The impact of climate change on ecosystem carbon dynamics at the

Scandinavian mountain birch forest - tundra heath ecotone

Sofie Sjögersten[1] Philip A Wookey[2]

[1]Sofie Sjögersten

Lecturer in Environmental Science

School of Biosciences, University of Nottingham

University Park, Biology Building

Nottingham, NG7 2RD, UK

[2]Philip A Wookey

Reader in Ecosystem Ecology

School of Biological & Environmental Sciences

University of Stirling

Stirling, FK9 4LA, UK

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Abstract

Changes in temperature and moisture resulting from climate change are likely to modify strongly the ecosystem carbon sequestration capacity in high latitude areas, both through vegetation shifts and via direct warming effects on photosynthesis and decomposition. This paper offers a synthesis of research addressing the potential impacts of climate warming on soil processes and carbon fluxes at the forest – tundra ecotone in Scandinavia. Our results demonstrated higher rates of organic matter decomposition in mountain birch forest than in tundra heath soils, with markedly shallower organic matter horizons in the forest. Field and laboratory experiments suggest that increased temperatures are likely to increase CO_2 efflux from both tundra and forest soil providing moisture availability does not become limiting for the decomposition process. Furthermore, colonization of tundra heath by mountain birch forest would substantially increase rates of decomposition, and thus CO_2 emissions, from the tundra heath soils, which currently store moderately large amounts of potentially labile carbon. Mesic soils underlying both forest and tundra heath are currently weak sinks of atmospheric methane, but the strength of this sink could be increased with climate warming and/or drying.

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Introduction

High latitude ecosystems are currently under severe threat from climate change; the predicted average warming at high latitudes during this century is ca. 4 ^{o}C (Prentice et al. 2001). Increased temperature is likely to have both direct and indirect effects on ecosystem carbon cycling. Currently, northern ecosystems store ca. one third of the global soil carbon pool due to slow decomposition (Gorham 1991, Schelsinger 1997), and there is considerable concern that a substantial proportion of this carbon (C) can be lost to the atmosphere, thus providing a positive feedback (i.e. further strengthening warming) on the climate system. The effect of climate change on ecosystem C balance will be determined by the difference between C inputs (both quality and quantity) and decomposition rates. There is evidence that even small changes in temperature could enhance decomposer activity and the release of carbon dioxide (CO_2) and nutrients from organic matter in these soils (Lloyd and Taylor 1994, Jonasson et al. 1999, Kirschbaum 2000). Indeed, experimental warming of understorey vegetation in mountain birch forest and tundra heath has shown that ecosystem respiration responds more strongly than photosynthesis, leading to a net loss of carbon from the system; however the magnitude and longevity of such a response remains unclear (Rustad et al. 2001). In addition to the strong effect of temperature, ecosystem processes in these areas are also commonly limited by nutrient availability due to the slow release of nutrients in plant

available form from soil organic matter (SOM) (Nadelhoffer et al. 1991, Press et al. 1998, Arft et al. 1999, Jonasson and Shaver 1999, Rustad et al. 2001, Hobbie et al. 2002), as well as moisture availability (Rosswall et al. 1975, Robinson et al. 1995, Latter et al. 1998, Illeris et al. 2004, Sjögersten et al. 2006b) and both these factors will affect the response of high latitude ecosystems to climate warming.

In addition to direct warming effects, the shifts in the distribution of major vegetation zones that have been suggested in response to increased temperature (Emanuel et al. 1985, Kittel et al. 2000, White et al. 2000, Holtmeier and Broll 2005, Kaplan and New 2006, Kullman 2007) are likely to have profound effects on ecosystem carbon cycling: For example, a doubling in net primary production in northern Sweden is predicted by 2070 -2100 (Koca et al. 2006). The effects of such vegetation changes on ecosystem function can be predicted to be greatest at ecotones. At high latitudes the most striking vegetation transition is the boreal forest-tundra ecotone: Here changes in ecosystem processes, such as litter production as well as soil C dynamics and respiration, may occur over short distances in relation to above ground vegetation and microclimate (Krosshavn et al. 1992, Raich and Schlesinger 1992, Couteaux et al. 1995, Korner 1998, Callaghan et al. 2002). Soil temperature is considered a primary control on tree growth at the forest-tundra ecotone through its impact on plant nutrient availability (Weih and Karlsson 2001, Korner and Paulsen 2004). Stabilising mechanisms such as herbivory

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and competition for space might counteract forest advances in response to climate change (Skre et al. 2002, Olofsson 2006). However, the mountain birch forest-tundra heath ecotone area in Abisko (Swedish Lapland), for example, has been responsive to increased temperatures during both the 20th century, as well as during earlier parts of the Holocene (Holmgren and Tjus 1996, Barnekow and Sandgren 2001). Shifts in the forest tundra ecotone have also been observed more widely in the Scandes mountains suggesting that the ecotone is already responding to climate warming (Kullman 2001, 2002, 2007). A shift of the boreal forest-tundra ecotone would likely significantly affect soil processes such as carbon and nutrient cycling in these areas, and the soils themselves would influence vegetation responses through, for example, altered nutrient supply and water holding capacity (McGuire et al. 2002, Berninger et al. 2004).

This paper presents a synthesis of work on ecosystem carbon C dynamics at the mountain birch forest-tundra heath ecotone (subsequently referred to as the forest-tundra ecotone) in Scandinavia, and evaluates the impacts of climate warming on the C cycling in understorey vegetation and soils in this area. The study was part of a broader EC-funded project entitled "dynamic response of the forest–tundra ecotone to environmental change" (acronym DART: http://www.dur.ac.uk/DART/). In order to determine the impact of climate warming at the ecotone we combined experimental

warming with natural gradient studies and transplant experiments in three ecotone areas of the mountain birch forest – tundra heath in Scandinavia. We tested the following two primary hypotheses: (i) that vegetation shifts will have an overriding effect on soil C dynamics and methane (CH_4) fluxes compared to direct effects of warming on the present ecosystem; and (ii) that colonisation of tundra areas by mountain birch forest will result in losses of stored organic C from tundra soil.

Study areas

The ecotone was studied at three locations in the Scandes mountain range where the mountain birch (*B. pubescens* Ehrh. ssp. *czerepanovii* (Orlova) Hämet-Ahti) is replaced by tundra heath vegetation. The study areas were Dovrefjell (Norway), Abisko (Sweden) and Joatka (Norway). These form a gradient in both latitude and continentality, with Dovrefjell being the most southerly and maritime, and Joatka the most northerly and continental (Table 1). The climate at the site in Dovrefjell is sub-alpine and the growing season is from late May to mid September. The sites at Dovrefjell usually have a deep snow cover during winter due to their more maritime climate; furthermore, the upper forest sites trap snow at all locations leaving forest sites snow-covered during a longer period in spring. The Abisko sites have a sub-arctic climate with approximately three months growing season from early/mid June to early

Table 1. Summary environmental information on the three field sites, Dovrefjell (D), Abisko (A) and Joatka (J), in the Scandes mountains.

