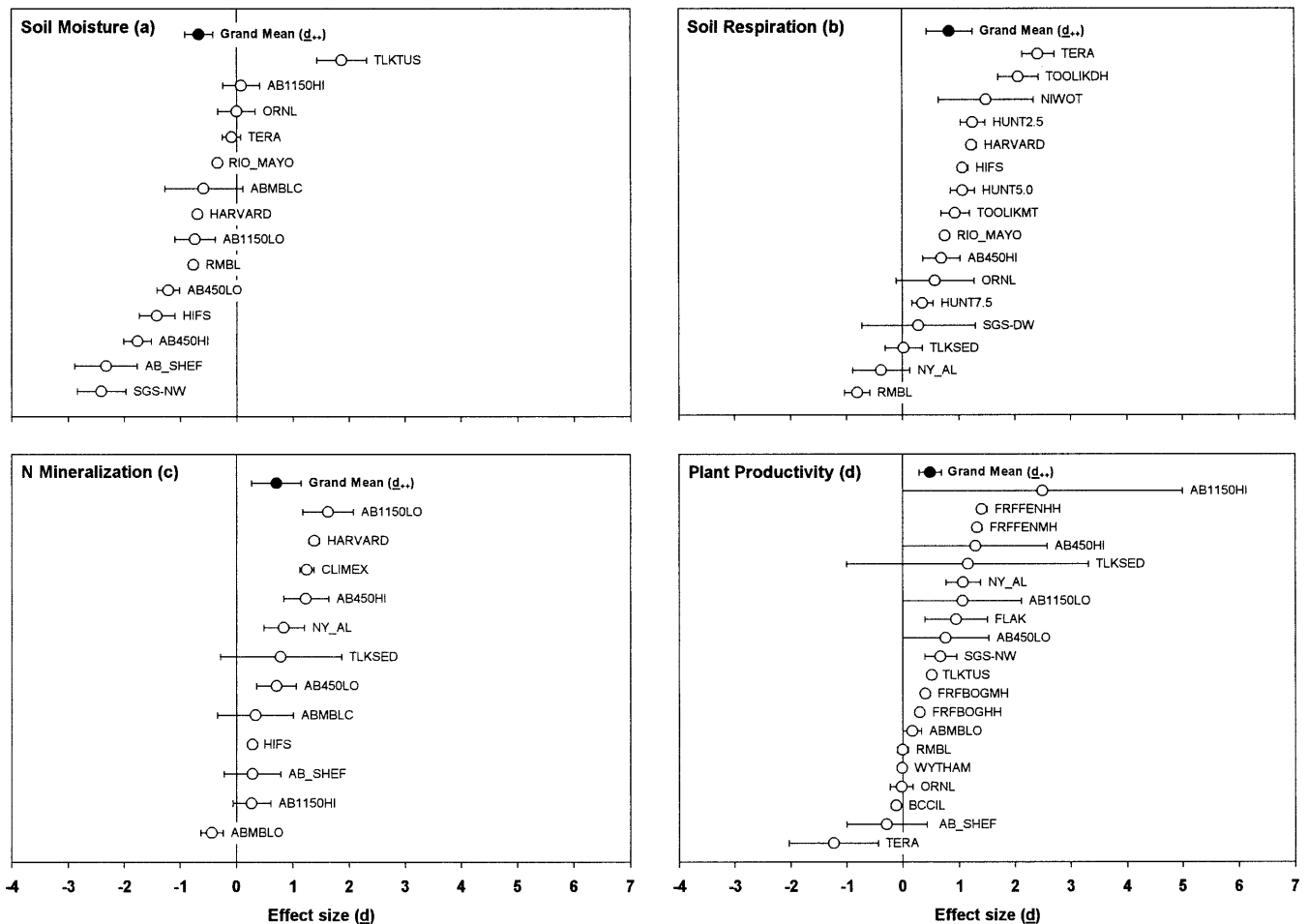
Fig. 2 Mean effect sizes (*d*; open circle) and 95% confidence intervals for individual sites included in the meta-analysis for **a** soil moisture, **b** soil respiration, **c** N mineralization, **d** and plant productivity. Grand mean effect sizes for experimental warming (d_{++}) and 95% confidence intervals for each response variable are given at the top of each panel (*closed circle*)

and plant productivity between the heated plots compared to the control plots were calculated as a weighted average (calculated as a back-transformed natural logarithm response ratio; Hedges and Olkin 2000). All meta-analyses were run using MetaWin 2.0, a statistical software package for meta-analysis (Rosenberg et al. 1997).

Standard unweighted statistical analyses

In addition to using meta-analysis to evaluate the outcome of experimental warming across sites, we also used standard unweighted regression analysis to investigate the relationships between soil respiration and net N mineralization rates in the control plots and latitude, mean annual and growing season temperature and precipitation, length of the growing season, foliar N, and forest floor C, N, C/N, and pH. All unweighted (standard linear regression) analyses were run using SAS (SAS 1995).

Results

Temperature and moisture

The mean experimental increase in soil temperature across all 32 studies was 2.4°C, with a range of

0.3–6.0°C. The response of soil moisture to this experimental increase in temperature was measured at 14 of the 32 sites. Results showed that soil moisture was significantly lower in the heated plots compared to the controls at nine sites, significantly higher in the heated plots compared to the controls at one site, and showed no significant change at four sites (Fig. 2a). The higher soil moisture in the heated plots compared to the control plots was typically due to pre-existing conditions. The overall grand mean effect size (d_{++}) for the response of soil moisture to warming was –0.67, which indicated that across all sites for which we had data, soil moisture was significantly lower in the heated plots than the control plots.

Soil respiration

Mean rates of soil respiration in the control plots ranged from a low of 0.4 mg CO_2-C m^{-2} h^{-1} at the high latitude Ny Alesund site in Svalbard, Norway to a high of 687 mg CO_2-C m^{-2} h^{-1} at the Shortgrass Steppe-day warming site in Colorado, USA, with a mean rate across all sites of 130 mg CO_2-C m^{-2} h^{-1} (Table 1). When the Oak Ridge National Laboratory site was excluded from the analysis as an outlier, (due to the exceptional combination of relatively high mean growing season temperature

Table 1 Mean soil respiration rates for control and heated plots; mean delta soil temperature; mean upper organic horizon N, C and C:N; and mean foliar N at 17 experimental ecosystem warming sites. *na* Not available

