Differential responses of soil CO_2 and N_2O fluxes to experimental warming

Junliang Zou[a,b,c,*], Brian Tobin[d], Yiqi Luo[b,c,e], Bruce Osborne[a,f]

[a] UCD School of Biology and Environmental Science, University College Dublin, Belfield, Dublin 4, Ireland
[b] Ministry of Education Key Laboratory for Earth System Modeling, Department of Earth System Science, Tsinghua University, Beijing, 100084, China
[c] Joint Center for Global Change Studies, Beijing, 100875, China
[d] UCD Forestry, School of Agriculture and Food Science, University College Dublin, Belfield, Dublin 4, Ireland
[e] Center for Ecosystem Science and Society, Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ, USA
[f] UCD Earth Institute, University College Dublin, Belfield, Dublin 4, Ireland

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ABSTRACT

Land-use conversions and elevated temperature can impact on carbon dioxide (CO_2) and nitrous oxide (N_2O) emissions, both of which are important greenhouse gasses (GHGs). Afforestation activity has increased significantly over the last century with a significant focus in recent years directed at offsetting GHG emissions, as forests have a large capacity to store carbon (C) and nitrogen (N) as well as affecting CO_2 and N_2O emissions. However, the impact of warming on GHG offsetting is unclear. This study was conducted in a forest and a grassland to investigate the effect of afforestation and warming, using infrared heaters, on soil fluxes of CO_2 and N_2O. Warming significantly increased the daily mean soil temperatures at a depth of 5 cm by 1.7 °C and reduced the soil moisture by ∼5% in the forest from March 2014 to February 2016. In the grassland, there were no significant increases in temperature and moisture with warming and no impact on the soil fluxes of CO_2 and N_2O. In the forest, elevated soil temperature enhanced the average soil CO_2 efflux by 23% but had no effect on soil N_2O fluxes. Warming decreased the temperature sensitivity by 13% and 23% at the forest and grassland, respectively. The soil fluxes of CO_2 increased exponentially with temperature and decreased linearly with the reduction in soil moisture, and were much larger in the grassland compared to the forest. However the grassland proved to be a larger sink for N_2O than the forest. Irrespective of warming treatments, all measured pools were significantly larger in the grassland compared to the forest. Our results imply that afforestation may have a bigger effect than warming on soil CO_2 and N_2O fluxes within the range of temperatures used and that afforestation dramatically lowers the inorganic, organic and microbial C and N pools, that could, in turn, impact on the responses of forest soils to future global warming.

1. Introduction

Anthropogenic emissions of carbon dioxide (CO_2) and other greenhouse gases (GHGs) have altered the global climate, causing temperatures to increase worldwide, with global air temperatures projected to increase by 1.8–6.4 °C by the end of the century. The pace of climate warming is also expected to accelerate with greater warming occurring in ecosystems at higher latitudes and altitudes but with significant although often overlooked regional variations (IPCC, 2013). Regional climate model simulations by Dunne et al. (2008), for instance, using different Atmosphere-Ocean General Circulation Models (AOGCM) with different emission scenarios, project that temperatures in Ireland will increase by 1.2–1.4 °C by mid-century, and up to 3.4 °C towards the end of the century, with the greatest warming taking place in the south and east of the country. These values are at the lower range of global estimates and emphasises the importance of using appropriate regional information to provide realistic assessments of the impacts of rising temperatures.

The gasses CO_2 and nitrous oxide (N_2O) contribute about 60% and 6%, respectively, of the global warming potential of all the GHGs (IPCC, 2013). As soils can switch between being sinks and sources of GHG emissions, depending on the prevailing conditions (Jungkunst and Fiedler, 2007), any changes could have a large impact on atmospheric concentrations of GHGs, as soils are a large store of C and N (1500 Pg organic C and 136 Pg total N; Batjes, 1996; Lal, 2003). Therefore, identification of the factors determining the net exchange rate of the two principal GHGs, CO_2 and N_2O, between the soil and atmosphere, as well as their responses to climatic warming, is an important global research topic. Information on soil CO_2 and N_2O emissions and their sensitivity to warming and land-use, will enhance our understanding of

ecosystem C and N cycling processes and improve our predictions of the response of ecosystems to global climate change (Fang et al., 2012; Merbold et al., 2014).

Soil warming is known to influence the emissions of CO_2 and N_2O (Luo et al., 2001; Zhou et al., 2012). Rising temperatures may alter the composition and activities of soil microbial communities, the quantity and quality of soil C input, N mineralization, as well as impacting on C and N cycling (Smith et al., 2002; Zhang et al., 2012) and hence CO_2 and N_2O emissions. Climate warming generally increases soil CO_2 efflux in many biomes (Rustad et al., 2001; Wu et al., 2011), however, the warming effects may disappear or reverse in the longer term depending on a range of factors including the soil moisture conditions (Schindlbacher et al., 2012). Climate warming may increase N_2O fluxes by accelerating N cycling, but it may also decrease the fluxes from partially anaerobic soils because of declining soil moisture content (Bijoor et al., 2008; Cantarel et al., 2012; Goldberg and Gebauer, 2009).

One of the measures often put forward to offset GHG emissions is the creation or enhancement of C sinks through afforestation and re-forestation activities. Forests are one of the major pools of terrestrial C stocks and consequently play an important role in the global C cycle (Lal, 2005). This is due to both the extensive global forest area, covering about 4.1 billion hectares of the global land surface (Luo and Zhou, 2006) and also because forests can sequester large amounts of C in tree biomass, harvested products and their associated soils (Raich and Tufekciogul, 2000). Afforestation activity has increased significantly over the last century. In Ireland up to about 0.74 million ha (DAFM, 2010), mainly through land-use conversion from grassland sites, has been forested. The Irish forest estate is dominated by coniferous plantations (Farrell et al., 2001), among which Sitka spruce [*Picea sitchensis* (Bong.) Carr.] is the main species, representing 53% of the total (DAFM, 2012). Replacing grassland with coniferous forest can result in a number of biogeochemical modifications (i.e. soil C and N cycles) that impact on GHGs fluxes (Benanti et al., 2014; Black et al., 2009). Given the increasing emphasis on the use of afforestation for C/GHG offsetting, it is important to understand how this change in land-use, in particular, responds to elevated temperatures.

Soil CO_2 and N_2O production is determined by microbial activities, soil microclimate conditions and the quality and quantity of C and N inputs associated with dead and decaying plant material (Huang et al., 2004; Schindlbacher et al., 2015; Wan and Luo, 2003). Land-use change may influence soil temperature and moisture (Xiao et al., 2014) and the types and amounts of C and N inputs via differences in vegetation productivity, changes in the supply/availability of C and N via root exudates, root turnover and the decomposition of contrasting litter inputs (Jin et al., 2014). In mineral soils CO_2 and N_2O emissions are likely to be positively related to the concentrations of soil C and N, as these are resources for microbial metabolism (Huang et al., 2004). Emissions of both CO_2 and N_2O will likely relate to labile soil C and N pools and increasing temperature, as metabolic reactions generally proceed more rapidly at higher temperatures. Land use change may also be associated with alterations in the number and diversity of microbial populations, which can have contrasting effects on the gaseous emissions of CO_2 and N_2O, as these are a result of independent soil and vegetation-related processes.

Differences in the effects of warming on ecosystems depend greatly on the initial conditions of that ecosystem, including hydrological factors, chemical and physical properties, the concentration of soil nutrients, microbial populations and vegetation production, as well as the chemical composition and turnover rates of plant residues (Deng et al., 2016; Shaver et al., 2000). The response of soil processes to warming will also be influenced by land-use differences (Luo et al., 2001). More information on soil responses to warming under different land-uses could therefore provide a better understanding of the effect of climate change on terrestrial ecosystems.