Site	Location	Elevation (m a.s.l.)	Slope	Temperature[c]		Continentaliy[a]	Precipitation (mm)
				Min (°C)	Max (°C)		
D	62°18'N, 9°37'E	1000-1100	10° facing NW	-7.9 (Jan)	10.2 (June)	14.3	473
A	68°21'N, 18°49'E	520-600	8° facing NW	-11.9 (Jan)	11 (June)	21.5	304 [b]
J	69°45'N, 23°59'E	420-500	8° facing NE (tundra), SW (forest)	-14.0 (Feb)	11 (July)	24.9	354

[a] Gorzinski's continentality index $K = 1.7 \times A \times \sin \theta^{-1} - 20.4$ (A = annual temperature range, θ = latitude angle)

[b] (Alexandersson *et al.* 1991)

[c] Air temperature data (at 2 m) are monthly mean minima and maxima, respectively, based on 1961-1990 averages.

September. The site in Joatka has a harsher climate, with a short growing season
starting in late June and ending in late August.

The main species in the tundra heath areas are *Empetrum hermaphroditum*, *Vaccinium
uliginosum*, *V. vitis-idea*, and *Betula nana*, lichens and bryophytes (and additionally in
Dovrefjell, *Arctostaphylos uva-ursi*). Mesic areas within the mountain birch forest have
comparable understorey vegetation, although tending toward greater cover of *V.
myrtillus*. The structure of the mountain birch forest at the three sites differs
considerably, with denser forests and taller understorey vegetation at Dovrefjell. Also
the structure of the ecotone differs between sites, depending largely upon steepness of
slope and aspect. At Dovrefjell the ecotone is alpine and the transition from mountain
birch to prevailing tundra heath occurs over ca. 50 m. The study sites in Abisko are
located in a more gradual alpine/sub-arctic ecotone area where the transition occurs over
3-4 kilometres. At Joatka tundra prevails above 400 m a.s.l and the ecotone extends
over several 10's of kilometres. The sites selected for study are all mesic and the soils
are predominantly thin spodosols (principally orthods) developed within well drained
medium to coarse-grained till deposits. The bedrock is generally acidic with gneiss and
hard-shale, although some richer, more basic, out-croppings are present in Abisko.

Experimental Design

In order to evaluate the relative importance of climate warming and vegetation shifts we established four experimental sites at each of the three study areas, spanning the forest-tundra ecotone. Two of these sites have a mountain birch canopy (one at lower altitude and one at higher) and two sites represent tundra heath at different altitudes. Ten experimental plots (1×1 m) were established at each site, with five control plots and five plots which were randomly assigned an experimental warming treatment using ITEX (International Tundra Experiment) open top chambers (OTCs)(Marion et al. 1997, Hollister and Webber 2000). The OTCs created generally warmer soil and surface temperature but the effect was variable over the seasons and between sites. Mean July surface air temperature in 2000 was increased by 0.4 and 0.5°C by the warming treatment at the forest and tundra sites, respectively. The OTC's also increased the number of frost-free days. In addition to the field warming experiments we also carried out soil transplantation and incubation experiments in order to differentiate between substrate-related and environmental effects on soil respiration and the effects of warming under controlled conditions. The soil transplant experiment involved transplanting monoliths of forest soil to tundra and vice versa (n=10), as well as maintaining monoliths at their site of origin (n=10) by way of comparison. For the incubation experiment soil monoliths were brought to field capacity in the laboratory and subsequently incubated at 2, 7, 12 and 17°C (n=6) (Sjögersten and Wookey 2002a).

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A variety of techniques were implemented in order to investigate the carbon cycle at the ecotone. In this paper we synthesise data on net ecosystem exchange of CO_2 (previously unpublished data), soil respiration (Sjögersten and Wookey 2002b), litter decomposition (Sjögersten and Wookey 2004), soil carbon chemistry (Sjögersten et al. 2003) as well as CH_4 fluxes (Sjögersten and Wookey 2002b).

Methods

Where details have been published previously only a brief summary of methods is presented here.

Carbon dioxide flux measurements I: Soil respiration

Soil respiration (R_s) was measured made using a dynamic flow canopy cuvette (1 l and 14 cm in diameter) connected to a portable Infra Red Gas Analyser (IRGA) (EGM-2; PP Systems, Hitchin, Hertfordshire, UK) during the growing season of 1999-2001 from plots that were clipped prior to measurements (Sjögersten and Wookey 2002a).

Litter decomposition

A standard material - leaf litter from *B. pubescens* Ehrh. ssp. *czerepanovii* collected in Abisko - was used for a litterbag experiment (Sjögersten and Wookey 2004). Litterbags

were placed on plots in all study areas (Dovrefjell, Abisko and Joatka) in July 1998 and were sampled at regular intervals during the experiment until autumn 2001 for the determination of rates of mass loss together with changes in chemical composition of the litter.

SOM chemistry

To study the SOM chemistry in detail, solid state CPMAS ^{13}C NMR spectra were acquired using a Bruker MSL 300 spectrometer on the top 2 cm of the soil organic horizon (Sjögersten et al. 2003). An index for aromaticity was calculated from the signal of aromatic and phenolic compounds in each sample relative to the total signal.

Carbon dioxide flux measurements II: Net ecosystem exchange of CO_2

To estimate net ecosystem exchange (NEE) of CO_2 above the understorey vegetation at forest and tundra sites we measured CO_2 exchange using the same equipment as above. These measurements were carried out in ambient and warmed plots only at the sites in Abisko, with both ambient photosynthetic photon flux densities (PPFD) - on average 787 and 363 μmol m^{-2} s^{-1} at the tundra and forest site, respectively - to provide data on NEE of CO_2 and, in darkness, to provide ecosystem respiration (R_e). The measurement period in both light and dark was 2 minutes, and gross photosynthesis (GEP) was derived by subtracting R_e from NEE. These measurements were made as a one-off

campaign (7 measurement occasions at the tundra site and 3 measurement occasions at the forest site) during the growing season (July-August) in 2001 on fully-vegetated plots; this was two years after the experimental plots were established and plexi-glass frames that were used as the base for the canopy cuvette were inserted in order to provide time for vegetation recovery following the disturbance. The measurements were made at between 10 am and 4 pm and therefore represent NEE during solar zenith and presumably at maximum rates of CO_2 assimilation. For the tundra heath plots the measurements properly represent NEE, while within the forest only understorey vegetation and soil (including tree roots) were included, not the tree canopy. For this reason the forest measurements are denoted NEE-T and GEP-T ('minus trees'). Negative NEE values represent uptake of CO_2 from the atmosphere whilst positive values represent a net loss of CO_2 from the ecosystem to the atmosphere.

