Climate Variation and Soil Carbon and Nitrogen Cycling Processes in a Northern Hardwood Forest

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ABSTRACT

We exploited the natural climate gradient in the northern hardwood forest at the Hubbard Brook Experimental Forest (HBEF) to evaluate the effects of climate variation similar to what is predicted to occur with global warming over the next 50–100 years for northeastern North America on soil carbon (C) and nitrogen (N) cycle processes. Our objectives were to (1) characterize differences in soil temperature, moisture and frost associated with elevation at the HBEF and (2) evaluate variation in total soil (TSR) and microbial respiration, N mineralization, nitrification, denitrification, nitrous oxide (N_2O) flux, and methane (CH_4) uptake along this gradient. Low elevation sites were consistently warmer (1.5–2.5°C) and drier than high elevation sites. Despite higher temperatures, low elevation plots had less snow and more soil frost than high elevation plots. Net N mineralization and nitrifica-tion were slower in warmer, low elevation plots, in both summer and winter. In summer, this pattern was driven by lower soil moisture in warmer soils and in winter the pattern was linked to less snow and more soil freezing in warmer soils. These data suggest that N cycling and supply to plants in northern hardwood ecosystems will be reduced in a warmer climate due to changes in both winter and summer conditions. TSR was consistently faster in the warmer, low elevation plots. N cycling pro-cesses appeared to be more sensitive to variation in soil moisture induced by climate variation, whereas C cycling processes appeared to be more strongly influenced by temperature.

Key words: carbon dioxide; climate change; mineralization; nitrification; nitrous oxide; meth-ane.

INTRODUCTION

Understanding the long-term effects of climate change on forest ecosystem processes is a great challenge that requires multiple approaches (Carpenter 1998; Parson and others 2003). Short-term manipulation experiments only provide information on the immediate effects of often dramatic changes (Shaver and others 2000), and whereas modeling studies evaluate long-term ef-fects, it is difficult to evaluate the validity of model predictions (Gerten and others 2008; Luo and others 2008; Canham and others 2003). Compar-ative studies along natural climate gradients allow for evaluation of the long-term effects of climate-

driven variation in temperature and moisture on ecosystem processes (Whittaker 1967; Smith and others 2002; Hart 2006; Griffiths and others 2009). Although gradient approaches suffer from spatial variation in factors other than climate (McDonnell and Pickett 1990), they provide opportunities to evaluate the effects of long-term variation in both winter and summer climate on intact ecosystems (Koch and others 1995; Kelly and Goulden 2008).

The Hubbard Brook Experimental Forest (HBEF) in the White Mountains of New Hampshire, USA is an excellent location for climate gradient studies. This long-term ecological research (LTER) site is located in an approximately 3,000 ha valley that encompasses significant variation in climate with relatively little variation in vegetation (northern hardwood forest, Schwarz and others 2003) and soils (Spodosols) with elevation. Variation in biogeochemical processes within the valley has been well studied (Johnson and others 2000; Bohlen and others 2001; Venterea and others 2003; Likens and Buso 2006), but little work has focused on climate as a driver of this variation. The variation in temperature within the Hubbard Brook valley ($\sim$2.0°C) is similar to what is predicted to occur with climate change over the next 50–100 years in northeastern North America (Hayhoe and others 2006; Campbell and others 2007).

Two important uncertainties about the long-term impacts of climate change on temperate forest processes are the effects of changes in summer soil moisture and winter snow cover. Summer soil moisture is a strong driver of plant and microbial processes that underlie decomposition, nutrient cycling, and ecosystem C dynamics, and is the integrated product of variation in temperature, precipitation, and plant water use (Hanson and others 2005). Winter climate change has received increased attention in recent years due to the realization that significant amounts of nutrient cycling activity take place during winter in many ecosystems and that this activity is sensitive to changes in snow cover, which regulates soil freezing dynamics (Williams and others 1996; Brooks and others 1999; Groffman and others 2001a; Campbell and others 2005; Henry 2008; Öquist and Laudon 2008).

Variation in winter climate and summer soil moisture affect multiple processes; litterfall, mineralization, nitrification, denitrification, leaching, microbial respiration and root respiration, turnover and exudation either directly by affecting soil temperature and moisture, or indirectly by influencing plant production and uptake of water and nutrients (Rastetter and others 2005; Borken and

others 2006). Changes in these processes will regulate the effects of climate change on ecosystem services related to primary production, water and air quality issues related to reactive N (Galloway and others 2003), C sequestration, and atmospheric chemistry (Campbell and others 2009).

In the present study, we exploited the natural climate gradient at the HBEF to evaluate the effects of climate variation similar to what is predicted to occur due to global warming over the next 50–100 years in northeastern North America. Our objectives were to, (1) characterize differences in soil temperature, moisture, and frost associated with elevation at the HBEF and (2) evaluate variation in soil C and N cycle processes (total soil and microbial respiration, mineralization, nitrification, denitrification, N_2O flux, and CH_4 uptake) along this gradient. The study was designed to complement ongoing long-term monitoring (Likens and Bormann 1995), experimental manipulation (Groffman and others 2001a), and modeling (Chen and Driscoll 2005) efforts to address the complex effects of climate change on the northern hardwood forest. The study was also designed to be more detailed than previous landscape-scale biogeochemical studies at HBEF that have generally been broad surveys with little repeated sampling or analysis of in situ process rates. Here the objective was to build on these previous surveys as a platform for more detailed measurements of actual process rates at a smaller number of sites.

METHODS

Study Sites

The HBEF is located in the White Mountain National Forest, New Hampshire USA (43°56′N, 71°45′W). The forest is dominated by northern hardwoods, with increased importance of red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* L.) at higher elevations (Schwarz and others 2003). Soils at HBEF are dominated by shallow (75–100 cm), acidic (pH 3.9) Spodosols developed from unsorted basal tills.

Our experimental design consisted of four 10 m × 10 m plots (Table 1), two low elevation south-facing sites approximately 350 m apart at the HBEF valley bottom (380 and 480 m), and two high elevation north-facing sites approximately 100 m apart on Mt. Kineo (755 and 790 m). The valley bottom and Mt. Kineo plots were approximately 8 km apart. Each plot was split into three distinct subplots for repeated sampling. The major tree species in our plots were *Acer saccharum*

Table 1. Description of Two Low Elevation (Valley) and Two High Elevation (Kineo) Study Sites Located in the Hubbard Brook Experimental Forest, NH USA

Site	Elev (m)	Aspect	Slope (%)	Forest floor depth (cm)	Forest floor C:N	Forest floor pH	Dominant tree species[1]
Lower valley	380	105 East	9	5–8	21.8	3.8	BEAL, ACPE, FAGR, PIRU
Upper valley	480	190 South	35	11–19	18.2	3.9	ACSA, FRAM, BEAL, FAGR
West Kineo	755	352 North	12	3–14	19.4	4.0	BEAL, ACSA, FAGR, ACPE, PIRU
East Kineo	790	350 North	20	3–10	18.4	3.9	BEAL, ACSA, PIRU

Beal Betula alleghaniensis Britt., ACPE Acer rubrum L., FAGR Fagus grandifolia Ehrh., PIRU Picea rubens Sarg., ACSA Acer saccharum Marsh., FRAM Fraxinus americana L.

Marsh., *Betula alleghaniensis* Britt., *Picea rubens* Sarg., *Fagus grandifolia* Ehrh., *Fraxinus americana* L., and *Acer rubrum* L. (Cleavitt and others 2008, Table 1).