To address this question a field climate/warming manipulation experiment was carried out at adjacent grassland and afforested sites, to explore the impact of increased soil temperature and land-use conversion on soil fluxes of CO_2 and N_2O.

2. Materials and methods

2.1. Experimental sites

The field study area was located in Dooary Forest, Co. Laois, central Ireland (52°57′N, 7°15′W; altitude of 260 m). The climate of the study area is characterized as a cool temperate oceanic climate, the 30-year (1978–2007) mean annual temperature and precipitation at this site are 9.9 °C and 857 mm (Saunders et al., 2014). The establishment of the forest and its management is under the control of Coillte, a semi-state company involved in forest-based land management. The selected study forest was planted in 1988 on a previously unmanaged grassland, with a planting density of 2300 stems per ha and currently consists of even-aged stands of one main species, Sitka spruce. The size of the forest stand covers an area of 42 ha and is made up of two management compartments, which are 25.8 ha and 16.2 ha in size, respectively. The measurements for this investigation were conducted in the 25.8 ha stand in close proximity to an eddy covariance tower used for long-term (begun in 2002) measurements of C fluxes, biomass and climatic data, as part of a long-term forest C sequestration and greenhouse gas emissions study. Shallow surface drains were cut across the site prior to afforestation to improve soil drainage, site cultivation involved ripping lines every 2 m and trees were planted every 2 m to one side of a rip line; this resulted in trees being arranged roughly in a 2 × 2 m grid.

An adjacent grassland, approximately 700 m away from the forest site, was selected as a control of the land-use conversion comparison. The soil type and climate conditions for this land use were as similar as possible to the forest and this aided in the comparative assessment. The semi-natural grassland is privately owned by a local family, and the main ground vegetation species are presented in Table S1.

The dominant soil type in the area is a wet mineral soil classified as a low humic gley. The main soil properties for both sites are detailed in

Table 1
Soil properties in the forest and grassland site. Significant differences shown at * P < 0.05; ** P < 0.01. ns, not significant. Values are mean (SE). BD, bulk density; STC, soil total carbon; STN, soil total nitrogen; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; DOC, dissolved organic carbon; DTC, dissolved total carbon; DTN, dissolved total nitrogen; DON, dissolved organic nitrogen; NH_4^+, ammonium; NO_3^-, nitrate.

Variables	Unit	Forest		Grassland		Significance
BD	g cm^{-3}	0.83	(0.04)	0.78	(0.06)	ns
STC	%	4.22	(0.58)	7.05	(0.61)	*
STN	%	0.27	(0.01)	0.55	(0.01)	**
STC:STN	–	15.38	(1.69)	12.81	(0.92)	ns
MBC	mg kg^{-1} soil	983.94	(233.08)	3184.30	(464.34)	**
MBN	mg kg^{-1} soil	107.70	(26.98)	319.00	(56.47)	**
MBC:MBN	–	9.38	(0.75)	12.94	(2.04)	ns
DOC	mg kg^{-1} soil	317.41	(25.88)	497.77	(29.43)	**
DTC	mg kg^{-1} soil	318.32	(26.76)	503.39	(29.27)	**
DTN	mg kg^{-1} soil	70.76	(12.15)	109.9	(14.58)	P = 0.051
NH_4^+	mg kg^{-1} soil	6.51	(0.83)	14.17	(2.22)	**
NO_3^-	mg kg^{-1} soil	2.51	(1.06)	1.83	(0.50)	ns
DON	mg kg^{-1} soil	61.74	(11.56)	93.98	(14.69)	ns
pH	–	3.90	(0.12)	4.38	(0.10)	**
DOC:DON	–	6.67	(0.97)	6.92	(1.27)	ns
DTC:DTN	–	5.64	(0.80)	5.36	(0.66)	ns

Table 1.

2.2. Warming treatments

Infra-red heaters (IR, 165 × 15 cm, MSR-2420, Kalglo Electronics Inc., Bethlehem, PA, USA) were used to simulate the effects of climate warming in this study by raising the temperature of the air above the vegetation and soil continuously year-round. This approach has been used in a number of warming experiments, including long-term studies (Luo et al., 2010; Morin et al., 2010), extreme event simulations (Smith, 2011; Van Peer et al., 2004), night-time-only warming (Mohammed and Tarpley, 2009), and in various ecosystems, including grassland (Wan et al., 2002; Zhou et al., 2012), forest (Jarvi and Burton, 2013; Zhao et al., 2014), and cropland (Liu et al., 2016). Although the efficacy of IR heaters under turbulent air conditions may be reduced, and the power consumption cost is rather high, this method of heating was used to better represent natural climate warming where ambient air temperatures transfer to the rest of the ecosystem, including soil, in an even manner and without artificial disturbance. Although other forms of heating the experimental area, such as soil-based heaters, were considered these would have been difficult to implement due to the extensive belowground biomass and would have involved considerable disturbance to the system, as well as resulting in an unrealistic pattern of heat distribution through the soil.

2.3. Experimental design

Three pairs of 2 × 2 m plots (n = 3) were located in the forest and grassland sites. One plot was warmed (W) continuously using IR heaters and the other, a control (C), was exposed to ambient conditions. Individual IR heaters were suspended 1.2 m above the ground in each warmed plot. Based on continuously monitoring soil temperature with a pre-experiment on grassland at UCD Rosemount Environmental Research Station from May 2013 to August 2013, an output of around 1000 W could lead to an increase in soil temperature of approximately 2 °C. Therefore, heaters were turned on continuously (day and night) from 18th Dec 2013 in both sites and set at outputs of approximately 1000 W radiation to raise the soil temperature at 5 cm depth by approximately 2 °C. Given the inability, with the experimental layout and heaters available, to implement a significant warming increase of more than 0.33 °C in the grassland, this was stopped after one year. This was most likely due to the windy conditions that reduced the efficacy of the heaters. Therefore, no data associated with warming was available in the grassland after 2014. With a similar arrangement, temperature increments generated by the heaters were proved by Wan et al. (2002) to be relatively even over the entire area of each warmed plot. In the control plot, one 'dummy' heater made of aluminum with the same shape and size as the IR heater was suspended at the same height, in order to simulate the shading effects of the heater. For each paired plot, the distance between the control and the warmed plot was at least 5 m to avoid indirect heating.

2.4. GHG flux measurements

The CO_2 and N_2O fluxes were measured approximately bi-weekly using a 1412 Photoacoustic Field Gas Monitor (PAS, INNOVA Air Tech Instruments, Ballerup, Denmark). In the forest, measurements for both the C and W treatments were taken from March 2014 to February 2016. Whilst in the grassland, measurements for the C treatment were taken from March 2014 to February 2016, and measurements for the W treatment were taken from March 2014 until warming was stopped in December 2014. The PAS was connected to a static chamber (16 cm-inside diameter, 16 cm in height) placed on top of a permanently installed collar in each plot via 6 m plastic tubing of 3 mm diameter allowing access to all plots at either the forest or grassland site. In this method, six collars (16 cm outside diameter, 5 cm in height) were inserted into the soil, at each of the two sites, to a depth of 3 cm in the O horizon, and these kept clear of vegetation for the duration of the experiment. Before the actual flux measurements, ambient air was sucked into the PAS for about 30–40 min, until the readings for CO_2 and N_2O concentrations were stabilized. For each flux measurement, 5–6 PAS readings were taken in order to calculate the flux rate, which took approximately 8 min. Two additional readings of ambient air were also taken after the chamber was opened in between the chamber flux measurements for about 2 min. Therefore, the total time required per plot was around 10 min excluding the time required to move from one plot to the next.