Determination of C pool sizes

The above ground biomass (excluding trees) was harvested at peak biomass at forest and tundra from the plots used for the NEE measurements in Abisko as described above (the harvested turfs were 14 cm in diameter, used for the NEE flux measurements n = 5). The vegetation was sorted into functional types, dried at 70 °C and weighed. The C content of the understorey vegetation was calculated using a dry weight conversion factor of 0.495 (that is specific to Arctic vegetation) (Welker et al. 2005) and for

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conversion of mountain birch forest biomass to C a factor of 0.49 was used (Patenaude et al. 2004).

Soil carbon content in the organic horizon at forest and tundra site at Dovrefjell, Abisko and Joatka was determined by analysis of the C content using a Carlo Erba NA 2000 analyser. The C pool size was thereafter calculated using the density and depth of the organic horizon.

Methane flux measurement

Headspace frames were inserted into plots during 1998 and CH_4 flux measurements were made during the thaw seasons of 1999 and 2000. The closed chamber technique was used, initial samples and samples after 1 hour were taken with syringes through a rubber septum in the headspace cap (Sjögersten and Wookey 2002b). Samples were analyzed the following day using a Perkin Elmer AutoSystem XL Gas Chromatograph (GC) fitted with a flame ionization detector. Negative CH_4 fluxes represent uptake of CH_4 from the atmosphere whilst positive values represents a net efflux of CH_4 from the soil to the atmosphere.

Temperature and soil moisture measurements

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Soil temperature data were collected year-round at all three main sites on an hourly

basis using TinyTag data-loggers (INTAB Interface-Teknik AB, Stenkullen, Sweden)

with thermistor probes at 5 cm depth. Additional soil temperature (at 5 cm depth) and

soil moisture measurements were made at each plot in parallel with the flux

measurements. Soil water content was measured with a ThetaProbe and hand-held

ThetaMeter (Delta-T Devices, Burwell, UK).

Data analysis

Data were analyzed in SAS for Windows V. 8.2 primarily using generalised linear

mixed models (GLMM). These models were fitted by the method of residual maximum

likelihood (REML) with 'block' as a random effect. Denominator degrees of freedom

were estimated using Satterthwaite's approximation (Littell et al. 1996) and the residual

variances were modelled as constant to the mean using PROC MIXED. Autocorrelation

between measurements within plots was modelled as a first-order autoregressive (AR 1)

process (i.e. repeated measures). Effects of the vegetation and warming treatment on

key ecosystem processes (e.g. C fluxes and litter decomposition) were analyzed using

vegetation and warming as fixed effects. There were some occasions on which NEE

exceeded R_e. In the data analysis we included all NEE data points, whilst for

photosynthesis data points for which NEE $>R_e$ were set to zero as discussed in

Sjögersten et al. (2006a).

Figure 1.
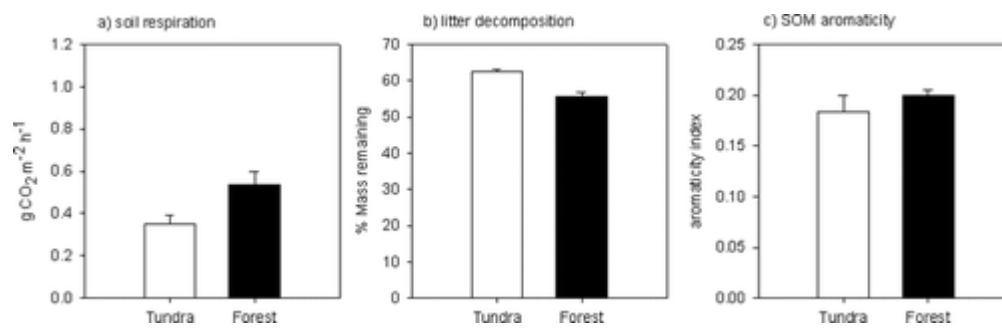
Indices of decomposition: a) soil respiration (Rs) measured at the Abisko sites around midday during the July 2001 growing season (mean and SE are shown, three measurement occasions, n = 10); b) litter decomposition of standard birch litter over 4 y at forest and subarctic/alpine tundra heath sites at Dovrefjell, Abisko, and Joatka, the litter decomposition is averaged over the three study sites (mean and SE are shown, n = 30); c) SOM aromaticity in forest and subarctic/alpine tundra heath sites at Dovrefjell, Abisko, and Joatka, the aromaticity is averaged over the three study sites based on data from 2000 (mean and SE are shown, n = 6), unfilled and filled bars represent tundra heath and forest sites, respectively.

Results and discussion

Effects of vegetation and experimental warming on CO_2 fluxes and decomposition

We found generally higher decomposition rates at forest sites using both soil respiration ($F_1 = 6.14$, $P < 0.05$) (Fig. 1a) and leaf litter decomposition ($F_1 = 26.31$, $P < 0.0001$) as indices (Fig. 2b), likely due both to more favorable microclimatic conditions and higher litter quality which can enhance decomposition of less labile litter by priming the decomposer community (as discussed by Quested et al. 2005) at the forest site (Sjögersten and Wookey 2002a, 2004). The slower decomposition rates in tundra soils $F_1 = 11.4$, $P < 0.05$) is reflected by lower aromaticity of the stored organic carbon ($F_1 = 11.4$, $P < 0.05$) (Fig. 1c) (Sjögersten et al. 2003, Sjögersten and Wookey 2004). There is an indication of greater soil C pools in tundra compared to forest soil at Abisko and Dovre fjell (Table 2), although it must be noted that the C soil pool data is based on five pooled samples from each site. The smaller difference in soil carbon storage between forest and tundra sites at Joatka is likely to be linked to the sparse structure of the mountain birch forest at this site, and hence a less marked environmental gradient controlling C storage between tundra and forest; the tree density at Joatka and Abisko is 399 and 747 trees ha^{-1}, respectively (Olofsson et al. 2004), and the forest at Dovrefjell is substantially denser than the Abisko site (although quantitative data for Dovrefjell are

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Table 2. Carbon storage (kg m^{-2}) in the soil organic horizon in forest and tundra sites, the values shown are mean values from each site.

	Dovre	Abisko	Joatka
Forest	6.3	1.3	2.0
Tundra	10.1	3.9	2.4

not available). In the context of C pool sizes it is also worth mentioning the greater understorey/tundra vegetation biomass in tundra than forest; 133 and 81 g m^{-2} at the tundra and forest site, respectively (data from Abisko). The carbon storage in the organic horizon in these tree-line soils is comparable, or higher than, C storage in soil (2.3 kg m^{-2} in mineral soil + forest floor down to 1 m depth) in the boreal zone in northern Sweden (Callesen et al. 2003), especially considering that our estimates of soil C pools excludes C stored in the mineral soil.