Site	Mean soil respiration control (mg CO_2-C m^{-2} h^{-1})	Mean soil respiration heated (mg CO_2-C m^{-2} h^{-1})	Data from the following years of the experiment	Mean △ soil temperature (°C)	Mean upper organic horizon N (%)	Mean upper organic horizon C (%)	Mean upper organic horizon C:N	Mean foliar N (%)	Species for foliar N
Abisko Nature Reserve, e.s.l. 450 m, high heat study	223.0	299.0	7	1.3	1.7	40	24	2.1	*Vaccinium uliginosum*
Harvard Forest	114.0	143.0	1–5	5.1	1.7	39	24	1.7	*Acer rubrum*
Howland Forest	35.0	43.0	1–3	4.3	1.0	42	42	1.1	*Picea rubens*
Huntington Wildlife Forest, 2.5°C study	72.0	105.0	1–2	2.6	na	na	na	2.4	*Fagus grandifolia*
Huntington Wildlife Forest, 5.0°C study	72.0	98.0	1–2	4.8	na	na	na	2.4	*Fagus grandifolia*
Huntington Wildlife Forest, 7.5°C study	72.0	82.0	1–2	6.0	na	na	na	2.4	*Fagus grandifolia*
Niwot Ridge	65.0	77.0	3	2.3[a]	na	na	na	2.2	*Dryas octopetala*
Ny Alesund	0.4	0.3	4	0.3	8.8	3	0	1.8	*Dryas octopetala*
Oak Ridge National Laboratory	28.0	30.0	3	1.6	na	na	na	2.1	*Acer saccharum*
Rio Mayo	9.0	13.0	1–3	1.9[a]	na	na	na	0.6	*Stipa sp.*
Rocky Mountain Biological Laboratory	193.0	179.0	4–5	1.2	na	na	na	2.0	*Artemisia tridentata*
Shortgrass Steppe – day-time warming	687.0	890.0	1	4.0[b]	na	na	na	na	na
Shortgrass Steppe – night-time warming	304.0	366.0	2	0.7	0.2	1	7	1.5	*Bouteloua gracilis*
TERA	138.0	201.0	2	1.5	0.9	37	41	0.8	*Pseudotsuga menziesii*
Toolik Lake – wet sedge study	36.0	36.0	6	3.2	2.0	34	17	1.7	*Carex rotundata*
Toolik Lake – dry heath study	55.0	78.0	2–4	1.5	na	na	na	na	na
Toolik Lake – moist tussock study	103.0	124.0	2–4	1.5	na	na	na	na	na

[a] Delta air temperature; soil temperature not measured
[b] Target delta soil temperatur

and relatively low soil respiration related to low root density in the experimental field chambers), conventional (unweighted) linear regression showed a significant positive relationship between mean rates of soil respiration in the control plots and mean growing season temperature ($r^2=0.45$, $P<0.012$). No other significant relationships were observed between soil respiration in the control plots and any of the other climatic or environmental variables evaluated in this analysis.

Mean d for individual sites ranged from a low of –0.8 at the Rocky Mountain Biological Laboratory (RMBL) site in Colorado, USA to a high of 13.3 at the Shortgrass Steppe-nightwarming (SGS-NW) site also in Colorado, USA (Fig. 2b; note, SGS-NW is not shown and was excluded from subsequent analyses because the mean d and variance for this site was over 6 times greater than for any other site, and thus SGS-NW was considered an outlier). The results appeared diverse when sites were examined individually: warming increased soil respiration at 11 of the 17 sites for which data were available, decreased soil respiration at one of the 17 sites, and had no effect on soil respiration at five of the 17 sites (Fig. 2b). However, d_{++} across all sites was 0.80, which was a large and statistically significant response to warming (Fig. 2b). Thus, across all sites, experimental warming significantly increased rates of soil respiration. The weighted mean increase in soil respiration in response to warming was 20% (with a 95% confidence interval of 18–22%), which corresponds to a mean increase of 26 mg CO_2-C m^{-2} h^{-1}.

The temporal pattern of response was investigated by grouping the data by year of study. Non-significant Q-between values indicated no significant differences in soil respiration response to warming among the years of study (Fig. 3a). However, a trend for a decrease in the magnitude of response was suggested by large and statistically significant positive effect sizes for year 1 (mean delta soil respiration=52 mg CO_2-C m^{-2} h^{-1}; $d_+=1.29$), year 2 (mean delta soil respiration=23 mg CO_2-C m^{-2} h^{-1}; $d_+=0.93$), and year 3 (mean delta soil respiration=14 mg CO_2-C m^{-1}; $d_+=1.30$), in contrast with small, non-significant effect sizes for year 4 (mean delta soil respiration=10 mg CO_2-C m^{-2} h^{-1}; $d_+=0.37$), and year 5 (mean delta soil respiration=9 mg CO_2 m^{-2} h^{-1}; $d_+=0.46$). This suggests that the response of soil respiration to warming may have been greater in the initial 3 years following treatment initiation than in later years. Results from the nine individual sites with 2 or more years of data showed a decline in soil respiration at four of the sites, and no trend at five of the sites.

Overall, effect sizes for the three biomes for which data were available (low tundra, forest, and grassland) were marginally different from each other at the 0.10 level (Fig. 3a). The high tundra biome was excluded from the analysis because there was only one high tundra site with soil respiration data. Effect size was greatest for the forest sites ($d_+=1.15$) followed by the low tundra sites ($d_+=0.98$), both of which were significantly greater than zero. Effect size for the grassland sites ($d_+=0.14$)

was small and non-significant. Similarly, effect sizes for the woody and non-woody sites were marginally different from each other at the 0.11 level (Fig. 3a). The effect size for the woody sites was large ($d_+=1.11$) and was significantly greater than zero, whereas effect size for the non-woody sites ($d_+=0.51$) wasnot significantly different from zero (Fig. 3a).

The effect of the method used to warm the treatment plots on d was evaluated by grouping the data by warming methods. Non-significant Q-between values indicated that there were no detectable differences among the three warming methods for which data were available (field chambers, cables, and greenhouses; Fig. 3a). Effect sizes, however, were larger and were significant for the field chamber and cable studies ($d_+=1.08$ and 1.02, respectively), whereas effect size was smaller and non-significant for the greenhouse studies ($d_+=0.10$).

Although soil respiration exhibited a strong positive response to warming across all the experimental sites, meta-analytic weighted regression analyses showed that the magnitude of d was largely independent of the geographic, climatic, and environmental factors evaluated in this study (Table 2). The only exceptions were length of the growing season which showed a slight but significant positive correlation with the magnitude of the response of soil respiration to warming ($P<0.002$), and upper organic horizon N concentration which showed a slight negative correlation with the magnitude of soil respiration response to warming ($P<0.04$) (Table 2). The negative correlation between upper organic soil horizon N concentration and d, however, was driven entirely by the high N (8.8%) combined with the negative d (–0.38) reported for the NY_AL site. In this polar semi-desert site, upper organic soil horizon N concentrations were based only on the organic soil under vegetated parts, which covered less than 50% of the plot, and upper organic soil horizon N on a whole plot basis (including bare mineral soil) would have been below 4%. No significant relationship between d and upper organic soil horizon N concentration was observed when this site was removed from the analysis. Finally, the magnitude of the increase in soil respiration was independent of the delta soil temperature, which was calculated as the mean temperature in the heated plots minus the mean temperature in the control plots.