2.5. Calculation of emission rates

GHG emission rates were calculated from the change in GHG concentration with time (slope in ppm GHG s^{-1}). Linear regression of GHG concentration against time was used to generate the slope. Flux rates were calculated from the linear increase or decrease in gas concentration over time for each chamber. Quality checks were applied for all flux measurements: thus for N_2O, the R^2 value of the linear regression analysis had to be larger than 0.7, and 0.9 for CO_2, otherwise the data were discarded (Unteregelsbacher et al., 2013). Emission rates in ppm GHG s^{-1} were converted to µmol GHG m^{-2} s^{-1} or mg GHG m^{-2} d^{-1} using the following equation.

$$\mu mol\,GHG\,m^{-2}s^{-1} = \frac{ppm\,GHG\,s^{-1} \times P \times V}{\frac{R}{1000} \times T \times A} \tag{1}$$

Where,

P = barometric pressure e.g. 1 atm

T = air temperature within the enclosure during sampling in K (K = °C + 273.15)

R = the universal gas constant (0.0820575 L atm./K mol)

V = the internal volume of the chamber (enclosure) (m^3)

A = the soil area enclosed by the chamber (m^2)

2.6. Environmental monitoring

At the center of each plot, air temperature and relative humidity were monitored using a HC2S3-L probe (Campbell scientific Inc., UK) at the height of 25 cm above the ground. The probes were put into PVC tubes with open ends (20 cm in length, 5 cm in diameter) which were horizontally fastened on wood stacks, through a small hole at the middle part and positioned. During gas sampling measurements, soil temperature and moisture at 5 cm depth were also determined using a portable sensor (WET sensor Delta-T Devices Ltd, Burwell, Cambridge, UK). An eddy covariance (EC) tower deployed on the same site was equipped with a meteorological station, so that other parameters, such as precipitation and wind speed at the time of sampling, were also available.

2.7. Soil sampling and analysis

Soil samples (n = 3) were collected at 0–10 cm depth, in close proximity to each chamber and subsequently mixed well to generate one composite sample. Each composite sample was passed through a sieve (4 mm diameter), so that any visible living plant materials and stones could be removed. The sieved soil was stored in a cold room at 4 °C prior to the analysis of labile soil C and N concentrations and microbial C and N. A subsample of each soil was air-dried and ground (< 250 µm) prior to further physical and chemical analysis.

Soil bulk density (BD) was determined using ring excavation (Grossman and Reinsch, 2002) with steel rings of known volume (100 cm^3) for this study. Total soil C and N concentrations were measured on 0.1 g soil samples, previously air dried and ground, using a CHN analyser (TrueSpec®, Leco Corporation, St. Joseph, USA). Soil pH

was measured using water extracts (Hendershot and Lalande, 1993) with a pH meter/probe (Thermo Fisher Scientific Inc., Waltham, Michigan, USA) with a 1:2.5 dry soil/water ratio. Soil mineral N, ammonium (NH_4^+) and nitrate (NO_3^-) concentration, and dissolved C and N were determined on 5 g samples of fresh soil based on a 2 M KCl solution extraction procedure (Maynard and Kalra, 1993). Soil ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were measured using a nutrient analyser (Lachat Quickchem®, 5600 Lindbergh Drive, Loveland, Colorado, USA). A sub-sample of the extracts was used to determine dissolved C and N concentrations with a TOC/TN analyzer (TOC-V Shimadzu Corp. Tokyo, Japan). The C and N concentrations in K_2SO_4 extracts (10 g dry weight equivalent soil/50 ml solution) of fumigated and non-fumigated soils were measured using the TOC/TN analyzer and MBC and MBN concentrations calculated by the differences between fumigated and non-fumigated samples divided by a factor of 0.45 (Wu et al., 1990).

2.8. Litter decomposition

Litter decomposition rates were determined using the litter bag method described by Robertson (1999). Although there are limitations associated with this method, such as the choice of mesh size (loss of material or exclusion of macrofauna), and modifications to the microclimate within the litter bag, this method is still the most widely used.

Sitka spruce litter samples from the forest site and above-ground grass material from the grassland were collected in October 2013, and then weighed (after drying at 65 °C for 48 h) into litterbags. After weighing, subsamples of the initial litter material for each litter type were milled, and measured for original C and N contents using the CHN analyzer.

The litter bags (approximately 8 × 8 cm dimension) were made of polyester curtain netting with a mesh size of 0.2 × 0.6 mm. This mesh size should allow most fungi, bacteria and soil organisms to colonize the litter materials but exclude larger organisms such as isopods and earthworms. All the bags were sown together using nylon thread. The bags were numbered using a permanent marker pen and weighed before they were filled with between 2.5 g and 9.0 g of plant material. The initial weights of the litter-bag contents were recorded for future use.

On 18th December 2013, the litter bags containing Sitka spruce needles and grass were anchored to the soil with iron wire to ensure firm contact with the surface. Ten bags of each litter type were placed on the soil surface of each of the three forest and grassland plots, respectively. A total of 120 bags were used in the study (2 sites × 2 treatments × 3 plots × 10 bags). The litter bags were sampled six times through 2013/2014 at approximately two month intervals. After the litter bags were collected, they were gently scraped to remove surface debris, dried at 65 °C for 48 h, and then brushed lightly to remove remaining debris. The dry mass of the contents of each litter-bag was then measured.

Specific decomposition rates (k) were determined by fitting an exponential function to data of the mass remaining after decomposition time (Olson, 1963) as:

$$\ln(\frac{M_t}{M_0}) = -kt + c \tag{2}$$

Where M_t is the mass remaining at time t, M_0 is the initial mass, t is the time in years, k is the decay constant, c is the intercept of the regression. This model was used to calculate one specific decomposition rate, k, for each species under each treatment.

2.9. Data analysis

The relationships between the soil fluxes of CO_2 ($\mu mol\, m^{-2}\, s^{-1}$) and soil temperature (T, °C) was analyzed using the following exponential model:

$$CO_2 = a \exp^{bT} \tag{3}$$

Where the coefficient a is the value of CO_2 at 0 °C, and coefficient b is the sensitivity of CO_2 to T.

The temperature sensitivity of CO_2 (Q_{10}), which is the relative increase in CO_2 for a 10 °C increase in T, for each treatment, was calculated using the coefficient b:

$$Q_{10} = \exp^{10b} \tag{4}$$

Where b is the regression coefficient in Eq. (3).

To correct for differences caused by differing temperature increases in each year and at each site the warming effect was normalized to provide a value per 1 °C increase by dividing the estimate by DT, which was the mean temperature increase each year at an individual site.

A one-way analysis of variance (ANOVA) was used to test warming effect at each site on CO_2 and N_2O fluxes, soil temperature and soil moisture. And one-way ANOVA was used to test the difference of soil variables and soil fluxes between the two sites. The assumption of normality of the residuals was tested by examining normal probability plots and stem-and-leaf plots of the residuals. The homogeneity of variances assumption was assessed visually by examining the side-by-side box plots and checked using Levene's test for equal variances. Regression analysis was used to investigate relationships between soil CO_2 and N_2O fluxes, soil temperature and soil water content. The effects were considered to be significantly different if P < 0.05. All these statistical analyses were performed using SAS software v9.3 (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Warming effects on soil microclimate at the forest and the grassland

Soil temperature and soil moisture at 5 cm depth showed a pronounced seasonal trend at both sites with higher values, as expected, during the warmer periods of the year (Fig. 1e–h). At the forest, warming increased soil temperature, on average, by 1.7 °C over the study period (P < 0.05, Fig. 1e, Table 2). In response to warming, the mean soil moisture declined significantly by ~5% (P < 0.05, Fig. 1g and Table 2). At the grassland, mean soil temperature at 5 cm depth was 0.3 °C higher in the warmed plots than control plots over the warming period in 2014, but the difference was not statistically significant. Accordingly, mean soil moisture was not changed significantly by warming (P > 0.05, Fig. 1f and h and Table 2).