Temperature was a major driver of *in situ* decomposition, and positive regressions between soil temperature and soil respiration were found both in tundra and forest soils; $R^2 = 0.37$ and 0.42, respectively (Sjögersten and Wookey, 2002), and between litter decomposition at the forest site and mean July temperature ($R^2 = 0.58$) (Sjögersten and Wookey, 2004). The response of soil respiration to temperature was strong early and late in the growing season of 2000, when soil temperatures were low and the microbial community was not limited by soil moisture. However, reduced moisture availability limited decomposition mainly during summer; for example, the relationship between R_s and temperature disappeared during a period of water deficit in mid-summer 2000 (Fig. 2). When moisture constraints were removed, however, during laboratory incubation of tree-line soil, increased temperature enhanced soil respiration from both forest and tundra soils ($F_1 = 7.34$, $P < 0.05$) as expected (Sjögersten and Wookey 2002a). Taken
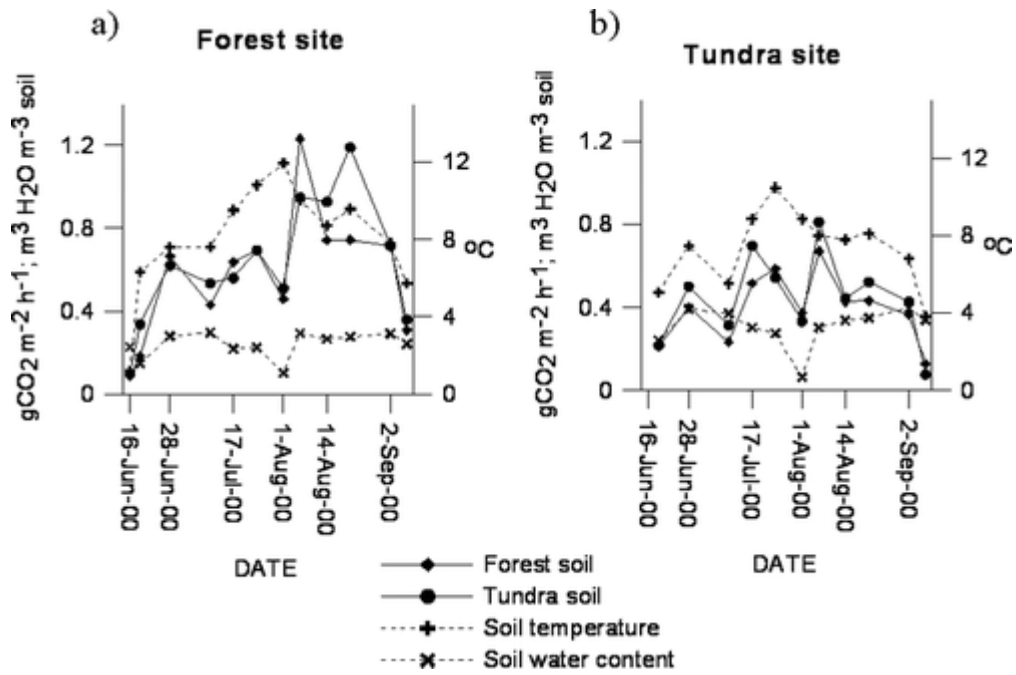
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Figure 2.

Seasonal variation in soil respiration measured in the field from control and transplanted soils a) at a forest site and b) at a tundra heath site in Abisko (mean values, n = 10). Data for soil moisture (on the left axis) and temperature (right axis) are also shown. Modified from Hollister and Webber (43).

together, these data clearly demonstrate the importance of temperature for decomposition processes, but they also illustrate the potential for summer water deficits to constrain responses to warming, even in these cold environments.

In general, the decomposition process proved rather tolerant of low temperatures. The apparently high temperature sensitivity we found at the beginning and end of the growing seasons, together with relatively rapid winter litter decompositions rates (3.8 % mass loss over winter (September – May) compared to 7.1 % mass loss during the summer (Sjögersten and Wookey 2002a, 2004)), suggest that the soil C storage at the forest tundra ecotone may be differentially sensitive to the predicted increases in temperatures during autumn, winter and spring in this region compared with the summer (Teng et al. 2006). This would be the case in particular if summer warming were accompanied by soil drying (as noted above). In the winter it is likely that changes in soil thermal and moisture conditions will be exerted principally via alterations in snow depth, snow-pack physical properties, and the longevity of cover. From soil temperature data measured at 5 cm depth it was clear that the thermal regime during winter differed between forest and tundra sites: at forest sites temperatures rarely fell below -5°C, while at the tundra sites temperatures were generally below -5°C. Since -5°C appears to be a threshold for biological activity in arctic soils (Mikan et al. 2002) this suggests that decomposition processes might continue (at a reduced rate) right

through the year at the forest sites. Winter CO_2 flux measurement in the Abisko area

suggests that respiration continues for a large part of the year, albeit at a lower rate

(Larsen 2001, Grogan and Jonasson 2005). These observations lend support to our

conclusion that the differences we detected in decomposition and SOM accumulation

between forest and tundra sites are a result both of summer and winter activity: Winter

processes cannot be ignored.

The net ecosystem exchange (NEE) and the NEE minus tree canopy (NEE-T) of CO_2 at

the tundra and forest site, respectively, during July and August 2001 responded to

experimental warming in markedly different ways ($F_{1,15} = 7.40$, $P < 0.05$) (Fig. 3). At

the tundra site warming increased the CO_2 efflux from the system whilst the opposite

was true at the forest site where the warming actually reduced CO_2 efflux. The pattern

we observed in NEE and NEE-T appeared to be largely due to the R_e response to

warming (dark measurements) rather than to any significant adjustments in GEP and

GEP-T. The significant interaction term could not be attributed to either abiotic (i.e.

light, temperature and soil moisture) or biotic (i.e. plant biomass) drivers. Our longer-

term data for soil respiration from clipped plots (R_s), taken together with the data on

ecosystem CO_2 exchange, suggest that a substantial component of the R_e is from

decomposition of SOM rather than recently assimilated carbon (e.g. via root respiration

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or rhizosphere processes): R_s contributed approximately 50 % of the R_e in both tundra and forest soil, respectively (Fig. 2, and Fig. 3 b & e).