Net N mineralization

Mean rates of net N mineralization in the upper organic soil horizon in the control plots ranged from a low of 0.02 g N m^{-2} $year^{-1}$ at the Abisko MBL OTC site in Sweden to a high of 4.13 g N m^{-2} $year^{-1}$ at the Howland Forest site in Maine (Table 3), with a mean of 1.05 g N m^{-2} $year^{-1}$ for all 12 sites. Conventional (unweighted) linear regression showed significant positive relationships between mean net N mineralization in the control plots and mean annual precipitation ($r^2=0.71$; $P<0.0006$), mean growing season precipitation ($r^2=0.68$; $P<0.0019$),

Fig. 3 Mean effect sizes of experimental warming (d_+) and 95% confidence intervals for year of study, biome, vegetation and warming method for **a** soil respiration, **b** N mineralization, **c** and plant productivity. *Q*-between values and significance level are given *in parentheses*
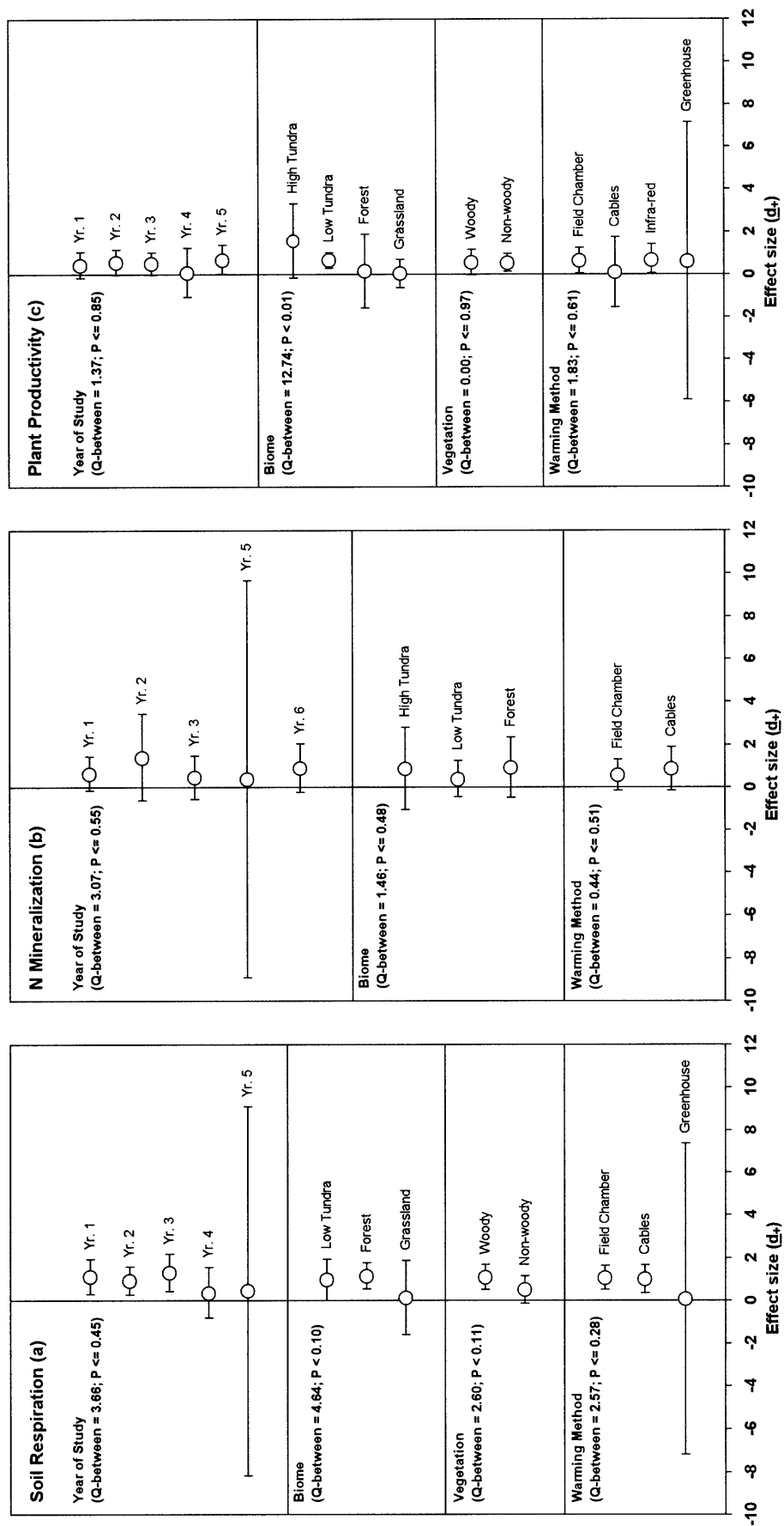
Table 2 Weighted regression analyses results for soil respiration, net N mineralization, and plant productivity

	Soil respiration			N mineralization			Plant growth		
	Intercept	Slope	P	Intercept	Slope	P	Intercept	Slope	P
Latitude	0.85	−0.001	0.986	1.31	−0.010	0.579	−0.36	0.017	0.166
Annual temperature	0.77	0.017	0.555	0.70	0.019	0.657	0.68	−0.051	0.027
Growing season temperature	0.14	0.049	0.321	0.38	0.036	0.641	1.11	−0.047	0.231
Annual precipitation	0.44	0.001	0.305	0.32	0.001	0.202	1.06	−0.001	0.072
Growing season precipitation	0.56	0.001	0.458	0.35	0.001	0.009	0.71	0.000	0.656
Growing season days	0.14	0.007	0.002	0.48	0.000	0.522	0.93	−0.002	0.373
Ambient soil temperature	0.46	0.028	0.809	0.98	−0.035	0.686	0.85	−0.025	0.523
Delta soil temperature	0.46	0.028	0.809	0.50	0.087	0.432	0.67	−0.032	0.856
Tindex	0.48	1.011	0.429	0.41	1.265	0.541	1.25	−2.418	0.018
Pindex	0.41	1.121	0.351	0.22	1.419	0.194	1.16	−1.849	0.096
PTindex1	0.47	1.327	0.329	0.28	1.897	0.310	1.20	−2.456	0.026
PTindex2	0.50	2.634	0.225	0.44	2.720	0.268	0.94	−3.697	0.022
Upper organic horizon N	1.48	−0.236	0.040	0.46	0.075	0.451	0.43	0.168	0.032
Upper organic horizon C	−0.49	0.041	0.098	1.15	−0.010	0.517	0.64	0.003	0.805
Foliar N	1.50	−0.459	0.172	0.32	0.332	0.291	1.06	−0.335	0.337

Pindex (r^2=0.68; P<0.0009), Tindex (r^2=0.39; P<0.0313), and PTindex2 (r^2=0.65; P<0.0016). Mean net N mineralization also showed a trend of increasing rates with increasing mean annual temperature (r^2=0.29; P<0.0738) and mean measured soil temperatures (r^2=0.30; P<0.0678). A significant negative relationship was observed between mean net N mineralization and latitude (r^2=0.47; P<0.0133).

Mean ds for individual sites ranged from a low of −0.44 at the ABMBLO site in Sweden to a high of 1.62, at the nearby Abisko fellfield low heat site (AB1150LO) (Fig. 2c). As shown for soil respiration, the results at first appear to be contradictory: warming increased rates of net N mineralization at seven of the 12 sites for which data were available, decreased rates of net N mineralization at one of the 12 sites, and had no effect on net N mineralization at four of the 12 sites (Fig. 2c). However, there was a large and statistically significant effect of warming on net N mineralization when averaged across all sites. The general mean effect size (d_{++}) was 0.71, indicating that, on average across all experiments, warming increased rates of net N mineralization (Fig. 2c). The weighted mean increase in net N mineralization due to warming was 46% (with a 95% confidence interval of 30–64%) or 0.48 g N m^{-2} year^{-1}.

While there was a strong and statistically significant overall effect of warming on rates of net N mineralization, no significant differences were found among classes when the data were grouped by year of study, biome (high tundra, low tundra, forest), or warming method (field chambers, cables) (Fig. 3b). In some cases there were confounding effects among classes. For example, the comparison of field chambers versus cables was largely a comparison of tundra field chambers versus forest cables. Differences between vegetation types could not be evaluated because we had only one non-woody site. With one exception, meta-analytic weighted regression analyses showed no significant relationships between the magnitude of d and the geographic, climatic and environmental factors, or between the magnitude of d and delta soil temperature (Table 2). The exception was a significant positive relationship between net N mineralization and growing season precipitation (P<0.009).

