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Two Decades of Experimental Manipulations of Heaths and Forest Understory in the Subarctic

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Abstract Current atmospheric warming due to increase of greenhouse gases will have severe consequences for the structure and functioning of arctic ecosystems with changes that, in turn, may feed back on the global-scale composition of the atmosphere. During more than two decades, environmental controls on biological and biogeochemical processes and possible atmospheric feedbacks have been intensely investigated at Abisko, Sweden, by long-term ecosystem manipulations. The research has addressed questions like environmental regulation of plant and microbial community structure and biomass, carbon and nutrient pools and element cycling, including exchange of greenhouse gases and volatile organic compounds, with focus on fundamental processes in the interface between plants, soil and root-associated and free-living soil microorganisms. The ultimate goal has been to infer from these multi-decadal experiments how subarctic and arctic ecosystems will respond to likely environmental changes in the future. Here we give an overview of some of the experiments and main results.

Keywords Tundra · Warming · Field experiments · Plant–microbe interactions · Carbon and nitrogen cycling

LONG-TERM ECOSYSTEM MANIPULATION STUDIES OF PLANT–MICROBE–SOIL INTERACTIONS

During the previous two decades, a large number of plot-scale field manipulations of the environment have been established and maintained across the subarctic and arctic, many of which include soil and air warming with various types of passive greenhouses (Callaghan et al. 2004; van Wijk et al. 2004; Elmendorf et al. 2012). In some of the experimental sites, the scientific focus has been on plant–microbe–soil interactions and biogeochemistry. One of the earliest experiments, involving factorial manipulation of light, temperature, and nutrient availability has been maintained during more than two decades at a mesic treeline heath near Abisko, northern Sweden (Jonasson et al. 1999; Rinnan et al. 2007a) (Fig. 1a). This represents one of the longest ongoing ecosystem manipulation experiments in northern latitudes. The experiment consists of summer warming by open top, passive 1.2 × 1.2 m tent-like greenhouses, addition of fertilizer (simulating enhanced nutrient availability as an indirect effect of warming), and attenuation of 50 % of the light (simulating enhanced cloud cover) (Michelsen et al. 1996). Similar greenhouses and open-top chambers (OTCs) have also been used in warming experiments near Abisko in mountain birch (*Betula pubescens* ssp. *czerepanovii*) forest understory (Press et al. 1998; Sjögersten and Wookey 2009; Olsrud et al. 2010), alpine fellfield heath (Jonasson et al. 1999), wet heath (Rinnan et al. 2008) (Fig. 1b), higher altitude dry heat, meadow and tussock tundra (Björk et al. 2007; Molau 2010) and a peat bog (Dorrepaal et al. 2009) and typically lead to 1–2 °C soil warming, and to 3–4 °C air warming above ambient summer temperature. By placing heating cables in the soil, additional soil warming in forest understory has been achieved (Hartley et al. 1999), also in an experiment which included combined treatment with elevated CO_2 (Olsrud et al. 2010). OTCs have furthermore been erected in late autumn and early spring to increase the frequency of freeze–thaw cycles in order to examine how these cycles affect microbes, soil arthropods, and nutrient availability (Konestabo et al. 2007). In winter, OTCs and snow addition have been applied on a peat bog in order to cause erratic snowmelt and to alter snow accumulation patterns (Aerts et al. 2006). In winter, warming has also