Forest and tundra soil transplanted reciprocally into tundra and forest sites, respectively, assumed similar respiration rates to the control (native) soils at each site (Fig. 2). The potential of tundra soils to increase and maintain their respiration rate over several years in response to the forest environment (Sjögersten and Wookey, 2002), combined with the storage of carbon in tundra soils in forms that are readily degradable (O-alkyls and acetals) (Sjögersten et al., 2003), suggest that carbon dioxide emission from tundra soils will increase if mountain birch colonizes tundra areas. We speculate that the differential warming response of R_e at the forest and tundra sites (Fig. 3) might be a result of carbon limitation at the forest site as a consequence of depletion of labile SOM here (it is worthwhile to note that a parallel study by Selander (2002) demonstrated that the soil respiration at the forest site was not nitrogen-limited). This may indicate a rapid loss of labile C in response to warming in the birch forest, and a sustained increase in CO_2 effluxes from tundra soils reflecting the larger pool of labile SOM in the latter. Since no data are available to demonstrate an initial stimulation of respiration with warming no firm conclusions can be drawn with respect to the cause of the reduced CO_2 efflux with warming at the forest site at this stage. However, rapid depletion of the labile carbon
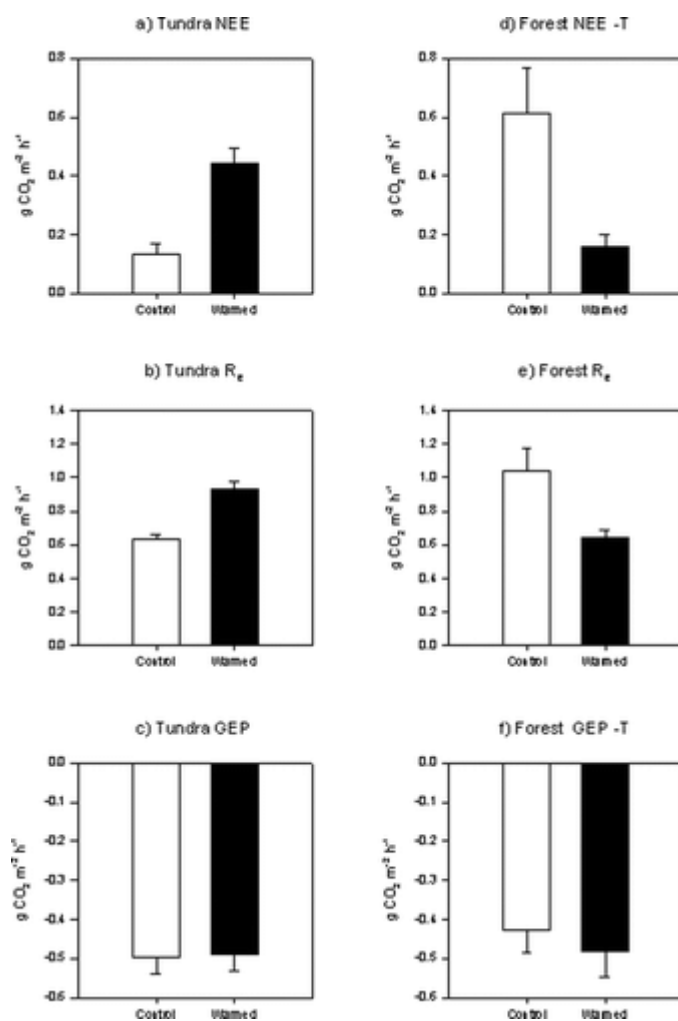
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Figure 3.

Net ecosystem exchange (NEE) of CO2, ecosystem respiration (Re), and gross ecosystem photosynthesis (GEP) at forest and tundra heath sites in Abisko 2001, following 2 y of experimental warming. Unfilled and filled bars represent ambient and warmed plots, respectively. Note that CO2 exchange measurements in the forest only included soils and understory vegetation; the forest trees themselves were excluded. For panels d, e, and f (forest) the fluxes are therefore denoted NEE − T and GEP − T to indicate the exclusion of aboveground tree components from the CO2 flux (tree roots, by contrast, were included, so Re remains the same). Means and SE are shown (n = 5); positive value represents a source of CO2 to the atmosphere, while negative values indicate a sink (ecosystem uptake).

pool in response to warming has been demonstrated previously: Transient effects of warming were found in a long term warming experiment in a mid latitude hardwood forest where substantial increases of CO_2 efflux were only noted in the first year of the experiment (Melillo et al. 2002). Additionally, the concept of a small, highly labile, pool of recently assimilated C contributing significantly to R_e is supported by (Grogan and Jonasson 2005) who found a large reduction in ecosystem and soil respiration after three years of removing the vegetation and litter layer at a nearby mountain birch forest.

Effects of vegetation and experimental warming on CH_4 fluxes

Methane fluxes did not differ significantly either between forest and tundra sites or across the 8° latitudinal gradient (Sjögersten and Wookey 2001). Mesic soils at the forest-tundra ecotone were found to be sinks for atmospheric CH_4 (Fig. 4) due to the activities of methane oxidizing bacteria (methanotrophs). Although the sink strength was weak compared to less harsh environments, the areas that act as sinks cover a large proportion of the landscape. The CH_4 fluxes were responsive to the OTC warming treatment ($F_1 = 4.04$, $P < 0.05$), and we observed significantly higher CH_4 uptake rates in warmed plots early in the growing season (Fig. 4). However, we found no clear relationship between CH_4 fluxes and either soil moisture content (in the mesic range) or soil temperature; in this respect our results are similar to those of Christensen et al. (1997). We suggest that the warming effect is linked to the earlier plant phenology
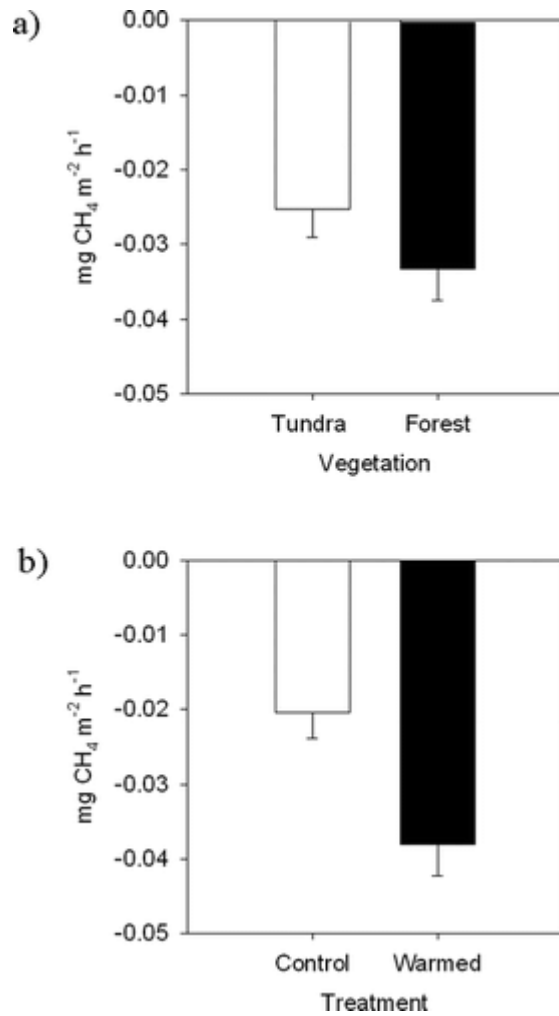
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Figure 4.