3.2. Warming effects on CO_2 fluxes at the forest and the grassland

Soil CO_2 efflux exhibited a similar pronounced seasonal trend as soil temperature between March 2014 and February 2016, with mean values in the control plots ranging from 0.22 $\mu mol\, m^{-2}\, s^{-1}$ to 4.62 $\mu mol\, m^{-2}\, s^{-1}$ and 0.47 $\mu mol\, m^{-2}\, s^{-1}$ to 7.35 $\mu mol\, m^{-2}\, s^{-1}$ for the forest and grassland sites, respectively (Fig. 1a and b). The soil CO_2 efflux in the warmed forest plots increased significantly by 21, and 23% in comparison to the control plots in 2014 and 2015, respectively. However, warming only marginally increased the flux rates by 5% at the grassland in 2014 (P = 0.111, Fig. 1b and Table 2). Averaged across the study period from 2014 to 2016, the CO_2 emissions were 3.26 ± 0.12 $\mu mol\, m^{-2}\, s^{-1}$ in the grassland control plots, which was more than double the emissions of 1.59 ± 0.08 $\mu mol\, m^{-2}\, s^{-1}$ in the forest control plots (Table 2).

A significant negative relationship between CO_2 efflux and soil moisture was found throughout the experimental period, while a significant positive relationship between CO_2 efflux and soil temperature was found at both sites (Fig. 2). At a given soil temperature, soil CO_2 effluxes were higher in the warmed plots than in the control plots and soil CO_2 efflux increased exponentially with soil temperature at 5 cm depth for both warmed and control plots (Fig. 2a and c). At the forest,
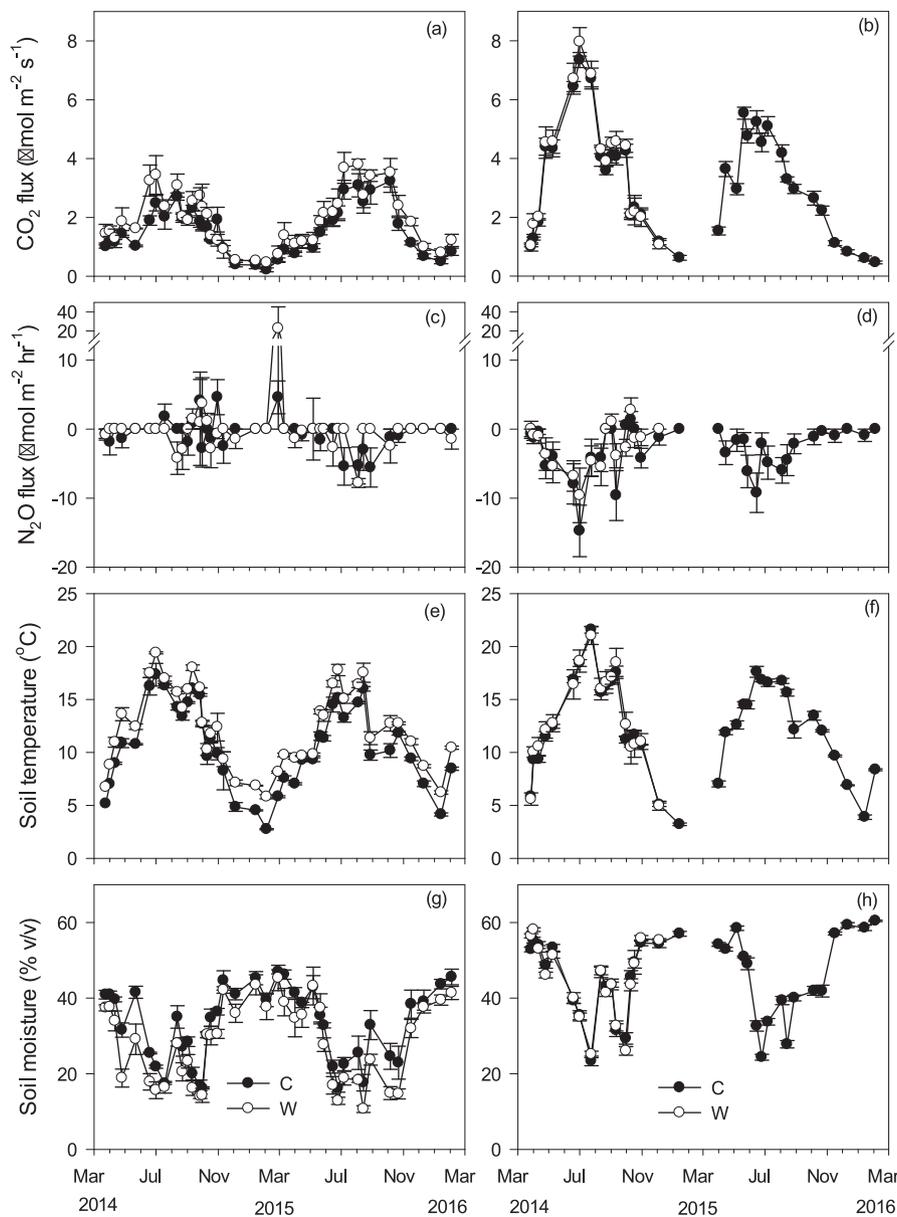
Fig. 1. Seasonal variations of CO_2 and N_2O fluxes, soil temperature, and soil moisture in the forest (a, c, e, g) and the grassland (b, d, f, h). Vertical bars represent the standard error of the mean (n = 3). C, control; W, warming.

the corresponding Q_{10} value in the control plots was 3.87 over the course of the experiment, being 13% higher than the warmed plots (Fig. 2a). Whilst at the grassland, the apparent Q_{10} values decreased by 23% from 4.33 in the control plots to 3.32 in the warmed plots (Fig. 2c).

3.3. Warming effects on N_2O fluxes at the forest and the grassland

There were periods when both positive and negative fluxes of N_2O were observed at the forest (Fig. 1c). In comparison negative fluxes of N_2O were generally found for the grassland soils, but with small

Table 2
Mean ± SE of soil temperature (T), soil moisture (M) and soil CO_2 and N_2O fluxes during the whole study period and separately for 2014 at both sites. Note that warming was only applied for one year (2014) at the grassland site. Data with different lowercase letters between control and warming indicate significant differences (P < 0.05). Note that the values for temperature and moisture were obtained from manual measurements.