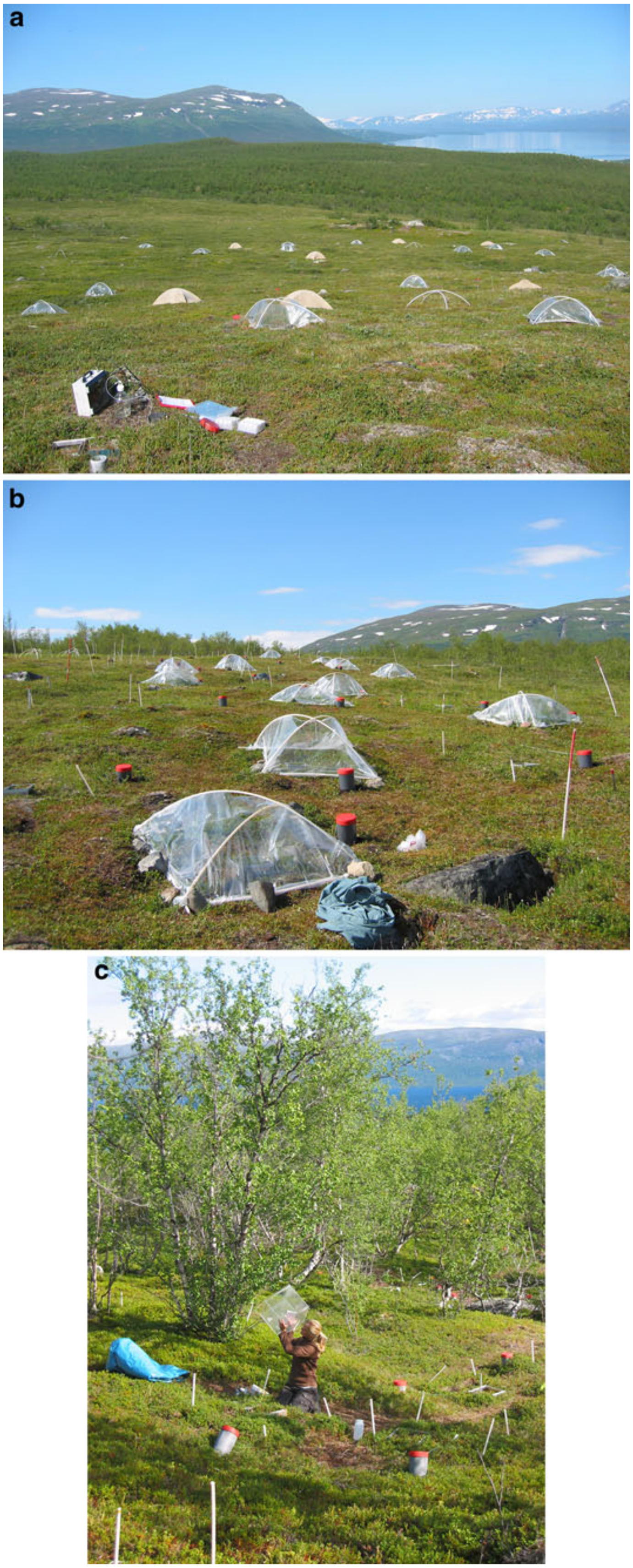

Fig. 1 Ecosystem manipulations near Abisko, Northern Sweden. **a** Mesic *Cassiope tetragona–Empetrum hermaphroditum–Betula nana* heath near the treeline, with manipulations of light (dome-shaped greenhouses with shading cloth), temperature (open-top plastic greenhouses), and nutrient availability (NPK fertilizer). **b** Mixed, wet dwarf shrub heath with open-top greenhouses and mountain birch litter addition plots in a fully factorial design. **c** Measurement of greenhouse gas exchange in species removal experiments in the understory of a mountain birch birch (*Betula pubescens* ssp. *czerepanovii*) forest. Photos by Anders Michelsen

been applied with infra-red heaters and soil cables to study the consequences of extreme winter warming events on heath ecosystem biota and processes (Bjerke et al. 2011; Bokhorst et al. 2011).

In addition to warming treatments, nutrients have frequently been added to experimental plots (Press et al. 1998; Jonasson et al. 1999). In high doses, responses to such additions (Jonasson and Michelsen 1996) increase our understanding of how nutrients act as drivers in these, often nutrient-poor ecosystems. In low doses, the additions are more similar to the natural pulse-increase in nutrient availability, which may take place periodically during, e.g., snow melt in spring or freeze–thaw cycles in autumn (Konestabo et al. 2007; Larsen et al. 2007a), with likely effects on microbial immobilization of nutrients (Andresen et al. 2008).

As an alternative to addition of inorganic nutrients, birch leaf litter has been added annually since 1999 in a long-term litter addition and warming experiment at a wet heath near Abisko (Sjursen et al. 2005; Rinnan et al. 2007b, 2008; Sorensen and Michelsen 2011) (Fig. 1b). The amount added each autumn is comparable to the litterfall in the mountain birch forest, now undergoing warming-induced expansion in Northern Scandinavia (Kullman and Öberg 2009; Rundqvist et al. 2011). The nutrients are gradually released from the litter by leaching and litter decomposition, and the experiment probably better simulates the stimulation of mineralization, as one of the probable effects of enhanced nutrient availability by warming (Rinnan et al. 2008).