Aboveground plant productivity

Aboveground plant productivity responses to warming were more variable than results for either soil respiration or net N mineralization, partly because of the different units in which it was measured. Furthermore, some of the sites had increasing plant biomass and increasing primary production among years while others were more mature sites, and had more uniform plant biomass and relatively constant annual productivity. Thus, it is not meaningful to present an overall mean value for plant productivity or the absolute response to warming in these experiments, or to regress plant growth on the geographic, climatic and environmental variables. However, because the raw data were converted to best represent the relative response of annual plant productivity to warming on a common scale, these responses could be compared across sites with meta-analysis. Mean ds for individual sites ranged from a low of −1.24 at the TERA site in Oregon, USA to a high of 2.50 at the Abisko fellfield high heat site in Sweden (Fig. 2d). As for the other response variables, there was a diversity of responses among sites, with experimental warming increasing plant productivity at 13 of the 20 sites for which data were available, decreasing plant productivity at two of the 20 sites, and having no significant effect on plant productivity at five of the 20 sites (Fig. 2d). There was a moderate and statistically significant d_{++} (0.49), indicating that, when averaged across all sites, experimental warming increased aboveground plant productivity. The weighted mean increase in plant productivity due to warming was 19% (with a 95% confidence interval of 15–22%).

Table 3 Mean net N mineralization rates for control and heated plots; delta soil temperature; mean upper organic horizon N, C, and C:N; and mean foliar N at 12 experimental ecosystem warming sites

Site	Mean N mineralization control (g N m⁻² year⁻¹)	Mean N mineralization heated (g N m⁻² year⁻¹)	Data from the following years of the experiment	Mean Δ soil temperature (°C)	Mean upper organic horizon N (%)	Mean upper organic horizon C (%)	Mean upper organic horizon C:N	Mean foliar N (%)	Species for foliar N
Abisko Nature Reserve, Sheffield study	0.44	0.54	3	0.4	na	na	na	1.0	*Empetrum hermaphroditum*
Abisko Nature Reserve, e.s.l. 1150 m, high heat study	0.04	0.06	6	1.6	0.9	21	25	0.8	Evergreen species
Abisko Nature Reserve, e.s.l. 1150 m, low heat study	0.04	0.11	6	0.9	0.9	21	25	0.8	Evergreen species
Abisko Nature Reserve, e.s.l. 450 m, high heat study	0.07	0.39	6	1.3	1.7	40	24	0.8	Evergreen species
Abisko Nature Reserve, e.s.l. 450 m, low heat study	0.07	0.25	6	0.6	1.7	40	24	0.8	Evergreen species
Abisko Nature Reserve, MBL cable study	0.05	0.06	5	4.8	1.2	41	34	1.8	*Vaccinium myrtillus*
Abisko Nature Reserve, MBL field chamber study	0.02	0.01	3	0.6	1.4	47	34	1.8	*Vaccinium myrtillus*
CLIMEX	3.93	7.26	1–2	3.5	2.0	46	23	na	na
Harvard Forest	1.61	2.96	1–5	5.1	1.7	39	24	1.7	*Acer rubrum*
Howland Forest	4.13	4.67	1–3	4.3	1.0	42	42	1.1	*Picea rubens*
Ny Alesund	0.19	0.40	3	0.3	8.8	3	0	1.8	*Dryas octopetala*
Toolik Lake – wet sedge study	2.00	2.92	6	3.2	2.0	34	25	1.7	*Carex rotundata*

Overall, no temporal patterns were observed in the response of plant productivity to warming (Fig. 3c). A significant difference in the response to warming was observed between the four biomes (Qb=12.74; P<0.01; Fig. 3c). The effect of warming on aboveground plant productivity was significantly greater than zero only for the low tundra biome, which includes the Minnesota bog and fen sites (d_+=0.68). The effect of warming was much larger in the colder, high tundra biome (d_+=1.22), but, due to the large confidence interval, was not significantly different from zero. The individual forest and grassland sites showed both positive and negative responses to warming, and their mean responses were near zero. The magnitude of the response to warming was independent of the method used to warm the plots (Fig. 3c).

Meta-analytic (weighted) regression analyses showed that the magnitude of d had significant or nearly significant inverse relationships with mean annual temperature (P<0.027) and mean annual precipitation (P<0.072) (Table 2), indicating that the positive response to warming was generally larger in colder systems with lower precipitation. This relationship was stronger when expressed relative to the climate indices. For example, there were significant inverse relationships between the magnitude of d and Tindex (P<0.018), PTindex1 (P<0.026), and PTindex2 (P<0.022). The only other environmental factor that appeared to influence plant response to warming was upper organic soil horizon N concentration, with d generally increasing with increasing organic soil horizon N concentration (P<0.032). However, no data were available on organic soil horizon N from three of the six sites that had negative responses to warming during 1 or more of the treatment years. No relationship was observed between the magnitude of d and delta soil temperature (Table 2).

Discussion

Results from this meta-analysis showed that across all sites, 2–9 years of experimental warming significantly increased soil respiration rates by 20%, organic soil horizon net N mineralization rates by 46%, and aboveground plant productivity by 19% across all sites. Because the evaluation of the effects of global warming on ecosystem processes is still a relatively new field of investigation, the database for this meta-analysis was small, with only 17 sites with soil respiration data, 12 sites with net N mineralization data, and 20 sites with aboveground plant productivity data. Despite these small sample sizes, the similarity in overall response patterns have important implications for terrestrial nutrient cycling and global C balance

Soil respiration

The increase in soil respiration in response to warming is consistent with results from individual in situ studies,

which have repeatedly demonstrated significant positive relationships between temperature and soil respiration (e.g., Witkamp 1966; Edwards 1975; Singh and Gupta 1977; Schleser 1982; Schlenter and Van Cleve 1985; Pinol et al. 1995). Given that soil respiration is one of the major fluxes in the global carbon cycle, with estimated annual emissions of 68–100 Pg C year^{-1} (Musselman and Fox 1991; Raich and Schlesinger 1992), a 20% increase in soil respiration would correspond to an increased release of ~14–20 Pg C year^{-1}. This is 2–3 times the estimated ~7 Pg C year^{-1} of CO_2 released to the atmosphere via combined fossil fuel combustion and land-use changes (Lal et al. 1995), and would provide a strong positive feedback to global atmospheric CO_2 concentrations and, consequently, warming. Caution, however, must be exercised in extrapolating results of this meta-analysis to a global basis. The increase in soil respiration reported here may be an overestimation because: (1) 13 of the 17 studies measured soil respiration only during the growing season, and the response may be smaller during the non-growing season when both roots and soil microbes are less active (Fahnestock et al. 1998; Jones et al. 1999), and (2) it is possible that the observed increases in soil respiration in response to warming are partly a transient response, reflecting the oxidation of only the most labile soil C compounds (Peterjohn et al. 1994). Once the labile soil C fractions are decomposed, the response of soil respiration to experimental warming may decline. A decrease with time in the magnitude of the response of soil respiration to experimental warming was observed at two of the nine sites for which multiple years of data were available: the Harvard Forest (Peterjohn et al. 1994) and the Huntington Forest sites (McHale et al. 1998). Results of this meta-analysis indicated a similar pattern and showed a significant positive effect of warming on soil respiration during the first 3 years of warming treatments, and no significant effect of warming on soil respiration during the fourth and fifth years of treatment (Fig. 3a). Differences in spatial and temporal response patterns may also be due to the different influences of warming on microbial vs. root respiration. These two components of total soil respiration have historically been very difficult to separate. Clearly, the longer-term response of microbial and root respiration to experimental warming is an area that warrants further study.