Site	Year	Treatment	T	M	CO_2	N_2O
Forest	2014–2016	C	10.69 ± 0.36 a	32.56 ± 0.94 a	1.59 ± 0.08 a	−0.499 ± 0.290 a
		W	12.37 ± 0.34 b	27.66 ± 1.00 b	1.95 ± 0.10 b	0.031 ± 0.650 a
	2014	C	11.70 ± 0.51 a	30.98 ± 1.26 a	1.63 ± 0.08 a	−0.007 ± 0.404 a
		W	13.12 ± 0.49 b	25.81 ± 1.23 b	1.98 ± 0.12 b	−0.302 ± 0.467 a
Grassland	2014–2016	C	12.70 ± 0.29	44.97 ± 0.73	3.26 ± 0.12	−3.011 ± 0.364
	2014	C	13.19 ± 0.47 a	44.23 ± 1.06 a	3.50 ± 0.20 a	−3.470 ± 0.635 a
		W	13.52 ± 0.45 a	44.15 ± 1.05 a	3.97 ± 0.22 a	−2.604 ± 0.539 a
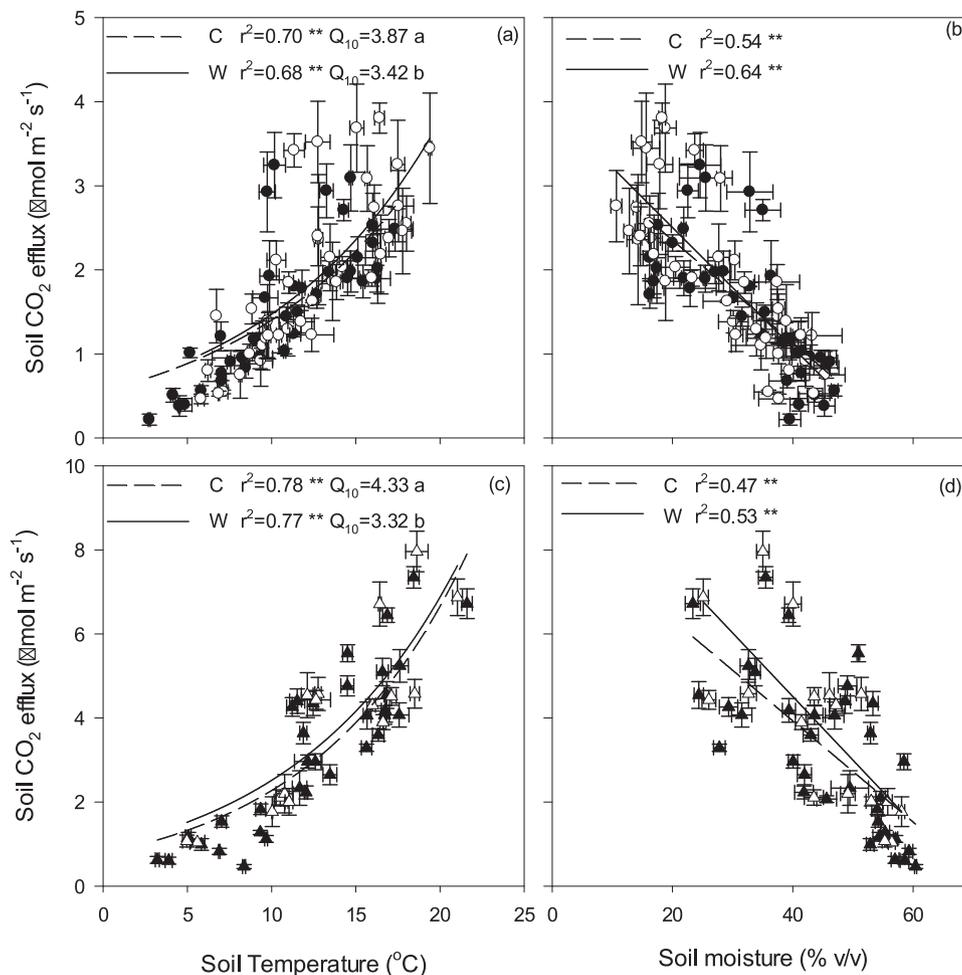
Fig. 2. Relationships between soil CO_2 flux, soil temperature (T) and soil water content (M) in the forest (circle) and the grassland (triangle). Vertical and horizontal bars represent the standard error of the mean (n = 3). ** Regression models are significant at P < 0.01, Q_{10} values with different lowercase letters indicate significant difference at P < 0.05. C, control (solid symbols); W, warming (open symbols).

emissions of N_2O observed on several dates. The highest uptake of N_2O was in summer, around July. During winter, the N_2O fluxes fluctuated close to zero (Fig. 1d). Experimental warming did not significantly affect N_2O fluxes across the study period at both sites (P > 0.05, Fig. 1c and d and Table 2). No obvious relationship was found between N_2O fluxes and soil temperature and soil moisture on an annual basis at the forest. However, N_2O fluxes at the grassland showed a positive relationship with soil moisture and a negative relationship with soil temperature (Fig. 3).

3.4. Warming effects on cumulative soil CO_2 and N_2O fluxes at both sites

Fig. 4 shows the cumulative soil CO_2 efflux in the control and warmed plots at the forest and grassland from March 2014 to December 2014 (2014) and from March 2014 to February 2016 (2014–2016). In 2014, cumulative soil CO_2 fluxes were 437.9 and 1068.2 g C m^{-2} for the control plots at the forest and grassland, respectively. Soil warming ($\sim 1.4\,^{\circ}$C) increased cumulative flux of CO_2 by 18.0% (P = 0.053) at the forest, and soil warming ($\sim 0.3\,^{\circ}$C) increased the cumulative flux of CO_2 by 7.8% (P = 0.161) at the grassland. During 2014–2016, cumulative soil CO_2 fluxes were 1071.6 and 2030.7 g C m^{-2} for the control plots at the forest and grassland, respectively. Warming ($\sim 1.7\,^{\circ}$C) increased forest cumulative CO_2 flux by 19.4% (P = 0.097). Cumulative soil N_2O fluxes were 21.0 and -366.6 mg N m^{-2} during 2014 and -113.6 and -676.2 mg N m^{-2} for the control plots at the forest and grassland, respectively. No obvious effects of warming on cumulative

N_2O fluxes were observed.

4. Discussion

Unlike many soil warming studies, which only examined warming effects in a single ecosystem, this study investigated warming effects at two adjacent and contrasting sites (a Sitka spruce forest and a grassland) on similar soils, to assess how increasing temperature affects soil processes in different ecosystems under comparable conditions. Greenhouse gas fluxes from cool-temperate ecosystems, such as the forest and grassland ecosystems used in the current study, are assumed to be particularly sensitive to projected future climate warming (Sturtevant and Oechel, 2013; Zhuang et al., 2007). In this study, IR heaters increased the mean air temperature by $\sim 0.8\,^{\circ}$C and the mean soil temperature by $\sim 1.7\,^{\circ}$C in the forest plantation during the three years from 2014 to 2016. Unfortunately, the air temperature sensors were damaged by wildlife in the grassland from the early stage of the experiment, thus only soil temperature was monitored in this ecosystem. Also IR heaters only elevated the mean soil temperature by $\sim 0.3\,^{\circ}$C on average in 2014 in the grassland. Given the inability, with the heaters available, to implement a significant warming increase of more than 0.3 °C in the grassland, this was stopped after one year. Therefore, no data associated with warming was available in the grassland after 2014. Soil temperature in the open grassland site did not respond to the same degree to warming as the more sheltered forest plots. Wind was probably the more significant factor making it difficult
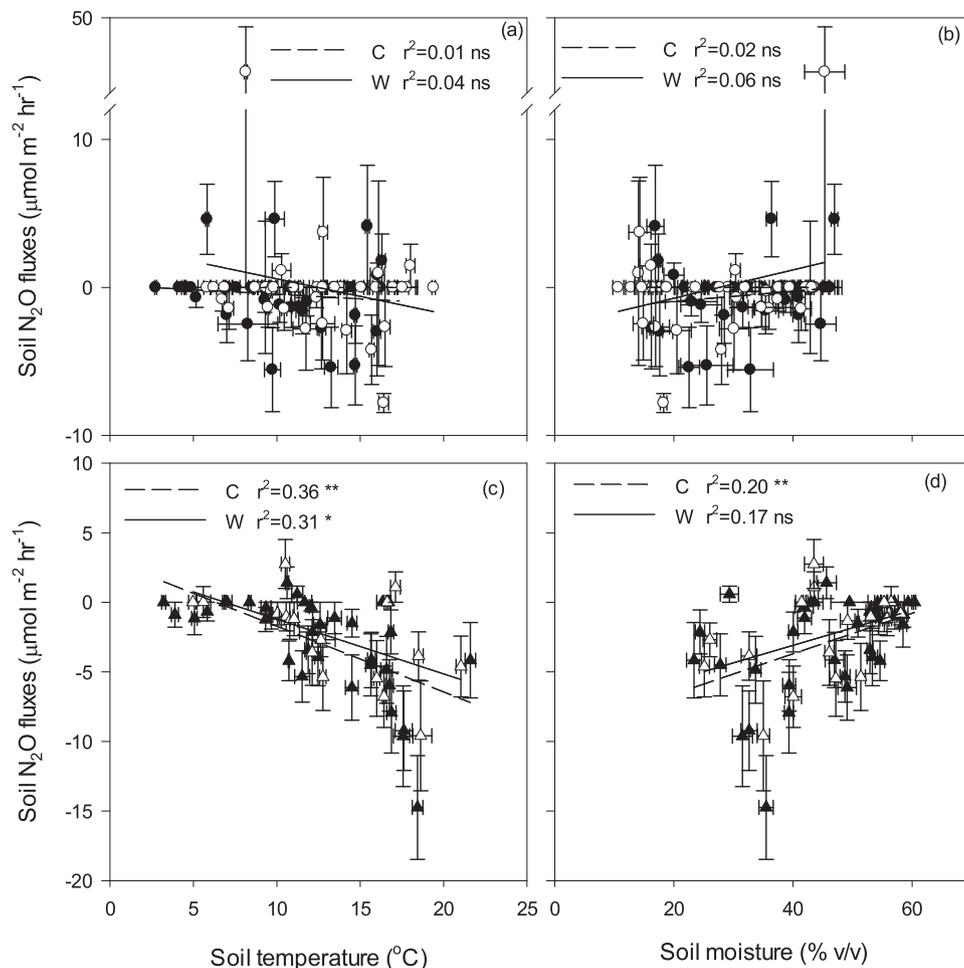
Fig. 3. Relationships between soil N_2O flux, soil temperature (T) and soil water content (M) in the forest (circle) and the grassland (triangle). Vertical and horizontal bars represent the standard error of the mean (n = 3). Regression models are significant at $P < 0.01$, **, $P < 0.05$, *, ns = not significant. C, control (solid symbols); W, warming (open symbols).