Other experiments in the Abisko region have included changes of substrate quality, nutrient availability, and microbial biomass by addition of labile carbon (sugar) to stimulate microbial growth, fungicide (benomyl) and bactericides (penicillin and streptomycin) to control specific microorganisms, and plant removals (Fig. 1c) to examine plant–plant and plant–microbe interactions (Christensen et al. 1999; Michelsen et al. 1999; Haugwitz and Michelsen 2011; Haugwitz et al. 2011; Faubert et al. 2012). In addition, effects of enhanced UV-B on vascular plant, lichen, and moss performance and on nitrogen-fixing potential of cyanobacteria associated with mosses have been evaluated in experiments conducted in the area (Solheim et al. 2002; Arroniz-Crespo et al. 2011).

PLANT FUNCTIONAL TYPES, NUTRIENT AVAILABILITY, AND RESPONSIVENESS TO CHANGES

The experiments in the forest understory (Press et al. 1998), the wet (Sorensen and Michelsen 2011) and the mesic (Graglia et al. 2001) heaths and the high altitude fellfield (Michelsen et al. 1996) have shown that both warming and, in particular, enhanced nutrient availability promote a higher biomass of dwarf shrubs, but that subcanopy mosses and lichens decline strongly as the plant canopy closes. Hence, plant species diversity is expected to be reduced in subarctic heaths following warming because of loss of cryptogams, while plant C accumulation is expected to increase as woody plants with large stem masses increase their cover. However, if extreme events of winter warming occur, this may counteract shrub expansion because vascular plants are more sensitive to damage than lichens (Bjerke et al. 2011). At the mesic heath, effects of warming have progressed during the two decades of study (Table 1). Warming already led to significant increases in evergreen shrubs during the first 5 years of treatment (Jonasson et al. 1999), while the effect became significant for deciduous shrubs first after a decade (Table 1). After two decades, these effects were maintained, with about 50 % increase in shrub cover, and a reduction of moss and lichen cover to one-third of that in unperturbed plots (Fig. 2). As in other subarctic heaths, grasses, and forbs had low cover and did not respond significantly, even after two decades of warming (Sorensen et al. 2012). These responses are consistent with a global assessment of experimental climate warming on tundra vegetation, which has shown that shrubs increase with warming only where ambient temperature is highest, i.e., in the Subarctic and Low Arctic, whereas graminoids increase primarily in high arctic sites (Elmendorf et al. 2012).

Warming has resulted in either unchanged or occasionally increased nutrient availability (Table 1). For instance, inorganic phosphorus (P) availability increased after 5 years of warming at the mesic heath (Jonasson et al. 1999) and soil ammonium concentration increased after 15 years of treatment at the same site (Rinnan et al. 2007a), while midsummer responses were insignificant in other years (e.g., Sorensen et al. 2008b). Increased concentrations are consistent with data from several other sites showing stimulated mineralization rates (Robinson et al. 1995; Schmidt et al. 2002), which is a prerequisite for enhancement of plant nutrient pool sizes (Sorensen et al. 2008a, b).

In initial phases of warming, the expanding evergreen shrubs at the mesic heath responded by a tendency towards reduced leaf N concentration (Table 1; Michelsen et al. 1996) due to accelerated growth but intensified N limitation. By contrast, deciduous plants showed increased leaf N concentration but first after more than a decade (Sorensen et al. 2008b), suggesting that N mineralization now was sufficient to meet plant demand. After two decades, the N concentrations in warmed plots were similar to controls (Table 1). However, these responses differ not only between different time-spans of the warming experiments but also between ecosystem types. In evergreens from warmed fellfield plots, leaf N was reduced still after a

Table 1 Medium and long-term plant and soil responses to experimental warming with open-top tents at mesic *Cassiope tetragona* heath at the treeline near Abisko, Northern Sweden since 1989

Response variable/Time span	5-9 yrs	10-14 yrs	15-19 yrs	20-23 yrs
Plant				
Deciduous shrub cover or biomass	–	↑	n.d.	(↑)
Evergreen shrub cover or biomass	↑	–	n.d.	↑
Herb cover or biomass	–	–	n.d.	–
Moss cover or biomass	–	↓	n.d.	↓
Lichen cover or biomass	–	↓	n.d.	↓
Fine root biomass	↑	↑	–	n.d.
Deciduous leaf N concentration	–	↑	–	–
Evergreen leaf N concentration	(↓)	–	–	–
Soil				
Soil inorganic N concentration	–	–	↑	n.d.
Soil inorganic P concentration	↑	–	–	n.d.
Soil fungal biomass	–	–	–	n.d.
Microbial biomass C concentration	–	–	↓	n.d.
Soil C stock	–	–	n.d.	n.d.