Soil and air temperatures were measured using a Campbell Scientific CR 10x data logger with thermistor probes (one per plot per depth) inserted horizontally at 10 cm intervals from 0 to 50 cm depth plus an aboveground probe. The data logger system recorded temperature readings every minute and stored hourly averages. Unfrozen volumetric soil water content was measured with duplicate Campbell CS615 time domain reflectometry (TDR) probes installed horizontally at two depths in the Oa and Bh horizons (approximately 0.05 and 0.15 m depth, respectively) that were the focus of our sampling for C and N cycle process measurements. These probes have been found to provide accurate measurements of volumetric water content in HBEF soils (Hardy and others 2001). Snow depths were measured throughout the winter using a metal meter stick at approximately 2-week intervals at between 10 and 100 randomly selected locations per plot. Frost depths were measured approximately weekly in two frost tubes (Ricard and others 1976; Hardy and others 2001) in each plot.

In Situ Net N Mineralization and Nitrification

Net N mineralization and nitrification were measured using an in situ intact core method (Robertson and others 1999). At each sampling date, six, 2 cm diameter × 25 cm depth intact cores were removed from each plot; two from each of the sampling subplots. Three of the cores (one from each subplot) were returned to the laboratory for extraction (2 N KCl) of inorganic N (ammonium (NH_4^+) and nitrate (NO_3^-)) and the other three were returned to the plot for in situ incubation. During the growing season, cores were incubated for approximately 4 weeks before removal and extraction. Cores overwintered from December to March. Inorganic N was quantified colorimetrically using a flow injection analyzer. Net N mineralization rates were calculated as the accumulation of total inorganic N over the course of the incubation. Net nitrification rates were calculated as the accumulation of NO_3^- over the course of the incubation. Values were converted to an areal basis (g N m^{-2}) using bulk density values from Bohlen and others (2001). Plot mean values were used in statistical analyses to avoid concerns about pseudo-replication.

Soil:Atmosphere Trace Gas Fluxes

Trace gas fluxes were measured using the in situ chamber design identical to that described by Bowden and others (1990, 1991). Chambers (three per plot) of 287-mm diameter (ID) by 40-mm high polyvinyl chloride (PVC) were placed on permanently installed PVC base rings immediately prior to measurement. At 0, 10, 20, and 30 min following placement of the chamber on the base, 9-ml gas samples were collected from gas sampling ports in the center of the chamber top by syringe. Samples were transferred to evacuated glass vials and stored at room temperature prior to analysis by gas chromatography (GC). N_2O and CO_2 were analyzed on a Shimadzu GC-14 GC with electron capture (N_2O) and thermal conductivity (carbon dioxide, CO_2) detectors. CH_4 was analyzed on a Shimadzu GC-8a GC with a flame ionization detector. These GC's were capable of detecting ambient levels of these gases. Fluxes were calculated from the linear rate of change in gas concentration, the chamber internal volume and soil surface area. Flux rate calculations were not corrected for actual in situ temperature and pressure. Single points were removed from regressions if they were more than 6 times higher or lower than the other three values or if they contradicted a clear trend in the other three points. This procedure prevents inclusion of high flux rates based on non-significant regressions.

Non-significant regressions were used in flux calculations to avoid biasing the statistical distribution of rates by setting all non-significant regressions to zero.

Measurements of Microbial Biomass and Activity and Ancillary Variables

Three samples (separate forest floor and mineral soil), distinct from the in situ N mineralization and nitrification samples described above, were taken from each plot in June 2002, April and June 2003, and April and June 2004. Samples were stored at 4°C between sampling and analysis (less than 1 week). Soil samples were hand sorted and mixed and held at field moisture for all analyses. Soil moisture content was determined by drying at 60°C for 48 h (McInnes and others 1994). Soil organic matter content was determined by loss on ignition at 450°C for 4 h (Nelson and Sommers 1996). Amounts of inorganic N (NO_3^- and NH_4^+) in soil were determined by extraction with 2 M KCl followed by colorimetric analysis with a Lachat Flow Injection Analyzer.

Microbial biomass C and N content was measured using the chloroform fumigation–incubation method (Jenkinson and Powlson 1976). Soils were fumigated to kill and lyse microbial cells in the sample. The fumigated sample was inoculated with fresh soil, and microorganisms from the fresh soil grew vigorously using the killed cells as substrate. CO_2 and NH_4^+ released during the incubation were assumed to be directly proportional to the amount of C and N in the microbial biomass of the original sample. CO_2 was measured by thermal conductivity gas chromatography and NH_4^+ was quantified colorimetrically after KCl extraction as described above. A proportionality constant ($k_c = 0.41$) was used to calculate biomass C from the CO_2 produced during the incubation. No proportionality constant was used for biomass N.

Inorganic N and CO_2 production were also measured in unfumigated "control" samples. These incubations provided estimates of rates of microbial respiration and potential net N mineralization and nitrification. Production of inorganic N and CO_2 in laboratory incubations can also be used as measures of pools of readily available or microbially labile N and C. Microbial respiration was quantified from the amount of CO_2 evolved over the 10-day incubation. Potential net N mineralization and nitrification were quantified from the accumulation of NH_4^+ plus NO_3^- and NO_3^- alone during the 10-day incubation. Ammonium and NO_3^- were measured as described above.

Potential denitrification (denitrification enzyme activity, DEA) was measured using the short-term anaerobic assay developed by Smith and Tiedje (1979) as described by Groffman and others (1999). Sieved soils were amended with KNO_3^-, dextrose, chloramphenicol (to inhibit synthesis of new enzymes), and acetylene, and were incubated under anaerobic conditions for 90 min. Samples were made anaerobic by repeated evacuation and flushing with N_2 gas. Gas samples were taken at 30 and 90 min, stored in evacuated glass tubes and analyzed for N_2O by electron capture gas chromatography as described above.

Statistical Analysis

Differences between elevations and annual or seasonal means of dependent variables were evaluated using analysis of variance (ANOVA) with elevation and/or year as main effects. Site means were used in all analyses to avoid concerns about pseudo-replication that could arise if within-plot replicates were included. Because trace gas fluxes were measured from the same permanent chamber bases at each sample date, repeated measures ANOVA was used to evaluate elevation effects on these fluxes. Repeated measures ANOVA was also used for the measurements of microbial biomass and activity and ancillary variables. Data were tested for normality using the Shapiro–Wilk statistic. When non-normal distributions were detected, elevation effects were evaluated using one-way nonparametric analysis of variance with the Kruskal–Wallis test. Relationships between variables were explored with Pearson product moment correlations. The Statistical Analysis System (SAS 1988) was used for all analyses.

RESULTS

The elevation gradient at HBEF produced a clear climatic contrast with the low elevation sites consistently warmer and drier than the high elevation sites. Air temperature differences ranged from 1.5 to 2.5°C, with no marked seasonal pattern (Figure 1). Soil moisture was consistently higher ($P < 0.01$) in the high elevation than low elevation plots in both continuous TDR (Figure 2) and occasional gravimetric (Table 3) sampling.