In reviews of the effects of temperature on rates of soil respiration, Schleser (1982) and later Kirshbaum (1995) hypothesized that the magnitude of the response of soil respiration to warming would be greater in colder, higher latitude ecosystems. Given that the soils in these ecosystems contain large amounts of organic C (Lal et al. 1995) and that the increase in temperature is expected to be greater at higher latitudes (IPCC 1996), global warming could result in a substantial release of C from soils to the atmosphere in high latitude ecosystems. Indeed, several studies have already suggested that some northern ecosystems have changed from a net C sink to a net C source (Oechel et al. 1993; Parton et al. 1995).

Results from this meta-analysis, however, showed no significant relationships between the magnitude of the response of soil respiration to warming (d) and mean annual temperature or precipitation, or mean growing season temperature or precipitation (Table 2). In fact, the only significant relationship between d and any of the climatic and environmental variables evaluated in the weighted regression analysis was a significant positive relationship between d and the length of the growing season (Table 2). This suggests that the response of soil respiration to warming was greater in *warmer* ecosystems. Further, there was no significant relationship between d and latitude, as had been hypothesized. The largest ds were observed for the forested sites (which tended to be mid-latitude), followed by the low tundra sites, and then the grassland sites (Fig. 3a).

In general, the mean rates of soil respiration reported here for the control plots were somewhat higher compared to rates reported in previous reviews (Raich and Schlesinger 1992; Raich and Potter 1995). This may be because the majority of the sites included in this synthesis measured soil respiration only during the warmer growing season, and thus did not include lower winter rates, whereas the previously published reviews selected only data sets with a full year of data. Despite this limitation, conventional (unweighted) linear regression showed a significant positive relationship between mean soil respiration rates in the control plots and mean growing season temperature. No significant relationships, however, were observed between mean soil respiration rates and mean annual temperature. Other analyses (Schleser 1982; Raich and Schlesinger 1992; Raich and Potter 1995) have shown significant positive correlations between mean annual or mean monthly rates of soil respiration and mean annual air temperature and mean annual precipitation, with mean annual air temperature being the single best climatic predictor of soil respiration. The relationship between soil respiration and mean annual temperature may be related in part to the significant relationship between fine root turnover and mean annual temperature (Gill and Jackson 2000).

Net N mineralization

Results of this meta-analysis showed that experimental warming significantly increased rates of net N mineralization of the upper organic soil horizon by a mean of 46% across the 12 sites for which data were available. Gross rates of N mineralization were likely higher than the values reported here for net N mineralization, because a large percentage of total mineralized N is typically quickly taken up and immobilized by the microbial community, particularly at nutrient-limited sites. The observed increase in net N mineralization is consistent with results from individual sites, which have demonstrated significant positive relationships between temperature and net N mineralization (Van Cleve et al. 1983, 1990; Emmer and Tietema 1990; Bonan and Van Cleve

1991; Goncalves and Caryle 1994; MacDonald et al. 1995; Hobbie 1996; Reich et al. 1997). For the 12 sites in this analysis, a 46% increase in net N mineralization corresponds to an increased internal production of 4.8 kg N ha^{-1} year^{-1}. This compares to atmospheric wet-plus-dry deposition inputs ranging from <5.0 kg N ha^{-1} year^{-1} in relatively pristine areas upwards to 50 kg N ha^{-1} year^{-1} or more in the heavily polluted areas of the northeastern USA and Europe (Gunderson and Bashkin 1994; Vitousek et al. 1997). Because N is generally considered to be one of the key limiting nutrients in terrestrial ecosystems (Vitousek et al. 1997), a warming-induced increase in the internal production of inorganic N could stimulate plant growth and net ecosystem productivity at N-limited sites. This would effectively transfer N from soil pools with typically low C/N ratios (i.e., 30 or less) to plant biomass pools, with typically higher C/N ratios (i.e., >30), thereby increasing net ecosystem C storage (Rastetter et al. 1991, 1997). However, in N-sufficient or N-rich environments, particularly those in the northern hemisphere which are already impacted by elevated atmospheric N deposition, a warming-induced increase in internal N production could lead to or further exacerbate conditions of "N saturation", where the input of N equals or exceeds the ability of an ecosystem to assimilate the added N (Aber et al. 1989, 1998). Joslin and Wolfe (1993) and Lukewille and Wright (1997), for example, have demonstrated warming-induced increases in soil leachate and run-off N. Symptoms of N saturation may include plant tissue nutrient imbalances, forest decline (and consequently declines in net ecosystem C sequestration), increased gaseous loss of N (with consequent feedback to global warming as NO and N$_2$O are "greenhouse" gases), and increased N leaching from soils with consequent declines in associated surface water quality (Vitousek et al. 1997; Fenn et al. 1998).

Results from this meta-analysis showed no temporal trends in the response of net N mineralization to warming, no differences between the biomes or vegetation types, and no significant relationships between the magnitude of d and any of the geographic, climatic or environmental variables investigated. However, given the limits of the data set (i.e., seven of the 12 sites were at the Abisko Nature Reserve in Sweden, none of the sites were below 42°N latitude, and no data were available for grassland sites), broad generalizations on temporal, geographic, or climatic response patterns cannot realistically be drawn from this analysis. This underscores the need for future ecosystem warming studies to include net N mineralization measurements in their analysis.

Although the response of N mineralization to experimental warming did not show any significant geographic or climatic trends at this scale of analysis, rates of mean control-plot net N mineralization increased significantly with increasing mean annual precipitation, and showed a trend of increasing rates with increasing mean annual and mean measured soil temperatures. This likely reflects greater rates of microbial activity, and hence N mineralization, at warmer sites characterized by greater

precipitation. No relationships were observed between rates of net N mineralization and organic soil horizon N concentration or C/N ratios, as has been reported in other studies (MacDonald et al. 1995; Fernandez et al. 2000; Rustad et al. 2000).

Aboveground plant productivity

Experimental ecosystem warming significantly increased aboveground plant productivity by a mean of 19% across the 20 sites for which data were available (Table 4). In general, the response was greatest in the colder ecosystems characterized by lower mean annual precipitation, with the strongest response observed in the high and low tundra sites. The warming-induced increase in plant productivity may be a direct effect of either increased rates of photosynthesis at higher temperatures or (in those experiments with year-round warming) longer growing seasons, or an indirect effect of increased nutrient availability, resulting from increased rates of litter decomposition and N mineralization. Both direct and indirect effects of warming could be particularly important in higher latitude arctic ecosystems, which tend to be both temperature and nutrient-limited.