Data are from measurements at peak plant biomass in late July or early August. Soil data are 0–10 cm depth. Direction of arrows indicates significant ($P < 0.05$) responses, evaluated with one-way ANOVA comparing warmed versus control plots ($n = 6$); "–" signifies no change; arrows in brackets indicate a tendency towards significance ($P < 0.05 < P < 0.10$); n.d. not determined

Data sources: Responses after 5–9 years: Jonasson et al. (1999), Ruess et al. (1999), Graglia et al. (2001); 10–14 years: Graglia et al. (2001); Clemmensen et al. (2006), van Wijk et al. (2004), Sorensen et al. (2008a, b), Michelsen and Jonasson (unpubl.); 15–19 years: Rinnan et al. (2007a, 2011b); 20–23 years: van Driel and Michelsen (unpubl.), Sorensen et al. (2012)

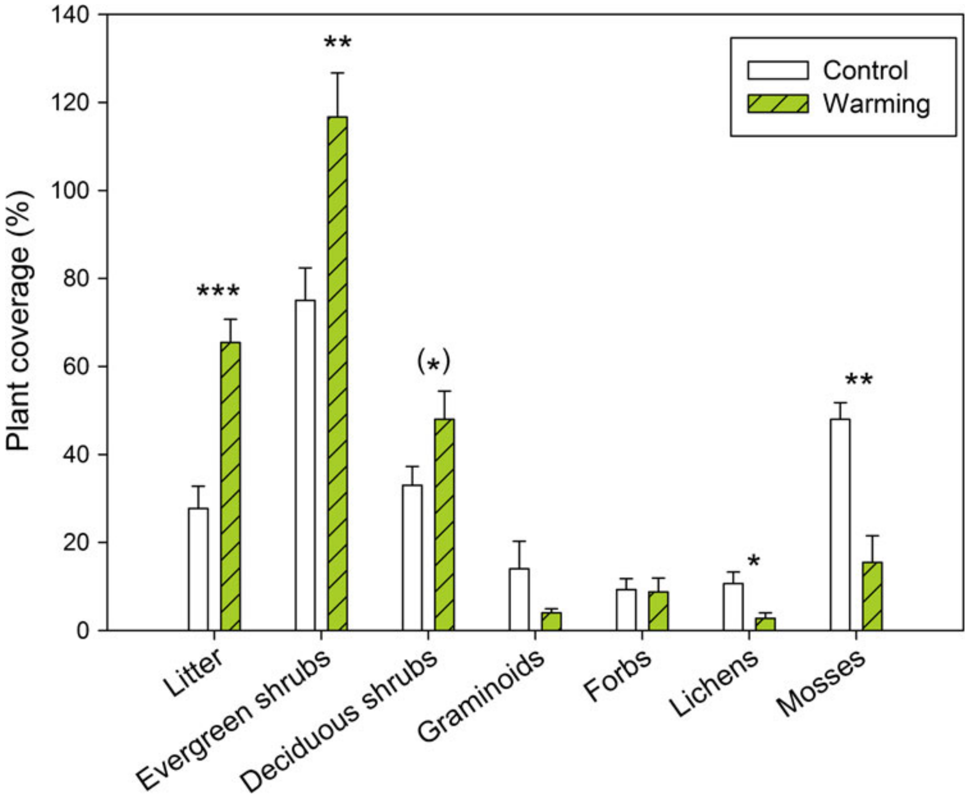

Fig. 2 Plant coverage at mesic treeline heath near Abisko, N. Sweden after 20 years of summer warming with open-top plastic greenhouses. Mean coverage (%) of different plant functional types (± SE, $n = 6$) in the control and warming treatment in analysis of 100 pin-points in July 2008. Results of one-way ANOVA's for different plant functional groups are indicated; (*) $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Modified from Sorensen et al. (2012)

decade and the tannin to N ratio was increased (Hansen et al. 2006). Consequently, if these responses persist in the fellfield, the changes could lead to lower tissue quality for herbivores and reduced decomposition, because of higher recalcitrance of litter.