We did not measure precipitation at our plots, but this was measured at numerous other sites within the HBEF (www.hubbardbrook.org). Precipitation at the gage nearest our low elevation sites (raingage #1) was 1309, 1639, and 1329 mm in
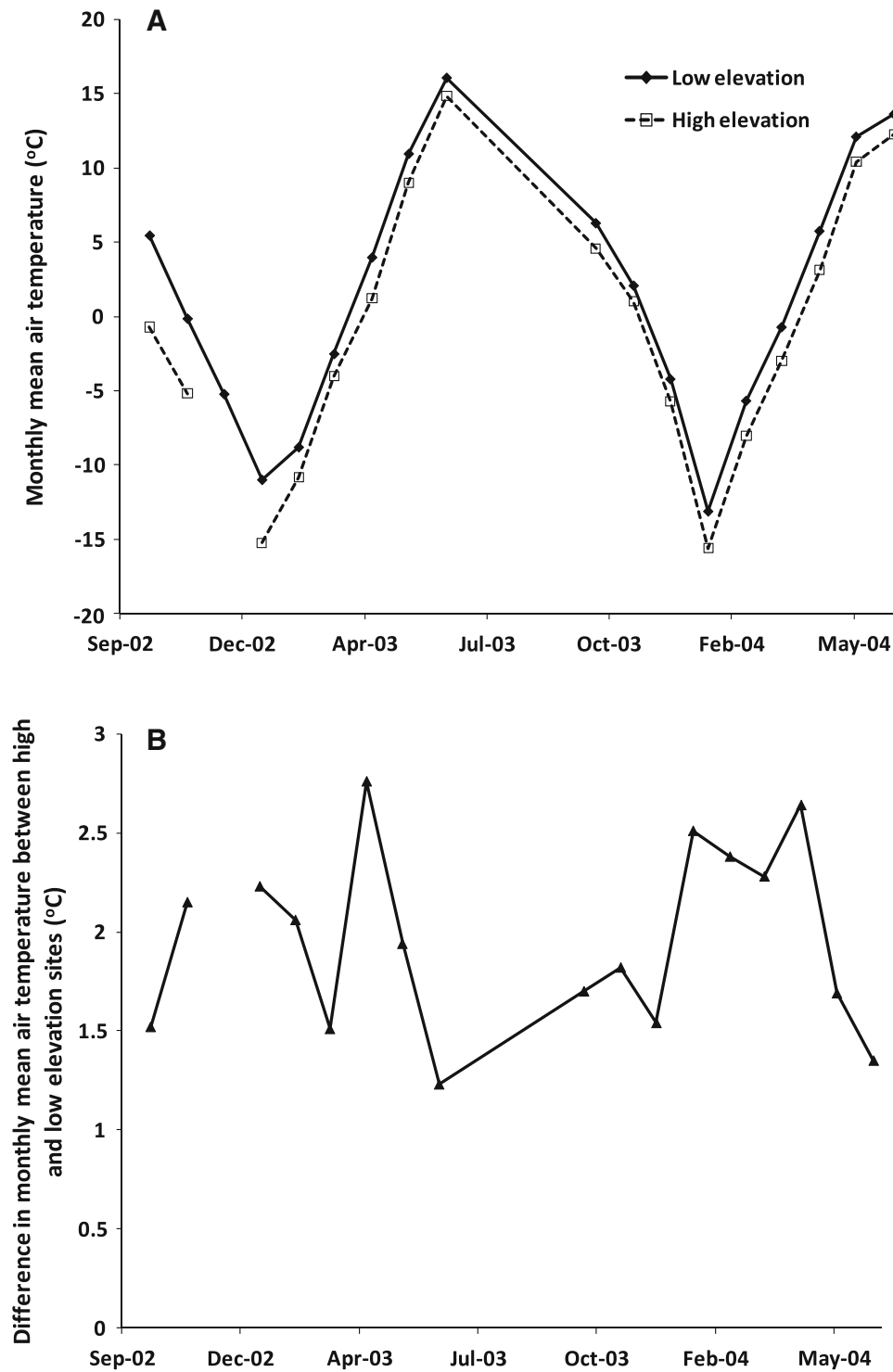
Figure 1. Monthly mean air temperature in low and high elevation sites (**A**) and the difference in monthly mean air temperatures between sites (**B**) from Fall 2002–Spring 2004. There was one meteorological station located at the low elevation (lower) site and one at the high elevation (west) site.

2002, 2003, and 2004, respectively. Precipitation at the gage nearest our high elevation sites (raingage #13) was 1326, 1704, and 1365 mm in 2002, 2003, and 2004, respectively.

Despite higher temperatures, low elevation plots had deeper ($P < 0.001$) soil frost for a longer period than high elevation plots (Figure 3). In winter

2002/2003, high elevation plots had almost no soil frost (<4 cm) throughout most of the winter and only one of the low elevation plots had persistent frost (Figure 3A). Mean soil frost depth was 3.7 cm at low elevation and 0.6 cm at high elevation in winter 2002/2003. Frost was deeper ($P < 0.001$) on all plots in winter 2003/2004 but was consistently
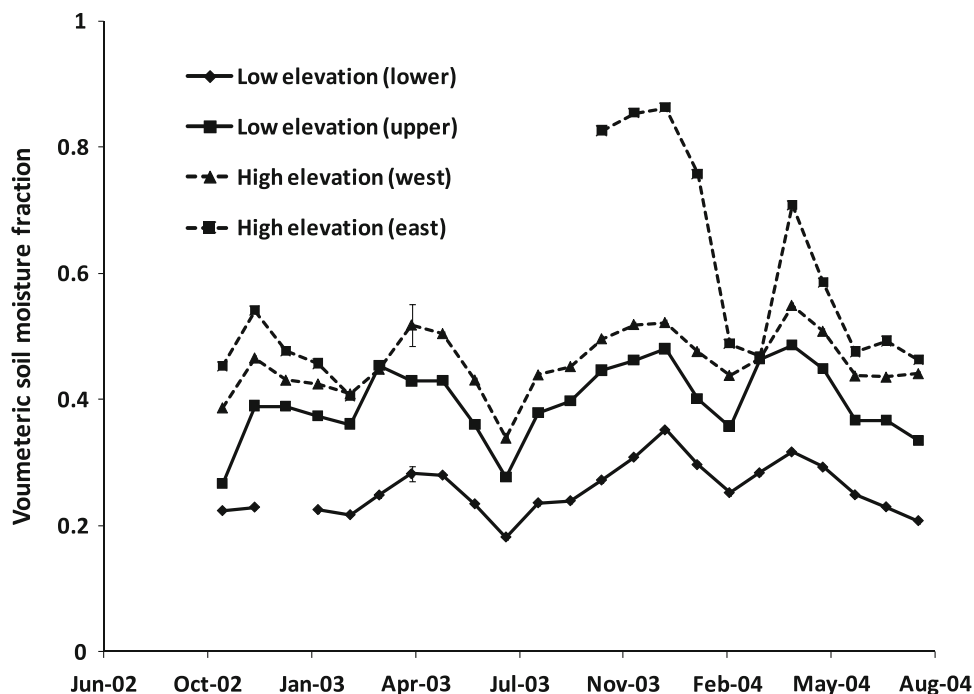
Figure 2. Mean monthly volumetric soil moisture in the forest floor of two low elevation and two high elevation plots from Fall 2002–Summer 2004. Datalogger failure resulted in loss of data at the high elevation (east) site from fall 2002 through summer 2003. Values are monthly means of hourly values from four soil moisture probes; two at 5 cm and two at 15 cm depth in each plot ($n = \sim 1400$ for each point). Example error bars are shown to illustrate typical variability.

deeper ($P < 0.001$) on the low elevation plots (Figure 3B). Mean soil frost depth was 9.2 cm at low elevation and 4.5 cm at high elevation in winter 2003/2004. Spatial and temporal patterns of frost mirrored patterns of snow accumulation which was deeper, earlier on the high elevation plots and in 2002/2003. On 7 January 2003 (the year with lower soil frost), there was 77.3 cm of snow on the high elevation plots and 35.4 cm on the low elevation plots ($P < 0.0011$). On 7 January 2004 (the year with more soil frost) there was 48.3 cm of snow at the high elevation plots and 19.8 cm of snow on the low elevation plots ($P < 0.0398$). Both winters had near average ($-4.7°C$) temperatures; $-5.8°C$ in 2002/2003 and $-4.5°C$ in 2003/2004.