for the radiated heat to penetrate the grass vegetation and reach the soil (De Boeck and Nijs et al., 2011; Kimball et al., 2008; Wan et al. 2002). More evaporative cooling under grass could also have been another reason that temperatures did not increase as much as in the forest. These factors made the grassland warming treatment less effective than in the forest where there was a closed canopy of trees that reduced any effects due to wind, and where there was little/no understory vegetation and a somewhat lower soil moisture content. The different vegetation types and the implementation of comparable warming treatments was a considerable constraint in many experimental manipulations directed at elevating temperature under field conditions, as well as differences in the microclimatic conditions. Therefore, it may be necessary to introduce systems that regulate the warming in relation to the ambient temperatures, which have been used in some studies (Braun et al., 2002; Lin et al., 2011; Marchand et al., 2004; Mohammed and Tarpley, 2009; Morin et al., 2010; Sherry et al., 2008; Wan et al., 2002), although these are more complex and difficult to implement in remote locations.

In addition to the practical difficulties of implementing consistent warming effects, both in contrasting ecosystems and on an annual basis, a number of studies have also shown that warming lowers the soil moisture content and this effect also needs to be taken into account (Allison and Treseder, 2008; Luo et al., 2001; Rustad et al., 2001). For example, a 2.0 °C increase in temperature decreased soil moisture by 6.4% in a tall grass prairie (Luo et al., 2001). In the current study warming-induced reductions in soil moisture content differed by land cover with a ~5% decrease in the forest and a < 1% decreases in the

grassland, again reflecting ecosystem specific effects, related in part to the degree of warming. However, because the soil moisture content was very high, due to frequent rainfall in the study area and a high water table, soil moisture consistently remained at > 20% in the warmed plots over the growing season, indicating that any warming-related impacts on soil water availability are unlikely to have had a significant impact on belowground processes.

An increase in soil CO_2 efflux in response to warming has been observed in various ecosystems (Rustad et al., 2001; Wu et al., 2011). The warming-related increase in soil CO_2 emissions during the experimental period in the forest was consistent with these finding. The average increase in soil CO_2 efflux due to warming (~1.7 °C) during the first two years (23%) in the current study was at the lower end of the range (24–76%) found in other soil warming experiments conducted in various forest ecosystems (Bronson et al., 2008; Hagedorn et al., 2010; Melillo et al., 2002; Peterjohn et al., 1994; Rustad and Fernandez, 1998; Schindlbacher et al., 2009), but was much higher than the reported 12% mean increase obtained in a recent meta-analysis, where the temperature increase was normalized to 2 °C across all biomes during the early warming years (Wang et al., 2014). As warming presumably did not alter labile C and N and had no effect on tree growth (data not shown), the observed increases in emissions are likely to be due more to a direct stimulation of litter decomposition rate (Fig. 5). This is not consistent with other studies where increased CO_2 efflux was reported to be due to an enhanced oxidation of labile soil carbon compounds in warmed plots (Lin et al., 2001; Peterjohn et al., 1993). Whilst significant increases in temperature or reductions in soil moisture were not
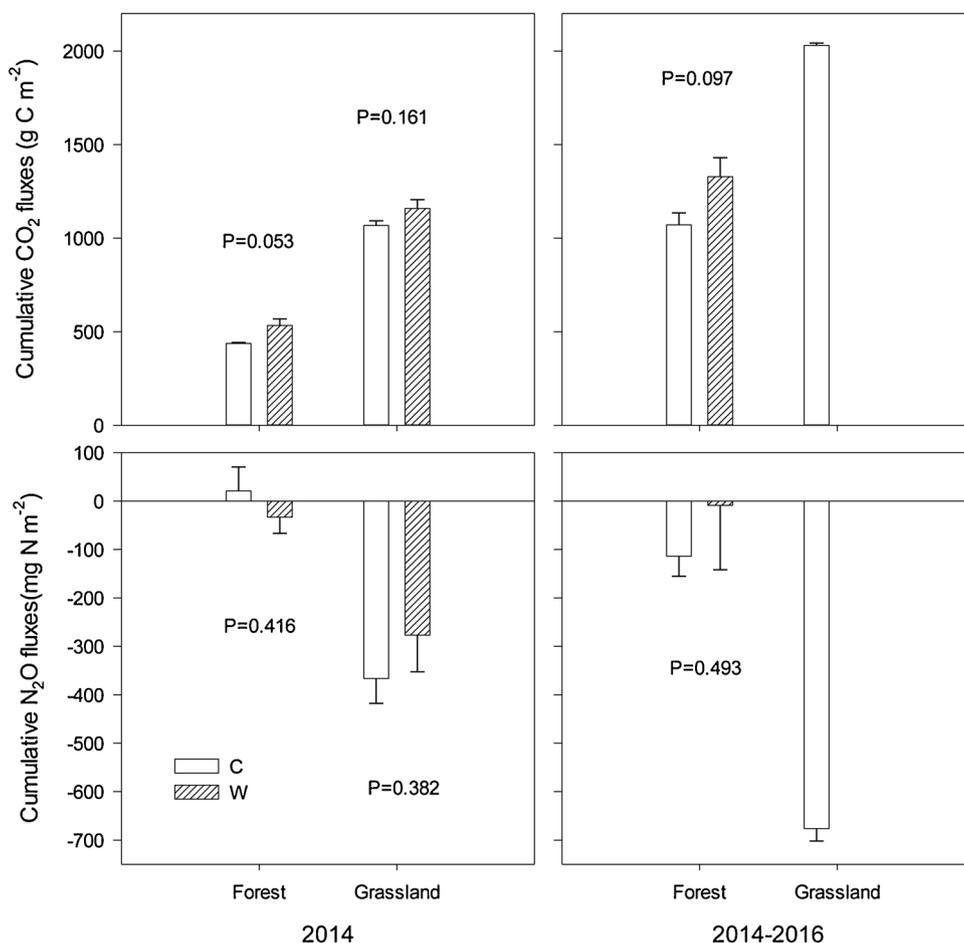
Fig. 4. Estimated cumulative fluxes of CO_2 across the study period. Vertical bars represent the standard error of the mean (n = 3). Treatments: C, control; W, warming.

found in the grassland because of technical limitations, there was a marginal stimulation of CO_2 emissions by warming (Fig. 4). Expressing these results on a per degree basis indicated that the stimulation of CO_2 emissions by warming was ∼15%, which is comparable to previously published studies on grassland (7–13%, Table 3; Graham et al., 2014; Peng et al., 2014; Peng et al., 2015; Wan et al., 2005; Zhou et al., 2006;

Zhou et al., 2007).