Methane fluxes a) at tundra heath and forest sites (unfilled and filled bars represent tundra and forest sites, respectively), and b) ambient and warmed plots (unfilled and filled bars represent ambient and warmed plots, respectively). The data have been averaged across the three study sites (i.e., Dovrefjell, Abisko, and Joatka). Means and SE are shown for the forest-tundra comparison (n = 30) and the control-warmed comparison (n = 60); positive values represent a source of CO2 to the atmosphere, while negative values indicate a sink (ecosystem uptake).

associated with warming (Arft et al. 1999), leading to increased water and nutrient uptake, as well as to increased rhizosphere activity, all of which have the potential to promote methanotrophy (Gulledge et al. 1997, Gulledge and Schimel 1998, Whalen 2000). The decrease in surface soil moisture content would likely reduce the diffusion barrier for atmospheric CH_4 through the soil, since the methanotrophs tend to have their maximum distribution at the top of the mineral horizon (at least in mountain birch forest soils; Sjögersten et al. 2007). These results suggest that CH_4 fluxes will be resilient to shifts in above ground vegetation communities but that warming is likely to increase CH_4 uptake rates, at least in mesic areas.

The landscape at the forest tundra ecotone is composed of a mosaic of contrasting vegetation communities nested within the predominant birch forest and tundra heath categories. These contrasts are related largely to heterogeneity in soil moisture conditions resulting from topographic and substrate variability in the area, together with controls exerted by mineralogy of the parent materials and the chemical composition of groundwater flushes. In our study the mesic areas represent the most active areas for CH_4 uptake (Sjögersten and Wookey, unpublished data); however, of particular importance for CH_4 fluxes in this region are the number of small lakes and mires that act as "hot-spots" for CH_4 production (methanogenesis) (Svensson et al. 1999, Nilsson et al. 2001). Thus the amplitude and net direction of CH_4 fluxes vary across the

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landscape, and this reflects the contrasting biotic and environmental controls on methanotrophy and methanogenesis (Schlesinger 1997). An understanding of regional CH_4 flux dynamics therefore requires information on the factors controlling both CH_4 uptake and emission, and how these will respond to environmental change. Methanotrophy tended to be rather resilient to fluctuations in both temperature and soil moisture, at least in the mesic range (Sjögersten & Wookey 2002a; Nordenmark, 2002). Generally, however, the rates of methane uptake decrease abruptly at higher soil moisture contents, while a more gentle reduction occurs in response to very dry conditions (and thus physiological water deficit for methanotrophic bacteria). These processes, operating with contrasting amplitude and direction (Fig. 5) mean that reduced soil moisture availability (e.g. in response to warming) might lead to increased methane uptake rates in some areas but reduce rates in others, and *vice versa*. Thus CH_4 fluxes need to be studied at the operational scale of the process rather than the km grid used in many models. This is a clear example of where plot-scale research is required to underpin regional flux estimates, including a CH_4 sampling framework that incorporates landscape variability and cuts across environmental gradients.

In order to make a ball-park comparison of the importance of CH_4 and CO_2 fluxes from a climate feedback perspective we converted the methane fluxes to kg CO_2 equivalents. We based the conversion on the 23 times greater global warming potential for CH_4
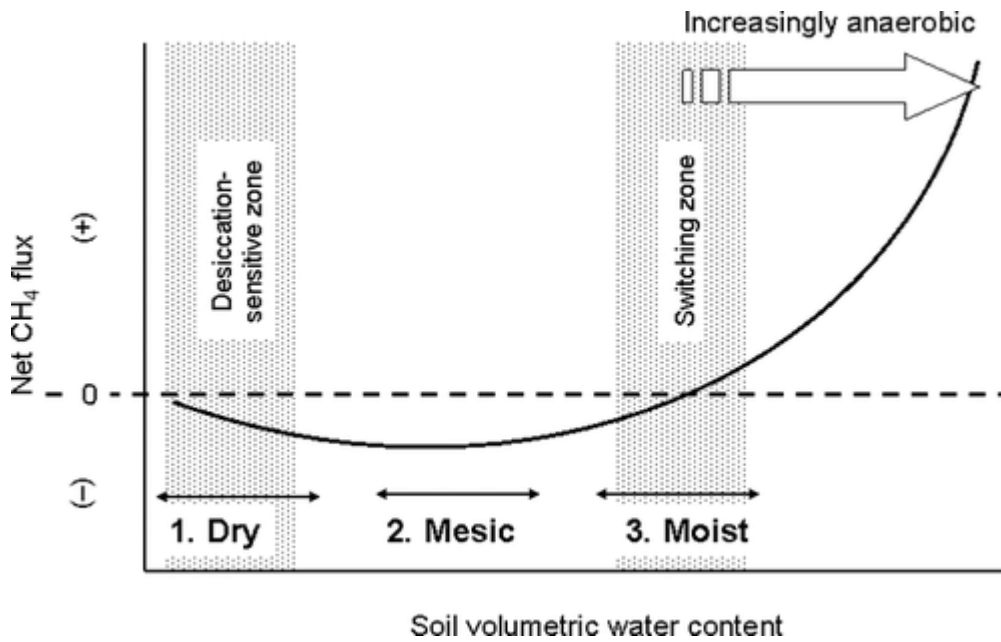
21

Figure 5.

Schematic diagram illustrating the moisture sensitive zones for net methane fluxes at the ground surface in relation to soil moisture content in the top 10 cm of soil. Values above the 0 line represents net methane emission at the ground surface, while values below 0 indicate net methane uptake. Note that an increase in moisture content across range 1 and 3 will produce opposite responses in terms of the direction of net CH4 flux, as will a decrease. Range 2, by contrast, is in the broad moisture-insensitive zone of net CH4 uptake (methanotrophy) from atmosphere to soil.

compared to CO_2 on a molar basis over a 100 yr period (Prentice et al. 2001). The negative feedback on global warming provided by CH_4 uptake at tundra sites is ca. 1.6 kg CO_2 equivalents km^{-2} hr^{-1}, whilst the CO_2 fluxes represent a positive feedback (based on midday NEE measurement), of a much greater magnitude: 133 kg CO_2 equivalents km^{-2} hr^{-1} from tundra heath. These are, however, gross extrapolations based on data from the period of maximum photosynthetic activity, and not accounting for diurnal fluctuations in C fluxes.