Rates of in situ net N mineralization and nitrification were faster in summer than in winter (Figure 4) and in high elevation plots than in low elevation plots (Table 2, $P < 0.0701$ for mineralization and $P < 0.0246$ for nitrification). Net nitrification was particularly slow on the lower valley low elevation plot. Winter mineralization activity ranged from 14 to 57% of annual activity in 2002/2003 and 7 to 23% of annual activity in 2003/2004 and was faster ($P < 0.0249$) in high elevation plots. Winter nitrification ranged from 6 to 25% of annual activity in 2002/2003 and from 0 to 29% of annual activity in 2003/2004 and was faster ($P < 0.0187$) in high elevation plots. Summer activity was strongly correlated with soil moisture (Figure 5A, $r = 0.75$, $P < 0.0500$ for mineraliza-

tion, $r = 0.96$, $P < 0.0007$ for nitrification). In winter, sites with more soil freezing had slower rates of nitrification, but the correlation between maximum soil frost and winter nitrification was not significant (Figure 5B, $r = -0.48$, $P < 0.5241$ in 2002/2003, $r = -0.81$, $P < 0.1854$ in 2003/2004). Because there were markedly different amounts of soil frost in the two winters of the study, correlations between soil frost and N cycling activity were done separately for each year, reducing the power of the analysis.

In addition to in situ net N mineralization and nitrification, other indices of N cycling were faster in the high elevation plots relative to the low elevation plots (Table 3). Potential net N mineralization and nitrification, pools of soil NO_3^-, microbial biomass N, and potential denitrification rates were faster (see Table 3 for P values associated with different variables and soil horizons) in high elevation plots than low elevation plots. Rates of microbial respiration/pools of labile C were also faster at high elevation (Table 3).

In contrast to rates of microbial respiration measured in the laboratory, in situ TSR was faster ($P < 0.0507$) in low elevation than high elevation plots, but the difference was more marked in summer (May–November, $P < 0.0342$) than in winter (December–April, $P < 0.1395$) when rates were much lower (Figure 6). Methane uptake was also faster ($P < 0.0441$) at low elevation, and again, the differences were stronger in summer ($P < 0.0347$) than in winter ($P < 0.1950$). There
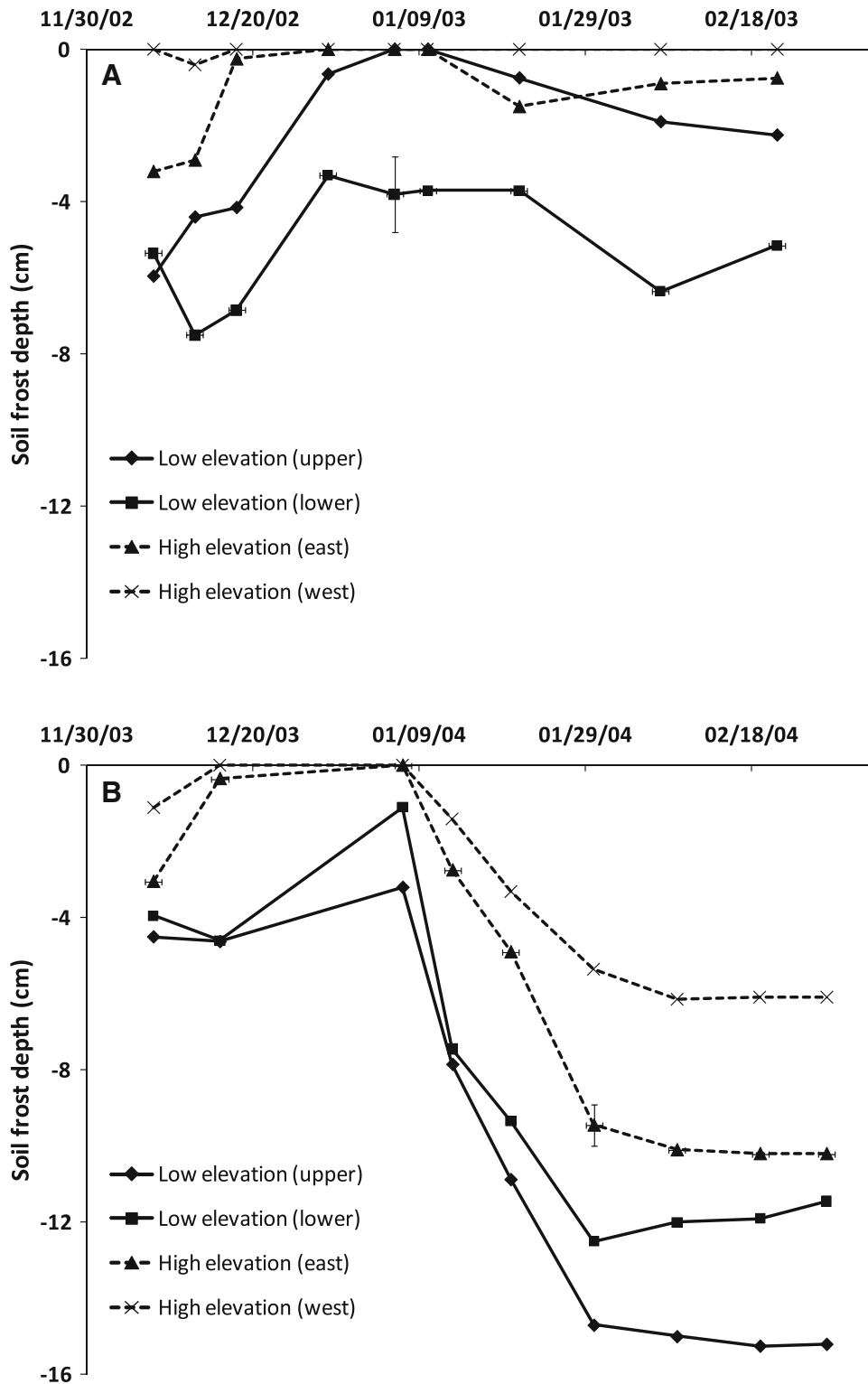
Figure 3. Soil frost in two low elevation and two high elevation plots in winter 2002/2003 (**A**) and winter 2003/2004 (**B**). Values are the mean of two frost tubes per plot. Example error bars are shown to illustrate typical variability.