Soil temperature and moisture are often considered the most important factors controlling soil CO_2 fluxes (Rustad et al., 2000). A variety of warming treatments have been reported to generally increase soil CO_2 efflux, but some studies have also reported unchanged soil CO_2 effluxes or even a decreased soil CO_2 efflux, depending on plant cover
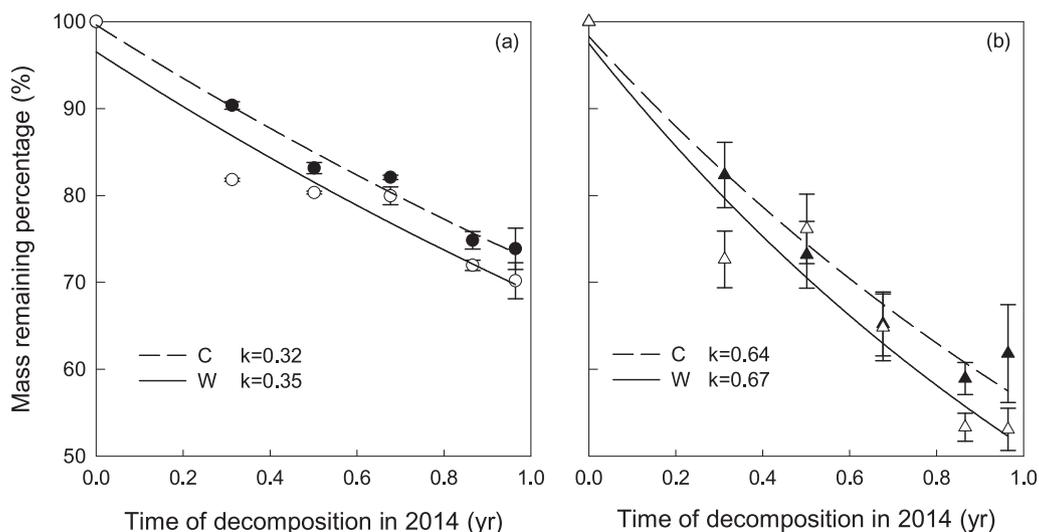
Fig. 5. Litter biomass remaining (%) and estimated annual decomposition rate of litter from the forest (a), and the grassland (b) among treatments. Vertical bars represent the standard error of the mean (n = 6). C, control; W, warming.

Table 3
Change in soil CO_2 emissions, soil temperature, and normalized soil CO_2 emissions of comparable warming experiments in forest and grassland ecosystems. NS indicates where soil CO_2 emissions were not significantly affected by warming.

Biome	Duration	Years	ΔT (°C)	ΔCO_2 (%)	$\Delta CO_2/\Delta T$	Reference
Black spruce	Jun–Oct	2004–2005	3.8	15.82	4.16	Bronson et al., 2008
Black spruce	Jun–Jul	2001–2002	0.9	20	22.22	Bergner et al., 2004
Scots pine	May–Oct	1997–2000	5	34.75	6.95	Niinistö et al., 2004
Red spruce	May–Nov	1993–1995	5	25	5	Rustad and Fernandez, 1998
Norway spruce	Apr–Nov	2008–2010	3.93	34	8.65	Schindlbacher et al., 2012
Dragon spruce plantation	May–Oct	2009	0.61	10.6	17.38	Xu et al., 2010
Spruce-fir-dominated natural forest	May-Oct	2009	0.56	15.4	27.5	Xu et al., 2010
Sitka spruce plantation	All year round	2014–2016	1.7	23	13.8	Current study
Semi-natural grassland	Mar–Dec	2014	0.3	5	15.2	Current study
Meadow grassland	Apr–Oct	2011–2013	1.03	ns	ns	Chen et al., 2016
Tussock grassland	Aug 2009–Oct 2011	2009–2011	3.1	41	13.23	Graham et al., 2014
Bromus japonicus Thunb.- dominated prairie	Jan 2010–Dec 2012	2010–2012	3.2	ns	ns	Li et al., 2013
Temperate desert steppe	Jul 2011–Aug 2012	2011–2012	2.87	ns	ns	Liu et al., 2015
Cottongrass tussock tundra	Field season	1995–1996	1.8	ns	ns	Oberbauer et al., 1998
Alpine meadow	May–Sep	2012–2013	1.78	17	9.58	Peng et al., 2014
Alpine meadow	All year round	2011–2013	2.32	21.5	9.27	Peng et al., 2015
Subalpine meadow	End of snow melt to mid Aug	1993–1994	0.78	−7.3	−9.41	Saleska et al., 1999
Tallgrass prairie	Jan–Dec	2001	2.2	15.6	7.09	Wan et al., 2005
Managed fescue field	Jun 2003–Dec 2004	2003–2004	1.45	ns	ns	Wan et al., 2007
Old-field tallgrass prairie	All year round	1999–2005	1.4	9	6.43	Zhou et al., 2007
Old-field tallgrass prairie	All year round	2003	1.48	13	8.78	Zhou et al., 2006
Old-field tallgrass prairie	All year round	2002–2004	2.735	22.9	8.37	Zhou et al., 2006

and climatic conditions (Rustad et al., 2001). The positive response of soil respiration to warming in the forest is broadly consistent with other warming manipulation studies conducted in similar coniferous forests (Table 3). However, as it is difficult to make direct comparison with other studies due to differences in the degree of warming, we normalised all the values to a 1 °C temperature increase. A 13.8% stimulation per degree warming falls well within the reported range 4.2%–27.5%, and is similar to the average value 13.1% among the comparable forests reported in Table 3. In contrast, warming experiments conducted in grasslands show variable results, including warming-related increases, no effect, or even a decrease in soil CO_2 emissions (Table 3). Further information on comparable forests and grasslands are available in Table S2.

This study demonstrated that warming can decrease the temperature sensitivity of soil CO_2 efflux (Fig. 2a and c). Previous studies have demonstrated that the temperature sensitivity of soil respiration (the increase in soil respiration per 10 degrees centigrade; Q_{10}) was negatively impacted by an increase in temperature (Luo et al., 2001; McHale et al., 1998; Niinistö et al., 2004; Strömgren, 2001; Wang et al., 2008; Xu and Qi, 2001; Zhou et al., 2006). Our results partly support this conclusion as the Q_{10} values were relatively smaller in the warmed treatments compared with the control. This is likely due to warming-induced soil drying which can offset some of the positive effects of warming (Allison and Treseder, 2008; Lellei-Kovács et al., 2008). It has also been found that soils with a low carbon content may have a lower temperature sensitivity (Luo et al., 2001; Pang et al., 2015). The temperature sensitivity was observed to be significantly greater in the grassland than in the forest, which may be a reflection of the fact that all measured soil C pools (including total soil C, DOC, and MBC) were larger in the grassland compared to the forest.