Warming-induced increases in plant productivity have been reported previously for individual subarctic tundra sites (Chapin et al. 1995; Jonasson et al. 1996; Press et al. 1998; Hartley et al. 1999). Increases in plant productivity would result in a greater storage of C in plant biomass (especially in systems with a significant woody component) and increased flux of C to soils in leaf and root litter. This could at least partially offset the warming-induced increase in C flux from soils to the atmosphere via soil respiration. Arft et al. (1999) reported a moderate but significant increase in plant growth during the first 3 years of treatments in the ITEX experiments, followed by no significant growth response for year 4. They suggested that the decline in growth response may be linked to resource limitations, particularly limitations in soil nutrients. In contrast, no temporal trends were apparent during the initial 5 years of warming treatments for the sites included in our analysis. The disparity in the temporal patterns presented in these two syntheses may be due to the wider range of sites included in our synthesis, with a greater representation of less nutrient-limited sites, or it could reflect differences in sample size bias. We cannot conclude from this analysis whether increases in plant productivity will compensate for greater respiratory losses of C. However, warming-induced changes in plant productivity may well alter the global C balance.

Variation in response

Although the general trend in response of soil respiration, net N mineralization, and aboveground plant productivity to warming was positive across all sites, large variation in the magnitude and even direction of response was

Table 4 Mean relative increase in plant productivity in heated plots compared to control plots; mean delta air temperature, mean delta soil temperature, mean upper organic horizon N, C, and C:N; and foliar N at 20 experimental ecosystem warming sites

Site	Mean % change in annual productivity	Data from the following years of the experiment	Mean Δ air temperature (°C)	Mean Δ soil temperature (°C)	Mean upper organic horizon N (%)	Mean upper organic horizon C (%)	Mean upper organic horizon C:N	Mean foliar N (%)	Species for foliar N
Abisko Nature Reserve, Sheffield study	−4.0	6	3.2	0.4	na	na	na	1	*Empetrum hermaphroditum*
Abisko Nature Reserve, MBL Field chamber study	9.1	3	5.1	0.8	1.4	47	34	1.7	*Vaccinium myrtillus*
Abisko Nature Reserve, e.s.l. 1150 m., high heat study	134.1	5	na	1.3	0.9	21	25	0.81	Evergreens
Abisko Nature Reserve, e.s.l. 1150 m., low heat study	64.5	5	na	0.6	0.9	21	25	0.81	Evergreens
Abisko Nature Reserve, e.s.l. 450 m., high heat study	53.8	5	na	1.2	1.7	40	24	0.79	Evergreens
Abisko Nature Reserve, e.s.l. 450 m., low heat study	33.0	5	na	0.6	1.7	40	24	0.79	Evergreens
Buxton Climate Change Impacts Laboratory	−0.7	1–5	na	3.0	0.7	7	10	1.46	*Festuca ovina*
Flakaliden	49.2	1–5	0.0	4.7	1.0	40	39	1.1	*Picea abies*
Minnesota Peatlands, bog, high heat study	9.8	1–3	na	1.6	1.1	42	38	0.89	*Sphagnum acutifolia*
Minnesota Peatlands, bog, medium heat study	13.1	1–3	na	2.0	1.1	42	38	0.89	*Sphagnum acutifolia*
Minnesota Peatlands, fen, high heat study	48.4	1–3	na	1.7	2.5	39	16	1.17	*Rhynchospora* spp.
Minnesota Peatlands, fen, medium heat study	46.1	1–3	na	1.4	2.5	39	16	1.17	*Rhynchospora* spp.
Ny Alesund	34.8	1, 3, 5	2.5	0.3	na	3	na	1.8	*Dryas octopetala*
Oak Ridge National Laboratory	11.2	1–4	3.3	1.6	na	na	na	2.05	*Acer saccharum*
Shortgrass Steppe – night-time warming	12.0	1–2	1.0	0.6	0.2	1	7	1.5	*Bouteloua gracilis*
Rocky Mountain Biological Laboratory	−1.8	1–4	na	0.5	na	na	na	2	*Artemisia tridentata*
TERA	−19.7	5	3.4	1.7	0.9	37	41	0.8	*Pseudotsuga menziesii*
Toolik Lake – wet sedge study	125.9	6	na	3.2	2.0	34	17	1.7	*Carex rotundata*
Toolik Lake – tussock study	37.6	3,9	na	2.2	0.4	17	43	1.8	*Carex rotundata*
Wytham Woods	−1.5	1–5	na	na	na	na	na	na	na

observed both between sites and between years at a single site. Understanding the exceptions to the general response trends can provide useful insights on the underlying mechanisms of ecosystem response to changes in temperature, and points to the need for caution in projecting responses based on averages.

Perhaps the most often cited explanation for the lack of response or negative response to increasing temperature is the concomitant decline in soil moisture often associated with warming. For example, at individual sites, reduced or lower soil moisture has been cited for declines in soil respiration response to warming by Peterjohn et al. (1994), McHale et al. (1998), and Rustad and Fernandez (1998a); for declines in litter decomposition by Robinson et al. (1995) and Verburg et al. (1999); for increases in CH_4 consumption by Torn and Harte (1995), and for declines in net C uptake by Saleska et al. (1999). Although not as commonly invoked, microbially-mediated responses to changes in temperature may also be affected by excess soil moisture that would limit O_2, thereby causing decreases in aerobic processes and concomitant increases in anaerobic processes (Alexander 1977). Year-to-year or site-to-site differences in soil moisture may thus explain some of the observed temporal and spatial variation in response to experimental ecosystem warming.

The supply of soil nutrient resources (particularly N and P) and the nature and quantity of soil organic matter could influence the magnitude of ecosystem response to warming. For example, several studies have reported limited ecosystem response to warming alone, but significant response to warming plus fertilization (Wookey et al. 1993, 1995; Parsons et al. 1994; Chapin et al. 1995; Press et al. 1998; Shaver et al. 1998). Arft et al. (1999) and Henry and Molau (1997) have hypothesized that the decline in the plant growth response to warming that was observed after only 3–4 years of treatment in the ITEX studies was due to limitations other than temperature, including depletion of soil nutrients. Rustad et al. (2000), meanwhile, suggested that the lower rates of soil respiration and more limited response to experimental warming at the Howland coniferous forest site compared to either the Harvard or Huntington Forest sites, both of which are northern hardwood forests, was due in part to the more recalcitrant quality of soil organic matter at the coniferous site. Similarly, Peterjohn et al. (1994) hypothesized that the marked decline in rates of soil respiration after just 1 year of warming at the Harvard Forest was due to the oxidation and resulting decline in labile soil C sources.

Higher mean annual temperatures will likely result in longer growing seasons and concomitant changes in plant phenology, including the timing of bud-break, flowering, and leaf abscission. Although this could result in greater NPP, negative effects are also possible. For example, leaf mass of *Pseudotsuga menzeisei* saplings grown for 4 years in outdoor, sunlit chambers was reduced in response to warming of the air by 3.5°C (Olszyk et al. 1998). The proposed explanation for this decline was that the buds were released from winter dormancy earlier in warmer chambers, as might be predicted, but this caused the needles to expand abnormally such that leaf area index, and hence plant growth, was reduced relative to that in control chambers (Apple et al. 1998). In a similar experiment with *Acer saccharum* and *Acer rubrum*, warming also increased the length of the growing season, but in this case stimulated productivity during the first year of warming in the heated chambers relative to the control chambers (Norby et al. 2000). In the second year of this experiment, however, unusually high summer temperatures caused stress responses in the trees in the heated chambers, and productivity was significantly reduced. This example illustrates that multiple responses to warming can occur simultaneously, and the net response may be difficult to predict.