was no difference in N_2O flux between the elevations. Mean CO_2 flux was 50% faster in the low elevation plots than the high elevation plots in summer (0.080 vs. 0.053 g C m^{-2} h^{-1}) and 300% higher in winter (0.021 vs. 0.007 C m^{-2} d^{-1}). The winter difference was driven by faster rates of total soil respiration at the beginning (December) and end (March) of the season when low elevation soils were snow free and markedly warmer than the high elevation plots.
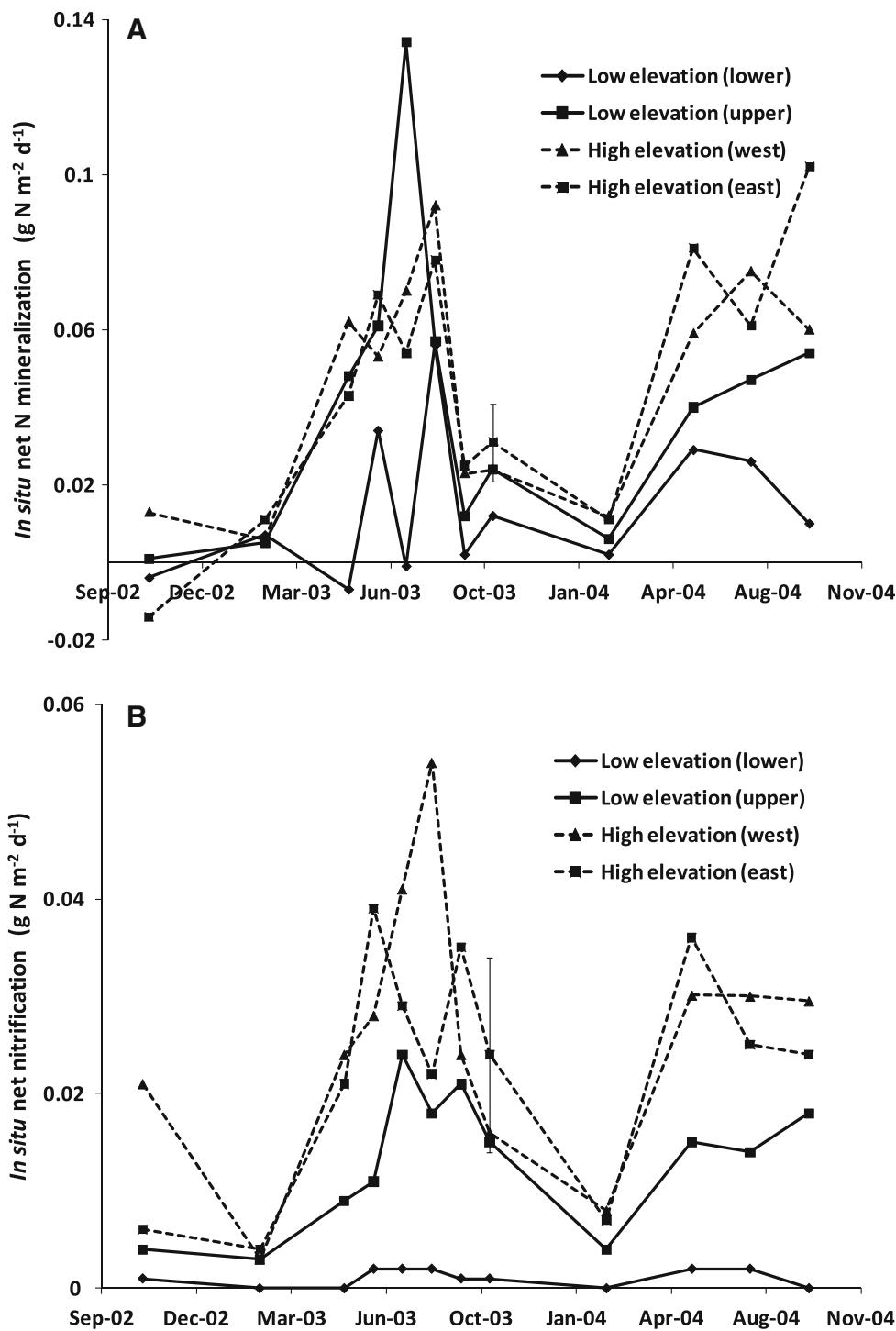
Figure 4. In situ net N mineralization (**A**) and nitrification (**B**) rates in two low elevation and two high elevation plots from Fall 2002–Fall 2004. Values are plot means over forest floor and mineral soil ($n = 1$ for each point). Example error bars (October 2003) are shown to illustrate typical within-plot variability.

DISCUSSION

Results from our analysis suggest that climate change in the northeastern US will produce drier soils that freeze more frequently and provide less N to support plant productivity. Soils in these ecosystems will export more CO_2, and consume more CH_4, with implications for their effect on atmospheric chemistry.

The Hubbard Brook Climate Gradient

The elevation gradient at HBEF produces consistent air temperature differences ranging from 1.5 to 2.5°C, similar to what is projected to occur with climate change over the next 50–100 years in the northeastern US (Hayhoe and others 2006). Climate change is also expected to increase precipitation in the region, but higher temperatures and a

Table 2. Winter and Annual In Situ Net N Mineralization and Nitrification Rates in Two Low and Two High Elevation Plots in 2002/2003 and 2003/2004

Site	Net N mineralization			Net nitrification		
	Winter (g N m^{-2} season)	Annual (g N m^{-2} y^{-1})	% Winter	Winter (g N m^{-2} season)	Annual (g N m^{-2} y^{-1})	% Winter
2002/2003						
Low elevation						
Lower	2.1	3.7	57	0.01	0.17	6
Upper	1.5	11.1	14	0.79	3.0	26
	**	*		**	**	
High elevation						
East	3.4	10.4	33	1.3	5.2	25
West	2.0	11.3	18	0.89	5.4	16
2003/2004						
Low elevation						
Lower	0.46	7.1	7	−0.04	0.51	0
Upper	1.9	13.0	15	1.1	5.2	21
	**	*		**	**	
High elevation						
East	3.8	19.1	20	2.5	9.8	26
West	4.3	18.7	23	2.8	9.6	29

**,*Indicates significant difference between elevations at P < 0.05 and 0.10, respectively, in a two-way analysis of variance with elevation and year as main effects. See text for specific significance values. There was no interaction between year and elevation. Annual N mineralization was higher (P < 0.0292) in 2003/2004 than in 2002/2003. Winter (P < 0.0839) and annual (P < 0.0594) nitrification were higher in 2003/2004 than in 2002/2003.

longer growing season are expected to lead to increases in drought (Huntington and others 2009).

Although elevation gradient studies provide opportunities to study climate change, their usefulness depends on a lack of variation in other factors that influence ecosystem processes. Within the HBEF, soil and geologic parent material is relatively uniform, with bedrock under our low and high elevation plots dominated by Devonian and Silurian schists and granulites (Bailey and Hornbeck 1992; Barton and others 1997; Likens and Buso 2006). The most important substrate variation within the HBEF landscape is depth to bedrock which is controlled by variation in accumulation of glacial till or the presence of other glacial features, for example, our lower valley site may be located on a kame terrace with a sandier substrate and deeper depth to bedrock than our other sites (see discussion below). Our other three sites have similar bedrock and soil depth.

Vegetation in the White Mountains between 300 and 800 m elevation (where our plots are located) is dominated by northern hardwoods of sugar maple–beech–yellow birch, whereas conifers become more common at higher elevations (Schwarz and others 2003). Given that rates of N cycle processes have been shown to vary strongly with vegetation at HBEF (Venterea and others 2003) and

in many other locations (Lovett and others 2002), it was important for us to restrict our climate gradient studies to this elevation band dominated by northern hardwood vegetation.

We consistently observed higher soil moisture at the cooler, high elevation sites, suggesting that climate change will lead to drier soils in these northern hardwood forest ecosystems. However, linking the higher soil moisture levels that we observed to climate variation depends on a lack of variation in precipitation along the elevation gradient. Long-term monitoring shows that there is on average 40–70 mm more precipitation at high elevation than low elevation rain gages at HBEF (Bailey and others 2003). Differences between the high and low elevation rain gages closest to our sites averaged 38 mm over the 3 years of our study, or 2.6% of average total precipitation of 1445 mm during this period, suggesting that differences in precipitation were not responsible for variation in soil moisture among our sites.