Nutrient addition led to increased vascular plant biomass in several subarctic ecosystem types (Press et al. 1998; Jonasson et al. 1999), but plant biomass changes may be dampened due to immobilization of nutrients in microbial biomass (Jonasson et al. 1999; Haugwitz et al. 2011). These results suggest that the strong microbial nutrient sink in subarctic and alpine heaths may mitigate changes in the plant biomass even if warming increases the mineralization rate.

BELOWGROUND C POOLS AND ENVIRONMENTAL CHANGES

In many subarctic heaths, the major part of the total ecosystem carbon (C) pool is found in the soil, due to temperature constraints on decomposition (Jonasson et al. 1999). Hence, although the total plant C pool may increase by warming (Fig. 2; Table 1), the changes in soil pools may be decisive for overall ecosystem C balance. For instance, at the mesic heath (Fig. 1a) soil C was unchanged following a decade of warming (but increased by fertilizer addition) (Clemmensen et al. 2006; Table 1). This contrasts with expectations of increased warming-induced losses of C to the atmosphere from tundra ecosystems (Mack et al. 2004). While more CO_2 is emitted from the system in warmed plots (Illeris et al. 2004), the soil C stock at least to 15 cm depth is unchanged (Clemmensen et al. 2006). This suggests that a major part of the respired C is derived from recently fixed labile C from litter and root exudates (Grogan et al. 2001), and another part possibly from deeper soil layers, emphasizing that gains in plant C pools must be compared to potential losses in soil pools in the entire soil horizon in order to estimate the long-term fate of C storage and release (Mack et al. 2004).

Warming significantly increased the biomass of fine roots at the mesic heath, both after 5 and 10 years of treatment (Table 1), and in higher altitude dry heath warming increased the specific root length in the fine root fraction (Björk et al. 2007). Likewise, at the wet heath (Fig. 1b), the root biomass and the dissolved organic C (DOC) concentration in the rooting zone also increased, by about 30 and 17 %, respectively (Rinnan et al. 2008), possibly due to a higher supply of root exudates (Rinnan et al. 2008). However, warming led to 30 % higher losses of DOC below the rooting zone at the mesic heath (Michelsen et al., unpublished data), suggesting that warming will increase CO_2 emission from subarctic streams and water bodies through DOC derived from terrestrial ecosystems (Christensen et al. 2007) and reduce the quality of drinking water.

MYCORRHIZAL FUNGI: FUNCTION, INTERACTIONS WITH HOST PLANTS, AND RESPONSES TO ENVIRONMENTAL CHANGES

Mycorrhizal fungi form an important part of the belowground microbial community at subarctic and arctic heaths (Michelsen et al. 1998). Responses to environmental changes in these microbial groups are important, because mycorrhizal fungi supply the host plants with nutrients from the soil in exchange for labile C from the plant, and because fungal composition and diversity influences plant productivity, stability and diversity. In the Subarctic and Low Arctic, most studies of fungal responses to warming and nutrient addition (Clemmensen and Michelsen 2006; Clemmensen et al. 2006) or plant species interactions (Urcelay et al. 2003) have focused on ectomycorrhizal fungi, because many of these fungi easily can be distinguished morphologically and because they colonize roots of widespread arctic shrubs species as dwarf birch (*Betula nana*) and willows (*Salix* spp). For instance, the ectomycorrhizal community on roots of the prostrate willow (*Salix herbacea x polaris*) at an arctic-alpine fellfield consists of at least seven fungal species, of which some may also be found in boreal forests. Despite a short growing season of only 2.5 months or less, the fungal colonization of short root tips is high, and gradually increasing from 60 % at snowmelt (late June) to 85 % in early autumn (late August) (Clemmensen and Michelsen 2006).

Eleven years of warming of the fellfield generally had modest effects on the fungal community, with a balanced increase in the number of colonized root tips of all fungal morphotypes and no change in the total percentage of colonized root tips (Clemmensen and Michelsen 2006). However, one dominant fungal species (*Cenococcum geophilum*) decreased by warming and fertilization, which may indicate that a shift from drought stress tolerant fungi towards a dominance of fungi more tolerant to high level of mineral nutrients may take place if nutrient availability increases substantially due to anthropogenic disturbances (Clemmensen and Michelsen 2006). At the mesic heath (Fig. 1a), fungal biomass in fine roots increased in warmed plots due to higher root mass (Clemmensen et al. 2006) but did not increase in the soil (Table 1). Increased abundance of ectomycorrhizal fungi in a warmer climate may contribute to increased belowground C sink in tundra ecosystems due to the role of fungal biomass in humus formation, while C turnover may be accelerated due to enhanced activity by heterotrophic fungi and bacteria.