Implication of a shift in the forest tundra ecotone for carbon dynamics

Comparing the effect of experimental warming with the effect of the dominant vegetation on CO_2 fluxes it seems likely that colonization of tundra heath by mountain birch would increase soil respiration rates and reduce soil C storage. These effects on C fluxes mediated by changes in vegetation may be of greater magnitude than the direct effects of warming on soil respiration and nutrient availability. By contrast, warming directly increased CH_4 fluxes from atmosphere to soil (net methanotrophy) but the presence or absence of mountain birch had no significant effect on the flux rates. The main differences between the two vegetation types, and the potential impacts of experimental warming on ecosystem carbon dynamics, are summarised in Fig. 6. The

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Figure 6.
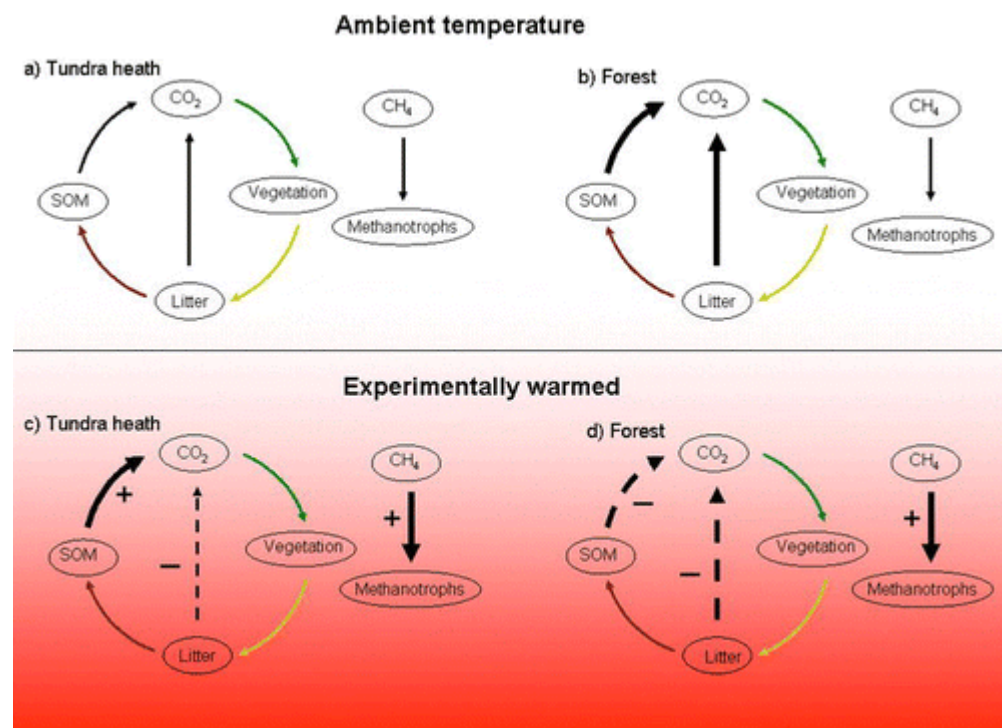
Conceptual model summarizing the significant differences in the carbon cycle between tundra heath (a and c) and forest (b and d) soils based on in situ measurements at ambient (a and b) and warmed (c and d) plots. Higher process rates are indicated by thicker arrows. Decreased or increased process rates with warming compared to the ambient situation is shown with dashed lines and a minus sign, or thicker lines and a plus sign, respectively.

different responses reflect the contrasting controls on CO_2 and CH_4 fluxes at the ecotone. Carbon dioxide fluxes are strongly linked to the environmental conditions associated with the above ground vegetation (Chapin 2001); this also applies indirectly to R_s due to litter inputs, root and mycorrhizal respiration, and rhizosphere processes. At forest sites the physical climatic conditions generally promote more rapid decomposition compared to tundra: Air temperature is higher, and a degree of shelter from high winds reduces evapotranspiration from the understorey and also allows snow to accumulate (ameliorating winter soil temperatures as well as providing moisture and nitrogen, from N deposition) (Sveinbjörnsson et al. 1995, Weih and Karlsson 1999, Sveinbjörnsson et al. 2002, Beringer et al. 2005, Sjögersten and Wookey 2005). The litter associated with mountain birch forest (mountain birch, deciduous shrubs and herbaceous plants) is generally also more labile than 'tundra litter' which is dominated here by evergreen shrubs and bryophytes (Cornelissen et al. 2004). By contrast, methanotrophy is less tightly controlled by these factors since methanotrophic bacteria are dependent upon atmospheric CH_4 as their principal energy and carbon source.

The overall impact of a shift in the tree-line on the C cycling in these regions will clearly also depend upon C sequestration by the trees, together with the implications of enhanced rates of SOM decomposition for nutrient cycling and release of plant-available nutrients (and hence plant growth/photosynthesis). Assimilation of CO_2 by

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mountain birch is substantial during summer; at a mountain birch forest site in northern Finnland (Petsikko), for example, net ecosystem assimilation was -1.5 gCO_2 m^{-2} h^{-1} (a net sequestration of CO_2) with photosynthetic rates of - 2.4 gCO_2 m^{-2} h^{-1} (Laurila et al. 2001). A comparison of the fluxes from the Finnish forest site with the tundra site in this study lends support to the hypothesis that the Abisko forest site would likely act as a sink for CO_2 during the thaw period, in contrast to the tundra site. In combination with the strong temperature controls found on growth in mountain birch at the ecotone (Weih and Karlsson 2002, Karlsson et al. 2004) this suggests that the medium- to long-term effect of forest establishment above the contemporary ecotone might be an increase of the carbon sink strength during the growing season. However, it is important to bear in mind that the birch forest will only act as a sink of CO_2 during the relatively short growing season (June-August) whilst decomposition processes are active over a substantially longer period (especially under the forest canopy, as discussed in relation to soil temperatures above). Indeed, a comparison of total ecosystem C storage in forest and tundra in the Abisko area, based on soil, understorey vegetation and mountain birch C pools (the mountain birch biomass in Abisko is 27.4 tonnes ha^{-1} (Dahlberg et al. 2004)), suggest that a shift in the tree-line could amount to a substantial loss of 18.9 tonnes C ha^{-1} (1.89 kg m^{-2}) to the atmosphere. However, such changes in ecosystem carbon storage will be highly spatially variable, and depend upon the relative amount of C stored in soil and above ground vegetation. For example, mountain birch biomass in

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northern Finland (8.35 tonnes ha^{-1} in an area relatively close to the Joatka site; Heiskanen (2006)) is substantially lower than in Abisko. Due to the lower C storage in tundra soils at Joatka this site might be less vulnerable to losses of C to the atmosphere following colonization by trees, despite the fact that birch forest here is relatively sparse compared to Abisko. The results from the simple 'space-for-time' model of climate change used for the calculations of C storage in this paper contrast with model predictions by BIOME4 which suggest that C storage in both plants and soil in the Arctic will double with a 2°C increase in global mean temperature (Kaplan and New 2006). The discrepancy between these two predictions likely reflects specific regional factors arguably unique to the mountain birch forest-tundra heath ecotone of Fennoscandia. Our study specifically addresses an ecotone area in Scandinavia where soil C storage within the forest is low compared to adjacent tundra heaths, and tree biomass is also low. The tree species here are also almost exclusively deciduous.