Finally, ecosystem response to warming will certainly be affected by differences or changes in plant species composition (Harte and Shaw 1995; Hobbie 1996; Cornelissen et al. 1999), with species composition affecting other ecosystem properties such as plant growth rates, litter quantity and quality (and consequently microbial dynamics and litter decomposition), canopy structure and architecture, shading, and rooting depth, to name a few. Because changes in species composition may occur over decades to centuries, particularly in long-lived forest ecosystems, these changes may be difficult to capture under experimental conditions, which emphasizes the need for more accurate and comprehensive models of ecosystem response to environmental perturbation.

Warming methods

A wide range of techniques have been used to experimentally warm ecosystems or ecosystem components, including heat-resistance ground cables, overhead infrared lamps, vented and unvented field chambers, and greenhouses. Because there has been some controversy on the merits of these different warming methods (Kennedy 1995; Marion et al. 1997), we examined whether the response to warming was affected by the warming techniques. Results showed no significant differences in effect size between techniques for any of the response variables evaluated in this analysis. Surprisingly, the magnitude of the effect size for the responses of soil respiration, net N mineralization, and aboveground plant productivity were also not significantly related to the magnitude of the warming treatment (delta temperature). This contrasts markedly to results from individual studies, which have demonstrated strong correlations, at least in the short term, between temperature and soil respiration (Peterjohn et al. 1994; Rustad and Fernandez 1998a), N mineralization (Goncalves and Caryle 1994; MacDonald et al. 1995; Reich et al. 1997), and plant growth (Jonasson et al. 1999). This suggests that, at the scale of this analysis (mean experimental response over 1–9 years), the magnitude of the response to warming was more sensitive to differences among sites, biomes, and vegetation types than to the magnitude of warming. This underscores the

need to understand the relative importance of specific factors at different spatial and temporal scales, and suggests that we should be cautious in "scaling up" responses from the plot and site level to the landscape and biome level.

Conclusions

Evidence continues to accumulate that mean global temperature has increased by 0.2–0.3°C during the last 40 years, and current general circulation models suggest that the mean global temperature will increase by another 1–3.5°C in the next century (IPCC 1996). Although the number of ecosystem warming experiments around the world is growing, there remains a paucity of data on whole ecosystem response to changes in temperature. Results from this meta-analysis demonstrate that across a wide range of ecosystem types and experimental methodologies, experimental warming in the range of 0.3–6.0°C significantly increases rates of soil respiration, net N mineralization, and aboveground plant productivity. These results are consistent with (though not a direct test of) the conceptual model where warming directly increases rates of microbial processes including litter decomposition and N mineralization, thereby increasing the availability of nutrients, and, particularly in nutrient-limited ecosystems, increasing plant productivity. The increase in plant productivity may also be a result of a direct effect of warming on rates of net photosynthesis, or an extension of the growing season.

Differences among biomes were apparent for the response of soil respiration and plant productivity to warming, with the response of soil respiration generally larger in forested ecosystems compared to low tundra and grassland ecosystems, and the response of plant productivity generally larger in low tundra ecosystems than forest and grassland ecosystems. No differences between the biomes were observed for the response of net N mineralization to warming, which may be due to small sample sizes. In general, the magnitude of the response of these three processes to experimental warming was not significantly related to the various geographic, climatic, or environmental variables that we evaluated. The primary exception to this was plant productivity, which showed a significantly larger response to warming in colder ecosystems.

Although our results represent the most comprehensive synthesis of ecosystem response to experimental warming to date, there were major limitations to the analysis, most notably the fact that above- and below-ground processes were not typically measured in the same studies. The focus of the individual experiments tended to be directed either at soil processes or plant processes, and thus it was difficult to test integrated hypotheses relating to whole ecosystem response to warming. In fact, perhaps the most significant conclusion that can be drawn from this synthesis is the observation that more comprehensive, whole ecosystem studies are needed in order to test the validity of both conceptual and quantitative models of ecosystem response to warming. Towards this goal, we make the following recommendations for future research on ecosystem response to global warming:

1. *Focus on whole-ecosystem warming experiments*. To date, the majority of studies have focused on either aboveground plant response or belowground soil response to experimental warming. Ultimately, we need to understand the integrated response of entire ecosystems to altered thermal regimes.
2. *Support longer-term experiments*. The magnitude and even the direction of the response to warming have been shown to change over time due to changing resource conditions, alterations in competitive interactions, and acclimation (Shaver et al. 2000). It is imperative to continue some studies beyond the typical 3-year funding cycle to distinguish transient response from longer-term trends.
3. *Add experiments in under-represented biomes*. To date, the majority of warming experiments have been conducted in north temperate, boreal and arctic ecosystems. These systems tend to be cool, moist, and strongly nutrient-limited. A clear need exists to understand the response of warmer and/or drier ecosystems to warming, including Mediterranean, desert, and tropical ecosystems, where the indirect effects of temperature on moisture will likely play a larger role in these ecosystems, and the possibility of exceeding temperature maxima should be considered.
4. *Encourage common protocols*. The comparison of ecosystem response to experimental warming at large temporal and spatial scales would benefit greatly from the establishment of common protocols across a coordinated global network of sites. This would allow a more direct comparison of results and would encourage continued data synthesis.
5. *Combine warming experiments with gradient studies*. Although experimental manipulations of soil and air temperature have provided useful insights on ecosystem response to warming on annual to decadal time frames, these types of manipulations do not simulate the gradual change in climate that occurs on the century to millennium scale. Combining results from warming experiments (annual to decadal time scale) with studies of ecosystem dynamics along natural climatic and environmental gradients (millennium time scale) would effectively put bounds on what is likely to occur on the century time scale (Callaghan et al. 1999).
6. *Investigate interactions with other vectors of environmental change*. Ultimately we must evaluate the response of ecosystems to a complex array of environmental changes, including warming, elevated atmospheric CO_2 concentrations, increased N deposition, and both increases and decreases in the quantity and distribution of regional precipitation. These additional forcing factors will undoubtedly influence the magnitude or even direction of response to warming alone.

Results from the existing, first-generation ecosystem warming experiments, many of which have been included in this meta-analysis, have shown that increases in temperature in the range of 0.3–6.0°C can have significant impacts on ecosystem function. Future ecosystem warming experiments need to: (1) more fully integrate the experiments at the ecosystem level, (2) investigate interactions with other vectors of environmental change, and (3) expand the spatial and temporal scales of analysis. To help accomplish this, the GCTE core project of IGBP has established a NEWS (GCTE-NEWS) to integrate and foster research on ecosystem-level effects of rising temperature. NEWS will promote the establishment of new research projects – using a variety of warming techniques including gradient and transplant studies – in biomes which are not currently investigated. The Network will carry out periodic synthesis of results and integration through modeling with other ongoing research efforts such as those on elevated CO_2 and N deposition.