Although ectomycorrhizal shrubs dominate many arctic shrub tundra types and roots of most boreal and subarctic tree species, the ericoid mycorrhizal fungi, which form symbiosis with plants in the heather family, are probably more important for biogeochemical cycling of C and N in many tundra types. This is, firstly, because wide areas of both arctic and subarctic tundra and subarctic forest understory are dominated by such plants, and secondly because these fungi to a larger extent than ectomycorrhizal fungi produce enzymes that break down soil organic matter. In addition to ericoid mycorrhiza, ericaceous roots also harbor the so-called dark septate endophytes (DSE), fungi with unknown ecological function (Olsrud et al. 2007). Both fungal groups consist of many individual species, and molecular analysis of the fungal community of ericaceous roots from a mire near Abisko showed that the fungal community consisted of more than 30 operational taxonomic units of ericoid mycorrhizal fungi and DSE fungi (Kjøller et al. 2010). Furthermore, while four co-existing ericaceous plants at local scale shared fungal symbionts, plants a few meters away hosted a different fungal community (Kjøller et al. 2010). It is uncertain whether this spatial distribution of fungal species is due to random founder effects, plant biomass or environmental conditions, as nutrient availability or temperature.

In order to couple fungal community characterization to ecosystem function, effects of enhanced CO_2 and warming on overall fungal colonization of ericaceous roots by ericoid mycorrhizal and DSE fungi was recently studied in a mountain birch forest understory with ericoid shrubs and a grass near Abisko (Olsrud et al. 2010). The ericoid mycorrhizal fungi increased under elevated atmospheric CO_2 concentrations, but did not respond to warming following 6 years of treatment. This suggests that the higher ericoid mycorrhizal colonization under elevated CO_2 might be due to increased transport of C belowground to acquire limiting resources such as N, which was diluted in the plant leaves under enhanced CO_2. By contrast, arbuscular-mycorrhizal fungi showed reduced colonization of grass roots in elevated CO_2, possibly because they could not match the enhanced root growth. The DSE fungi in grass roots increased by warming of the birch forest understory but did not respond to enhanced CO_2 (Olsrud et al. 2010). However, the implications for plant N uptake and soil C storage remain unclear as the ecological function of this fungal group is unknown, and more research on this fungal group is warranted.

NITROGEN CYCLING IN STRONGLY N-LIMITED ECOSYSTEMS

Characterization of the controls on nitrogen (N) cycling is critical to understanding the functioning of high latitude ecosystems, and to predicting responses to perturbations. Plant C accumulation is limited by the lack of N in many tundra ecosystems because N input with deposition is low (e.g., 0.23 g N m^{-2} $year^{-1}$ in the Abisko region in N. Sweden; Karlsson et al. 2009; Sorensen and Michelsen 2011), partly due to long distance to N sources such as industry, agriculture, and traffic. Nitrogen fixation in lichens with cyanobacteria as symbionts, and in cyanobacteria associated with mosses, contribute with "new" N of the same order of magnitude as N deposition, with high fixation in surface crusts with cyanobacteria, intermediate fixation in moss and lower fixation in dense heaths (Sorensen et al. 2006). Nitrogen fixation associated with mosses is promoted by enhanced precipitation, while lichen-associated N_2 fixation is sensitive to enhanced UV-B (Solheim et al. 2002). A decade of warming led to a doubling of N_2 fixation in the wet heath at ecosystem level (Fig. 3) (Sorensen and Michelsen 2011). However, N_2 fixation associated with specific moss species tended to be reduced in warmed plots, partly because of drying, and partly because the denser canopy formed by the shrubs in the longer term led to reduced moss and lichen cover (Fig. 2). Although litter addition stimulated N_2 fixation after 10 years of treatment of the wet heath (Fig. 3), probably due to the relatively high P content in birch litter (Sorensen and Michelsen 2011), the very high nutrient input with NPK fertilizer strongly reduced N_2 fixation at the mesic heath (Fig. 3) (Sorensen et al. 2012). If N input increases due to deposition, N_2 fixation is likely to decrease. Similarly, both dryer conditions and shading from an increased vegetation cover in the long run leads to a negative feedback on N_2 fixation.