Other than precipitation, the dominant controller of variation in moisture in HBEF soils is evapotranspiration (Hornbeck and others 1997). We suggest that the higher soil moisture that we observed at high elevation is due to slower rates of evapotranspiration at the lower temperatures at the high elevation sites. This conclusion is consistent
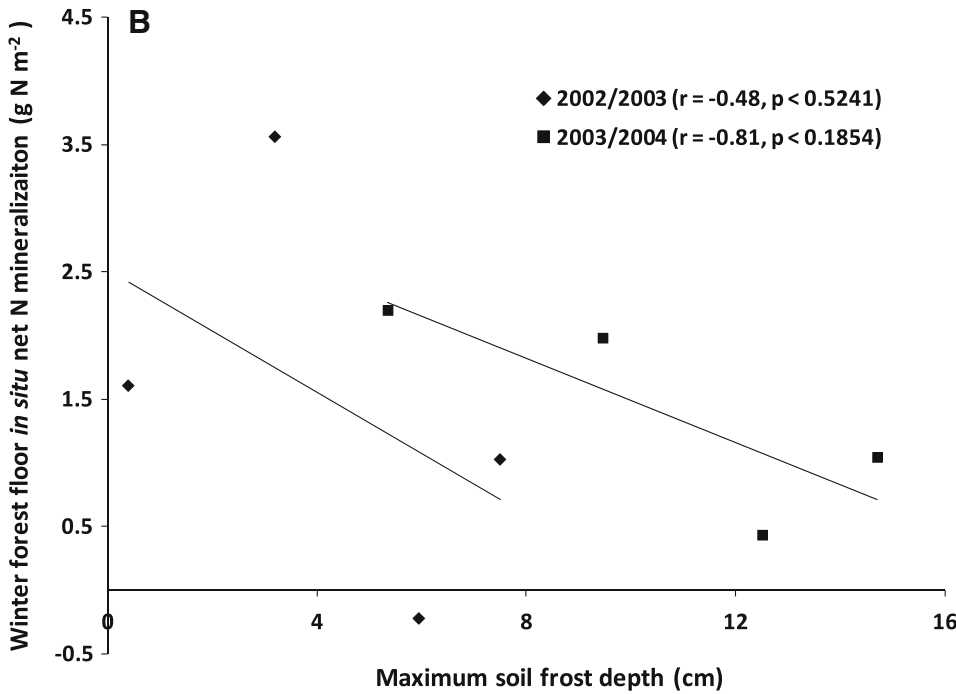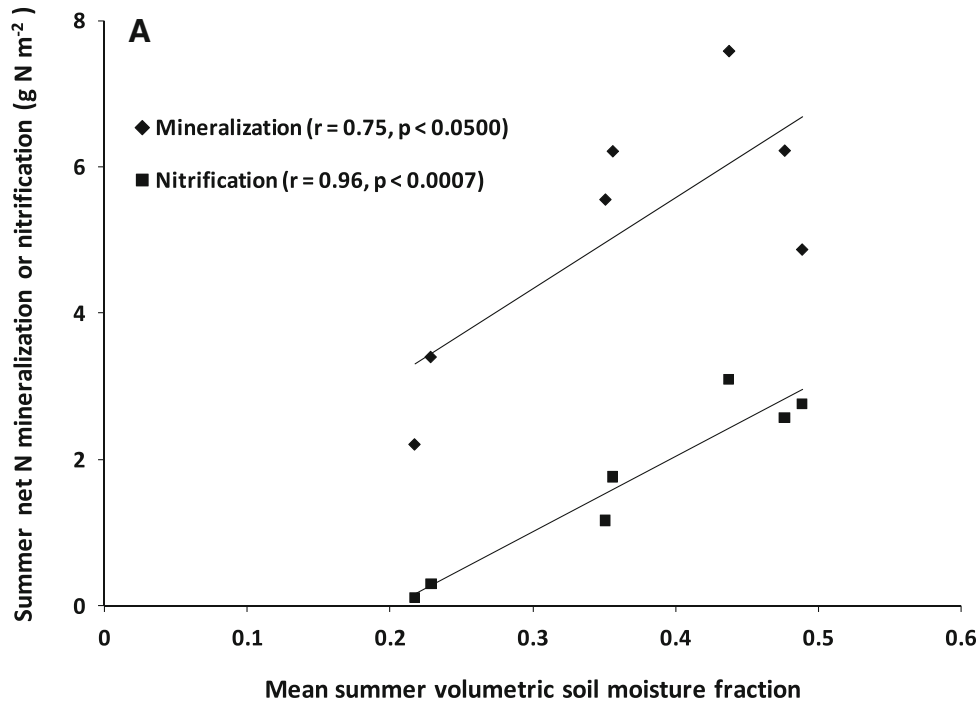
Figure 5. Summer in situ N mineralization and nitrification versus soil moisture (**A**) and winter in situ net N mineralization versus maximum soil frost depth (**B**) in two low elevation and two high elevation plots in 2002 and 2003. Soil moisture values for the high elevation (east) plot were not available for 2002 due to datalogger failure, hence there are only seven points in **A**. Due to marked differences in the amount of soil frost in the winters of 2002/2003 and 2003/2004, relationships in **B** are presented for each year separately, four points per year.

with modeling results produced by Aber and others (1995) evaluating the effects of increases in temperature on evapotranspiration at HBEF. The climate change relevance of our results is reduced, however, by the fact that we cannot account for predicted increases in atmospheric CO_2 levels that have a strong effect on plant water use efficiency.

The Aber and others (1995) modeling study suggested that a doubling of CO_2 yields a doubling in water use efficiency and compensates for the effects of up to a 6°C increase in temperature. Longer term monitoring will be necessary to determine if climate change will result in ''drier soils in a warmer world.''

Table 3. Soil Nitrate, Ammonium, Microbial Biomass C and N Content, Denitrification Potential, Microbial Respiration, Soil Moisture, and Potential Net N Mineralization and Nitrification Rates in Two Low Elevation and Two High Elevation Plots Sampled in Summer 2002, Spring and Summer 2003, and Spring and Summer 2004