Current predictions of forest establishment in tundra areas predict an 88% reduction in the aerial extent of tundra in north Western Europe (Kaplan and New 2006) in response to a 2°C global temperature increase (corresponding to a 3.2 - 4.5°C warming north of 60°N). Considering the large areas covered by tundra heaths in Fennoscandia (33 813 km^2 in Sweden alone, (Esseen and Lofgren 2004)) this would represent a dramatic change in the vegetation of the Scandes mountains. Indeed, it has been suggested that

the contemporary climatic conditions (or climatic 'envelope') in the northern parts of the Scandes will disappear entirely from this region by 2035 (Ohlemuller et al. 2006) which obviously will feed forward into changes in the vegetation community structure. However, the rate of a shift in the forest-tundra ecotone is likely to be highly variable depending on region, site and the physiological constraints of the tree species forming the ecotone, and there will be a substantial time lag in tree dispersal, establishment and growth compared to changes in climate (Grace et al. 2002). For example, Kullman (2002, 2006) recorded migration rates of 35 m yr^{-1} for pine seedlings at the tree-line in the Scandes Mountains, together with a rise in the maximum elevation for establishment of birch seedlings of 435 m since the 1950s. By contrast, a mean shift of the forest tundra ecotone of only 2 cm yr^{-1} was recorded at a black spruce ecotone in Québec, the very slow migration rates at this site are likely controlled by moisture deficit limiting tree establishment (Gamache and Payette 2005). In addition to moisture deficit, herbivory and available sites for germination (Grace et al. 2002, Olofsson et al. 2005) are likely to down-regulate the high forest migration rates (in the range 7.5 to 21 km yr^{-1}; Kaplan and New (2006)) predicted in the Scandes mountains as a function of warming, especially in areas subject to high grazing intensities (Cairns and Moen 2004). Furthermore, the net effect of changes in decomposition rates and tree growth will vary temporally as the forest matures, as illustrated by a study of peat accumulation rates over 53 years, together with a CO_2 flux measurement campaign at the tree-line in

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Alaska (Rouse et al. 2002), and a study of forest chronosequences in Europe (Magnani et al. 2007).

In conclusion, our results - based on measurements of CO_2 fluxes during the growing season, litter decomposition over both summer and winter, and SOM chemistry - demonstrate that decomposition is slower in tundra heath compared with mountain birch forest, which has resulted in greater C storage in tundra soils. Based on this evidence we predict that an advance of the mountain birch forest into tundra heath areas in Fennoscandia will result in an initial pulse of CO_2 released from soil to the atmosphere as labile C stored in tundra soils is metabolized by decomposer organisms. The implications of this for whole-ecosystem CO_2 fluxes will depend on the extent to which increases in photosynthesis (either in the understorey, or by the mountain birch trees themselves) might compensate for losses through respiration. A comparison of the soil C pools with above ground C pools in forest and tundra site in the Abisko area suggest that a shift in the tree-line will result in a net loss of stored carbon to the atmosphere if forest replaces tundra. However, future increases in forest productivity over and above the productivity of the current ecotone forest system in response to CO_2 fertilization and warming might dampen this positive feed back.

Acknowledgements

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Figures

Figure 1. Indices of decomposition: a) soil respiration (R_s) measured at the Abisko sites around midday during the July 2001 growing season, (mean and SE are shown, 3 measurement occasions, n = 10), b) litter decomposition of standard birch litter over four years at forest and sub-arctic/alpine tundra heath sites at Dovrefjell, Abisko and Joatka; the litter decomposition is averaged over the three study sites (mean and SE are shown, n = 30), c) SOM aromaticity in forest and sub-arctic/alpine tundra heath sites at Dovrefjell, Abisko and Joatka; the aromaticity is averaged over the three study sites based on data from 2000 (mean and SE are

shown, n = 6), unfilled and filled bars represent tundra heath and forest sites, respectively.

Figure 2. Seasonal variation in soil respiration measured in the field from control and transplanted soils a) at a forest site, and b) a tundra heath site in Abisko (mean values, n = 10). Data for soil moisture (on the left hand axis) and temperature (right hand axis) are also shown. Modified from (Sjögersten and Wookey 2002a).

Figure 3. Net ecosystem exchange (NEE) of CO_2, ecosystem respiration (R_e) and gross ecosystem photosynthesis (GEP) at forest and tundra heath sites in Abisko 2001, following two years of experimental warming. Unfilled and filled bars represent ambient and warmed plots, respectively. Note that CO_2 exchange measurements in the forest only included soils and understorey vegetation; the forest trees themselves were excluded. For sub-figures 3d, e and f (forest) the fluxes are therefore denoted NEE-T and GEP-T to indicate the exclusion of above-ground tree components from the CO_2 flux (tree roots, by contrast, were included, so R_e remains the same). Means and SE are shown (n = 5); positive value represents a source of CO_2 to the atmosphere, whilst negative values indicate a sink (ecosystem uptake).

Figure 4. Methane fluxes a) at tundra heath and forest sites (unfilled and filled bars represent tundra and forest sites, respectively), and b) ambient and warmed plots (unfilled and filled bars represent ambient and warmed plots, respectively). The data has been averaged across the three study sites (i.e. Dovrefjell, Abisko and Joatka). Means and SE are shown for the forest-tundra comparison (n = 30) and the control-warmed comparison (n = 60); positive value represents a source of CO_2 to the atmosphere, whilst negative values indicate a sink (ecosystem uptake).

Figure 5. Schematic diagram illustrating the moisture sensitive zones for net methane fluxes at the ground surface in relation to soil moisture content in the top ten cm of soil. Values above the 0 line represents net methane emission at the ground surface whilst values below 0 indicate net methane uptake. Note that an increase in moisture content across range 1 and 3 will produce opposite responses in terms of the direction of net CH_4 flux, as will a decrease. Range 2, by contrast, is in the broad 'moisture-insensitive' zone of net CH_4 uptake (methanotrophy) from atmosphere to soil.

Figure 6. Conceptual model summarising the significant differences in the carbon cycle between tundra heath (a & c) and forest (b & d) soils based on *in situ* measurements at ambient and warmed plots, (a & b) and (c & d), respectively. Higher process rates are indicated by thicker arrows. Decreased or increased process rates with warming compared to the ambient situation is shown with dashed lines and a (-) sign, or thicker lines and a (+) sign, respectively.