Appendix 1

Site characteristics and experimental design for the ecosystem warming studies

Site	Abbreviation	State, country	Latitude	Longitude	Biome	Vegetation	Ecosystem type
Abisko Nature Reserve, Sheffield study	AB_SHEF	Sweden	68 21'N	18 49'E	Low tundra	Woody	Open birch heath/woodland
Abisko Nature Reserve, e.s.l. 1150 m, high heat study	AB1150HI	Sweden	68 21'N	18 49'E	High tundra	Woody	Dwarf shrub fellfield
Abisko Nature Reserve, e.s.l. 1150 m, low heat study	AB1150LO	Sweden	68 21'N	18 49'E	High tundra	Woody	Dwarf shrub fellfield
Abisko Nature Reserve, e.s.l. 450 m, high heat study	AB450HI	Sweden	68 21'N	18 49'E	Low tundra	Woody	Dwarf shrub heath
Abisko Nature Reserve, e.s.l. 450 m, low heat study	AB450LO	Sweden	68 21'N	18 49'E	Low tundra	Woody	Dwarf shrub heath
Abisko Nature Reserve, MBL cable study	ABMBLC	Sweden	68 35'N	18 82'E	Low tundra	Woody	Dwarf shrub heath
Abisko Nature Reserve, MBL OTC study	ABMBLO	Sweden	68 35'N	18 82'E	Low tundra	Woody	Dwarf shrub heath
Buxton Climate Change Impacts Laboratory	BCCIL	UK	53 20'N	2 00'W	Grassland	Non-woody	Grassland
Climate Change Experiment	CLIMEX	Norway	58 23'N	8°19'E	Forest	Woody	Birch and pine mixture
Flakaliden	FLAK	Sweden	64 07'N	19°27'E	Forest	Woody	Planted evergreen forest
Minnesota Peatlands, bog, high heat study	FRFBOGHH	MN, USA	47 10'N	92°43'W	Low tundra	Non-woody	Bog peatland
Minnesota Peatlands, bog, medium heat study	FRFBOGMH	MN, USA	47 10'N	92°43'W	Low tundra	Non-woody	Bog peatland
Minnesota Peatlands, fen, high heat study	FRFFENHH	MN, USA	46 59'N	92°34'W	Low tundra	Non-woody	Fen peatland
Minnesota Peatlands, fen, medium heat study	FRFFENMH	MN, USA	46 59'N	92°34'W	Low tundra	Non-woody	Fen peatland
Harvard Forest	HARVARD	MA, USA	42 30'N	72°10'W	Forest	Woody	Northern hardwood forest
Howland Forest	HIFS	ME, USA	45 10'N	68°48'W	Forest	Woody	Spruce-fir forest
Huntington Wildlife Forest, 2.5°C study	HUNT2.5	NY, USA	43 59'N	74°14'W	Forest	Woody	Northern hardwood forest
Huntington Wildlife Forest, 5.0°C study	HUNT5.0	NY, USA	43 59'N	74°14'W	Forest	Woody	Northern hardwood forest
Huntington Wildlife Forest, 7.5°C study	HUNT7.5	NY, USA	43 59'N	74°14'W	Forest	Woody	Northern hardwood forest
Niwot Ridge	NIWOT	CO,USA	40 03'N	105°36'W	Low tundra	Non-woody	Alpine dry tundra

Site	Abbreviation	State, country	Latitude	Longitude	Biome	Vegetation	Ecosystem type
Ny Alesund	NY_AL	Norway	78 56'N	11 50'E	High tundra	Non-woody	*Dryas octopetala* community
Oak Ridge National Laboratory	ORNL	TN, USA	35 54'N	84 21'W	Forest	Woody	Planted deciduous trees
Rio Mayo	RIO_MAYO	Argentina	45 25'S	70 16'W	Grassland	Non-woody	Grass, shrub steppe
Rocky Mountain Biological Laboratory	RMBL	CO, USA	38 53'N	107°02'W	Grassland	Non-woody	Subalpine meadow
Shortgrass Steppe – day-time warming	SGS-DW	CO, USA	40 49'N	104°46'W	Grassland	Non-woody	Shortgrass steppe
Shortgrass Steppe – night-time warming	SGS-NW	CO,USA	40 49'N	104°46'W	Grassland	Non-woody	Shortgrass steppe
TERA trees	TERA	OR, USA	44 33'N	123°16'W	Forest	Woody	Planted evergreen
Toolik Lake – wet sedge study	TLKSED	AK, USA	68 38'N	149°34'W	Low tundra	Non-woody	Wet sedge meadow
Toolik Lake – tussock study	TLKTUS	AK, USA	68 38'N	149°34'W	Low tundra	Non-woody	Tussock tundra
Toolik Lake – dry heath study	TOOLIKDH	AK, USA	68 38'N	149°35'W	Low tundra	Non-woody	Dry heath
Toolik Lake – moist tussock study	TOOLIKMT	AK, USA	68 38'N	149°35'W	Low tundra	Non-woody	Moist tussock tundra
Wytham Woods	WYTHAM	UK	51 46'N	1 20'W	Grassland	Non-woody	Calcareous grassland

Mean annual temperature (°C)	Mean annual precipitation (mm)	Mean growing season temperatur) (°C	Mean growing season precipitation (mm)	Average growing season (days)	Warming technology	Replicate plots per treatment	Heating duration	Reference
–1	301	10	122	92	Field chamber	6	Field season	Press et al. (1998)
–5	500	6	150	61	Field chamber	6	Field season	Jonasson et al. (1993)
–5	500	6	150	61	Field chamber	6	Field season	"
–1	304	10	121	92	Field chamber	6	Field season	"
–1	304	10	121	92	Field chamber	6	Field season	"
0	228	9	126	122	Cables	4	Field season	Hartley et al. (1999)
0	228	9	126	122	Field chamber	12	Field season	"
8	1292	13	408	154	Cables	5	Winter only	Grime et al. (2000)
5	1400	11	810	183	Cables	1	All year	Lukewille and Wright (1997)
2	590	11	270	135	Cables	2	Field season	Bergh and Linder (1999)
3	634	13	488	183	Infrared	3	All year	Bridgham et al. (1999)
3	634	13	488	183	Infrared	3	All year	"
3	634	13	488	183	Infrared	3	All year	"
3	634	13	488	183	Infrared	3	All year	"
7	1102	13	765	177	Cables	6	All year	Peterjohn et al. (1994)
6	1100	11	na	168	Cables	2	Field season	Rustad and Fernandez (1998a)
4	1010	15	447	152	Cables	6	Field season	McHale et al. (1998)
4	1010	15	447	152	Cables	6	Field season	"
4	1010	15	447	152	Cables	6	Field season	"
–4	930	7	na	130	Field chamber	3	Field season	Welker et al. (1999)
–6	371	4	78	76	Field chamber	6	Field season	Robinson et al. (1995)
14	1322	22	772	184	Field chamber	3	All year	Norby et al. (1997)
8	150	11	14	152	Field chamber	10	Field season	Sala et al. (1989)
5	750	9	100	61	Infrared	5	All year	Harte et al. (1995)
9	322	18	225	135	Greenhouse	2	Field season	Burke and Lauenroth (1993)
9	322	18	225	135	Night warming	4	Field season	Alward et al. (1999)
11	1095	na	na	364	Field chamber	3	All year	Tingey et al. (1996)
–9	330	9	177	71	Greenhouse	2	Field season	Shaver et al. (1998)
–9	330	9	177	71	Greenhouse	4	Field season	"
–9	330	9	177	71	Field chamber	3	Field season	Jones et al. (1998)
–9	330	9	177	71	Field chamber	3	Field season	Jones et al. (1998)
10	682	12	420	245	Cables	5	Winter only	Grime et al. (2000)

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