	Low elevation			High elevation	
	Lower	Upper	P value	East	West
Forest floor					
Soil nitrate (mg N kg^{-1})	0.3 (0.3)	4.0 (2.7)	0.3178	3.8 (2.1)	7.5 (4.0)
Soil ammonium (mg N kg^{-1})	58 (43)	49 (22)	0.6602	50 (14)	65 (40)
Microbial biomass C (mg C kg^{-1})	2,455 (1,132)	3,008 (1,560)	0.1036	3,585 (1,288)	3,485 (1,765)
Microbial biomass N (mg N kg^{-1})	462 (201)	311 (169)	0.3503	487 (89)	470 (39)
Denitrification potential (µg N kg^{-1} h^{-1})	608 (836)	751 (756)	0.2620	975 (352)	2,028 (2,696)
Microbial respiration (mg C kg^{-1} d^{-1})	240 (175)	130 (68)	0.2782	284 (168)	304 (194)
Soil moisture (%, w/w)	56 (14)	59 (8)	0.0198	66 (4)	67 (3)
Potential net N mineralization (mg N kg^{-1} d^{-1})	6.4 (4.5)	8.9 (2.9)	0.1556	10 (4.2)	11 (5.7)
Potential net nitrification (mg N kg^{-1} d^{-1})	0.03 (0.06)	2.4 (0.9)	0.1825	3.4 (1.1)	4.4 (0.8)
Mineral soil					
Soil nitrate (mg N kg^{-1})	0.1 (0.2)	1.0 (0.8)	0.0848	2.9 (1.5)	4.7 (2.6)
Soil ammonium (mg N kg^{-1})	4.7 (2.6)	6.4 (3.2)	0.4109	7.8 (3.6)	5.9 (5.4)
Microbial biomass C (mg C kg^{-1})	730 (439)	912 (213)	0.3174	1,399 (358)	920 (205)
Microbial biomass N (mg N kg^{-1})	108 (30)	155 (111)	0.3673	145 (33)	217 (168)
Denitrification potential (µg N kg^{-1} h^{-1})	167 (168)	148 (83)	0.0064	403 (185)	371 (268)
Microbial respiration (mg C kg^{-1} d^{-1})	34 (18)	33 (13)	0.0004	77 (75)	77 (93)
Soil moisture (%, w/w)	29 (8)	35 (10)	0.1259	51 (6)	42 (1)
Potential net N mineralization (mg N kg^{-1} d^{-1})	0.6 (0.9)	1.3 (0.4)	0.0527	2.2 (1.0)	2.5 (2.9)
Potential net nitrification (mg N kg^{-1} d^{-1})	0.03 (0.03)	0.6 (0.3)	0.0389	2.0 (0.6)	2.5 (2.5)

Values are mean (standard deviation).

The elevation gradient at HBEF provided marked variation in snow depth and soil frost. Snowpack at low elevation developed later, and to less depth than at high elevation, facilitating the development and maintenance of soil frost. In 2002/2003, one of the high elevation plots had no soil frost and the other had minor and non-persistent frost. In 2003/2004 there was less snow and frost was observed on all plots, but it came earlier and was deeper on the low elevation plots. These results support the idea that there will be "colder soils in a warmer world" (or at least more soil freezing) in winter due to the loss of insulation provided by a snowpack (Groffman and others 2001a). These results are in contrast to recent modeling analyses (Henry 2008), including some at Hubbard Brook (Hong and others 2005), that have suggested that warmer temperatures will result in less soil freezing in many areas. Ultimately, soil freezing depends on soil temperature at critical periods when the snowpack is developing, for example, one outbreak of cold air before snowpack develops can cause soils to be frozen for the entire winter. Both winters in our study had near average temperatures so, although our results suggest that the likelihood of soil freezing is increased by later development of a snowpack under current "normal" temperature regimes, longer term monitoring that includes winters with above average temperatures will be necessary to determine if soil freezing will be increasingly common in a warmer world with less snow.

Soil N Cycling in a Warmer World

We consistently observed slower rates of net N mineralization and nitrification (both in situ and potential) in warmer, low elevation plots, in both summer and winter. In summer, this pattern appeared to be strongly driven by differences in soil moisture (lower soil moisture in warmer soils) and in winter the pattern was linked to differences in soil freezing (more soil freezing in warmer soils). Consistent with these results, levels of soil NO$_3^-$ and microbial biomass N were also lower in the warmer, low elevation plots. Denitrification potential, which is often limited by water and NO$_3^-$ availability in forest soils (Robertson and Tiedje 1984; Groffman and Tiedje 1989) was higher in the cooler, wetter, more N rich high elevation soils.
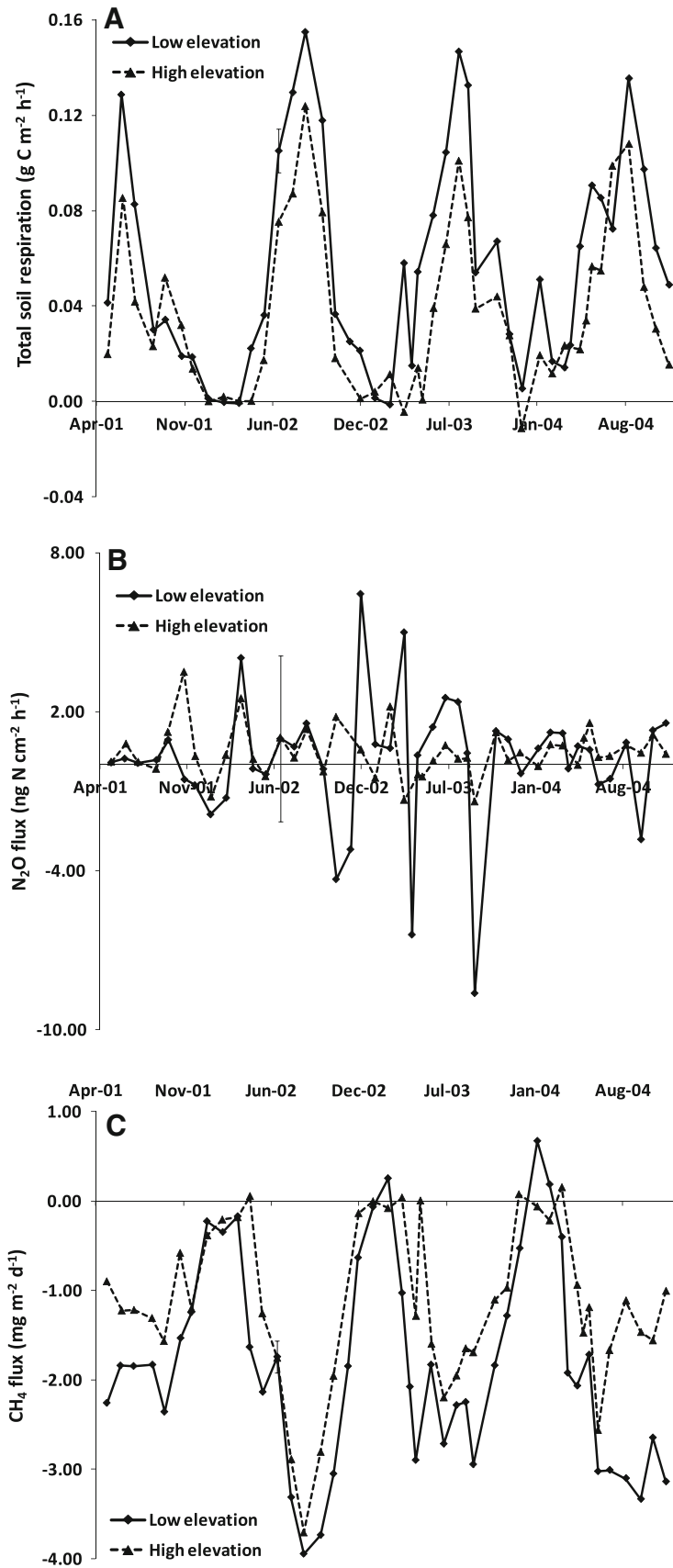
Figure 6. Soil: atmosphere fluxes of CO_2 (**A**), N_2O (**B**), and CH_4 (**C**) from Spring 2001 through Fall 2004. Values are means of two low elevation and two high elevation plots. Example error bars (June 2002) are shown to illustrate typical variability.

These data suggest that N cycling and supply to plants in these northern hardwood ecosystems will be reduced in a warmer climate due to changes in both winter (soil freezing) and summer (soil moisture) conditions. Winter changes in soil freezing have also been shown to accelerate hydrologic and (occasionally) gaseous N losses from these ecosystems (Fitzhugh and others 2001; Groffman and others 2006; Joseph and Henry 2008; Matzner and Borken 2008), which could exacerbate decreases in N supply to these ecosystems that are assumed to be N limited (Vitousek and Howarth 1991; LeBauer and Treseder 2008).