The present study found that the effects of soil temperature on CO_2 efflux could be described with a simple exponential regression model for both the warmed and control plots (Fig. 2a and c), consistent with a number of studies (Briones et al., 2004; Laganière et al., 2012; Shi et al., 2012; Zimmermann et al., 2009). Variations in soil temperature are one of the most important factors determining the seasonal variations in soil CO_2 efflux (Yuste et al., 2003), although water availability can also have a strong effect (Carbone et al., 2011; Moyano et al., 2013; Tang et al., 2006). Additionally, the relationship between soil CO_2 efflux and soil water content could be site-specific and no single model type that has quantified this relationship have been widely accepted (Davidson

et al., 1998; Peng et al., 2009). In this study, a significant negative correlation between CO_2 efflux and soil water content was found (Fig. 2b and d). Linear regression analyses could account for 51%, 53%, and 57% of the variability of CO_2 flux when the model included soil temperature (alone), soil water content (alone), and soil temperature and soil water content together, respectively, for the forest site. Similarly, linear regression analyses accounted for 66%, 37%, and 66% of the variability of the CO_2 flux when the model included soil temperature (alone), soil water content (alone), and soil temperature and soil water content, respectively, for the grassland. However, the lower impact of water at the grassland site could be linked to the higher water content in situ with relatively smaller seasonal variations in this open site. The combined effects of these two factors were additive, probably because higher temperatures may often lead to lower soil water content and vice versa (Davidson et al., 1998).

Seasonal fluxes of N_2O from different ecosystems are often highly variable, ranging from net uptakes to net emissions (Dijkstra et al., 2012), even in the same ecosystem (Benanti et al., 2014; Brummell et al., 2012). Similar results were found in the present study with both ecosystems switching intermittently between sinks and sources of N_2O during the study period. No significant warming effects were found for N_2O fluxes in this study, which is in agreement with another comparable study (Unteregelsbacher et al., 2013). Whilst the absence of any significant impact of warming on N_2O emissions at the grassland site is likely to be due to non-significant temperature increases, there was no evidence of any increases in N_2O at the forest site where warming resulted in significant increases in temperature/reductions in soil moisture. This indicates that other factors, such as labile substrate availability for microbial metabolism, could be regulating N_2O emissions at both the grassland and forest site. Soils are usually observed to be sources of atmospheric N_2O (Chapuis-lardy et al., 2007; Muñoz, 2010) and a previous study by Benanti et al. (2014) in the same forested area showed that the soil was a net source of atmospheric N_2O with emissions of 7.15 ± 2.38 kg N_2O ha^{-1} yr^{-1}. However, the soils can also be sinks depending on the soil conditions for converting N_2O to N_2 (Chapuis-lardy et al., 2007). The fluxes of N_2O in the present study indicated that both sites appear to be net sinks with the grassland showing more uptake than the forest. This contrasts with the results of Benanti et al. (2014), which may be due to the large spatial variability of N_2O emissions at this site, where values ranged from ~50 to ~200 µg m^{-2} hr^{-1} were found for the same sampling day (Benanti

et al., 2014). This variability was also detected in the current study where the high emissions of N_2O in March 2015 were caused by extremely high values for a single replicate. Inter-annual climatic variations may also contribute to the differences in soil N_2O fluxes. The generally observed uptake of N_2O by soil seems to hold across different ecosystems, including a temperate heathland ecosystem, a plateau peatland and a treeline ecotone (Carter et al., 2011; Karbin et al., 2015; Yang et al., 2014). It is believed that the uptake of N_2O by soils may be the result of denitrification occurring at the surface layers due to the reduced NO_2- availability for denitrifiers by nitrification (Jungkunst and Fiedler, 2007), converting atmospheric N_2O into N_2 (Wrage et al., 2004; Yu et al., 2000), which mainly occurs at high soil water contents and low NO_3- availability (Chapuis-lardy et al., 2007; Davidson and Schimel, 1995; Kato et al., 2011). One of the major factors controlling the magnitude of denitrification in soils is the availability of O_2. The high levels of soil water in our study site are likely to reduce O_2-availability/diffusion into the soil and, under these conditions, bacteria capable of denitrification may use nitrate as an alternative electron acceptor (Firestone and Davidson, 1989; Knowles, 1981). Furthermore, a large flush of soil CO_2 due to both microbial and plant activities may consume soil oxygen exacerbating oxygen depletion. Owing to the presumed low oxygen conditions, the major end product of denitrification may be N_2 rather than N_2O, thus resulting in a decreased $N_2O:N_2$ ratio (Davidson, 1991; Firestone and Davidson, 1989; Scholefield et al., 1997). Many authors have also reported links between net negative N_2O fluxes at the soil surface and very low concentrations of inorganic N, even in soils with an appreciable total N content (Clayton et al., 1997; Khalil et al., 2002; Ryden, 1983; Wagner-Riddle et al., 1997), as low nitrate levels would reduce the amount of N available for conversion to N_2O (Bremner and Blackmer, 1981). Consequently, N_2O may be the only electron acceptor left for denitrification due to the low concentrations of soil NO_3- found in our sites (Butterbach-Bahl et al., 1998; Goossens et al., 2001; Rosenkranz et al., 2006). As the grassland soil had an even lower NO_3- concentration compared to the forest soil, this difference in NO_3- concentration might be the reason for the higher uptake of N_2O in the grassland. Therefore, the negative fluxes found in this experiment could be ascribed to anaerobic denitrification under high soil water content and low NO_3-concentrations.

Soil temperature and moisture largely explained the seasonal variation of soil CO_2 and N_2O fluxes, however, the availability of soil resources and plant properties may be more important factors contributing to the difference in soil CO_2 and N_2O fluxes between sites (Davidson et al., 1998; Janssens et al., 2001; Raich and Schlesinger, 1992). These factors include the quality and quantity of SOM, available plant C and N pools, root traits, and plant residues, that could in turn respond differently to climate warming (Kuzyakov and Gavrichkova, 2010; Phillips et al., 2012; Potthast et al., 2010; Shaver et al., 2000). Therefore, land-use change is likely to influence the interactions between the C and N cycle and the impact of warming (Striegl and Wickland, 1998). Afforestation, as an important forest practice, often has profound impacts on soil properties. As reported in this study, almost all measured pools (labile, recalcitrant and total C, and N pools) were much higher in the grassland than in the forest. Obviously, this difference can further affect the responses of soil C and N fluxes to global warming. According to our study, the temperature related increase in the loss of soil C and N over this period will have been small based on the results of this project and the small temperature increase that has occurred over the last 20 years. However, afforestation of grassland can lead to a greater loss of soil C and N, and the soil C and N pools may not recover to their original levels after more than 26 years after afforestation, thus it may be important to maintain current grasslands in order to mitigate global warming.

5. Conclusions

The present study reported on a field soil warming experiment conducted in adjacent forest and grassland sites. The soils were observed to be sources for CO_2 but may have been 'sinks' for N_2O, with a larger emission of CO_2 and a stronger apparent 'uptake' of N_2O in the grassland compared to the forest. Irrespective of the warming treatments, all measured pools (total soil C and N pools, labile C and N pools, as well as microbial C and N pools) were significantly larger in the grassland compared to the forest. These results imply that afforestation through its ability to dramatically influence soil C and N pools, can further affect the responses of soil C and N cycling to global warming. Whilst a warming enhancement of only 1.7 °C amounted to an increase in cumulative CO_2 efflux of almost 20%, the change from a grassland to forest had the greater effect on GHG emissions, further emphasising the importance of accounting for land use changes in GHG budgets.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2018.04.006.

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