Many studies have shown growing season N mineralization and nitrification to be highly sensitive to soil moisture and temperature (Gilliam and others 2001; Knoepp and Swank 2002; Paul and others 2003). Results from a meta-analysis of experimental warming experiments at 32 sites showed that experimental warming in the range 0.3–6.0°C increased net N mineralization rates by 46% (Rustad and others 2001). However, consistent with our results, several recent studies in cool temperate climates suggest that moisture may be a more important driver of soil N cycling than temperature during the growing season (Morecroft and others 1992; Fernandez and others 2000; Bohlen and others 2001; Christ and others 2002; Bonito and others 2003; Venterea and others 2003; Johnson and others 2008; Griffiths and others 2009).

Over time, higher soil moisture conditions could lead to lowered soil N status due to increases in gaseous and hydrologic N losses. This does not appear to be the case at HBEF, where litterfall N also increases with elevation (Bohlen and others 2001) suggesting that plants are responding more to enhanced N availability than loss processes.

Our conclusion that winter soil N cycling and availability will be decreased in a warmer world relies on an increase in soil freezing in a warmer world with less snow. Winter microbial processes appear to be controlled by temperature, moisture, the availability of organic substrates, and the physiological potential of the microbial community (Monson and others 2006; Lipson 2007), all of which are affected by snow depth and soil freezing. Warmer winter temperatures allow for microbial production and consumption of N to go on simultaneously, and soil freezing reduces this activity (Grogan and Jonasson 2003; Schimel and Mikan 2005; Miller and others 2007; Kaste and others 2008; Matzner and Borken 2008; Stuanes and others 2008). In the present study, winter soil temperature was not a strong predictor of overwinter activity (data not shown). For example, overwinter temperatures were higher but overwinter mineralization was slower in the low elevation upper valley site than in the high elevation west site in both 2002/2003 and 2003/2004 (Table 2). Soil frost was consistently deeper, and overwinter mineralization and nitrification were consistently lower on the low elevation sites, suggesting that soil freezing is a stronger controller of overwinter activity than temperature. The ultimate effects of winter climate change on soil N cycling and availability at different sites will depend on the complex balance between temperature, snow cover and soil freezing discussed above.

One of our low elevation plots (lower valley) had slow net N mineralization and particularly slow net nitrification rates. Although we originally assumed that soils on this plot were the typical shallow (75–100 cm to a dense confining layer) Spodosols that dominate the landscape at HBEF, this plot appears to be located on a kame terrace with deeper, more freely draining sandier soils. In addition to having slow mineralization and nitrification, this plot had the lowest soil moisture levels. Interestingly, however, many variables (soil NH_4^+, microbial biomass, microbial, and total soil respiration) were not reduced on this plot relative to the other plots. If nitrification, which is a critical controller of hydrologic and gaseous N losses (Vitousek and others 1982), is particularly susceptible to drier soil conditions, then any reduction in internal N supply with climate change may be partially mitigated by increased competition for N that reduces nitrification and N losses. Results from this plot do not undermine the basic patterns of soil moisture and N cycling that we observed with elevation and climate. These patterns are supported by the much broader sampling (100 plots) done by Venterea and others (2003) and Bohlen and others (2001) at HBEF.

Annual rates of N mineralization (3.7–11.3 g N m^{-2} y^{-1}) and nitrification (from 0.2 to 5.4 g N m^{-2} y^{-1}) that we measured in 2002/2003 were similar to those reported for other, similar forest ecosystems, but the mineralization rates measured in 2003/2004 (7.1–19.1 g N m^{-2} y^{-1}) are high compared to other studies (Melillo 1977; Scott and Binkley 1997; Reich and others 1997; DeVito and others 1999; Ohrui and others 1999; Campbell and others 2000; Goodale and Aber 2001; Fisk and others 2002; Ollinger and others 2002; Joshi and others 2003; Jefts and others 2004; Latty and others 2004; Ste-Marie and Houle 2006; Zak and others 2006). It is important to note that our estimates include both the forest floor and the top

10 cm of the mineral soil, whereas many studies include little or no mineral soil activity. The rates and significant interannual variation reported here are similar to results for HBEF reported by Groffman and others (2001b) using the same methods.

Soil:Atmosphere Interactions in a Warmer World

Total soil respiration (TSR) was consistently faster in the warmer, low elevation plots. These results are consistent with a meta-analysis of experimental warming experiments that showed that experimental warming in the range 0.3–6.0°C increased soil respiration rates by 20% (Rustad and others 2001). However, the large increase that we observed (50% during the growing season) is somewhat surprising given recent analyses suggesting that humid temperate ecosystems like HBEF should not exhibit marked changes in TSR in response to changes in soil temperature and moisture of the magnitude observed in our field plots (Gerten and others 2008; Luo and others 2008).

The fact that microbial respiration was faster in the cooler high elevation plots might suggest that the increase in TSR that we observed was driven by increases in root respiration. The microbial respiration data were obtained in the laboratory, however, and therefore immediate temperature differences were not reflected in these measurements. Rather than suggesting that in situ microbial respiration was faster in the cooler, high elevation plots, our laboratory measurements likely reflected the long-term effects of altered site conditions on pools of labile C, which have been shown to be reduced by warmer soil temperatures (Rustad and others 2001; Melillo and others 2002; Bradford and others 2008; Garten 2008). Thus, it is likely that both root and microbial respiration were faster in the warmer, low elevation plots.

Our results are consistent with modeling analyses for the HBEF (Aber and others 1995) that predict significant increases in TSR with an increase in temperature. They are also consistent with laboratory studies (Koch and others 2007) showing that C mineralization is more temperature sensitive than N mineralization, making it reasonable for us to observe increases in C mineralization and decreases in N mineralization in warmer, drier soils. Fahey and others (2005) observed that TSR was only reduced at HBEF under extreme drought conditions and recovered quickly upon rewetting. It remains to be seen, however, how much of the increase in TSR that we observed was due to plant versus microbial processes. There may be important interactions between C and N cycle processes underlying this increase, for example, plants may be investing more resources belowground to obtain N in the face of reduced rates of net N mineralization (Finzi and others 2006). Overall increases in primary production associated with climate change may also underlie the increase in TSR (Shaver and others 2000; Piao and others 2008). The Rustad and others (2001) meta-analysis of warming experiments showed that experimental warming in the range of 0.3–6.0°C increased plant productivity by 19%. Any effects of warming on productivity will be complicated by the moisture and winter controls of N availability discussed above.

Similar to CO_2, CH_4 uptake was consistently faster in the warmer, low elevation plots. This uptake was likely stimulated by the low soil moisture on the warmer, drier low elevation plots as high soil moisture inhibits CH_4 diffusion to the microbes responsible for this process (Castro and others 1995; Borken and others 2006). Uptake may also have been inhibited by the relatively high soil N availability on the cooler, wetter high elevation plots (Steudler and others 1989; Mosier and others 1991).

It is somewhat surprising that we did not observe faster N_2O fluxes on the cooler, wetter more N rich high elevation plots as these conditions have been shown to increase these fluxes (Brumme and others 1999). However, these fluxes are notoriously variable (Parkin 1993) and it is thus difficult to establish differences with monthly sampling of a small number of sites.

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