As for the N input, also the N export from many subarctic ecosystems is presently very low. One reason may be that plants partition the dissolved N, so that the most productive plants take up the most abundant form of N, while less productive species tap less abundant forms (McKane et al. 2002). The availability of N in different forms (NO_3^-, NH_4^+, amino acids), and the cycling between plants, microbes, fungal mycelium and soil has been intensively investigated at Abisko, both in experiments designed to address fundamental questions on plant N acquisition and mycorrhizal function (Andresen et al. 2008; Clemmensen et al. 2008; Krab et al. 2008), and in climate change related experiments (Sorensen et al. 2008a, b; Olsrud and Michelsen 2009).

The ^{15}N natural abundance has been used as a tool to investigate plant and microbial N acquisition at subarctic and arctic heaths (Michelsen et al. 1998). Ericoid mycorrhizal plants are clearly the most depleted in ^{15}N, ectomycorrhizal plants less depleted and non- and arbuscular-mycorrhizal plants relatively more enriched in ^{15}N (Michelsen et al. 1998), a pattern which has been confirmed as global phenomenon, although much less pronounced than in subarctic and arctic settings (Craine et al. 2009). The pattern is probably both due to differences in N forms acquired by plants with different

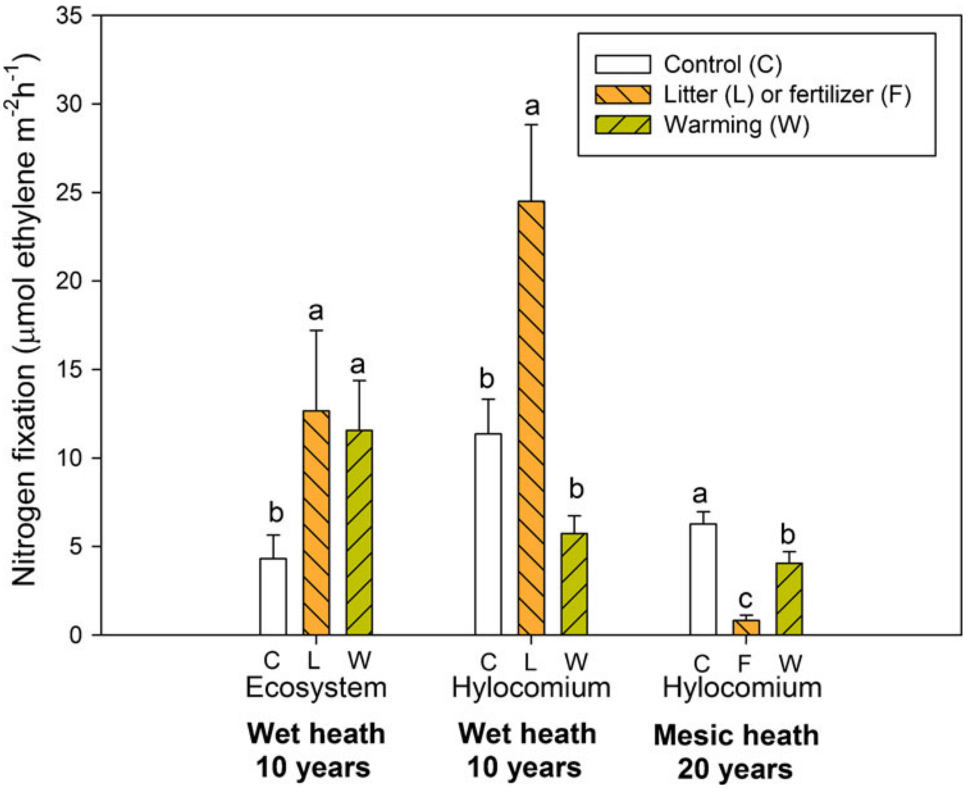

Fig. 3 Long-term effects of warming, litter addition and fertilizer addition on nitrogen fixation measured with the acetylene reduction method at ecosystem level (20 × 20 cm heath squares), and in plugs with the moss *Hylocomium splendens*. Data are from the wet heath after 10 years of treatment, and from the mesic heath after 20 years of treatment. Data are means across growing season, adapted from Sorensen and Michelsen (2011) and Sorensen et al. (2012). Significant differences between treatments investigated with repeated measures mixed model ANOVA with Tukey adjusted means comparison. Treatments influenced means in all cases, $P < 0.05$. Within site or type, *bars with the same letters* are not significantly different (± SE, $n = 6$)

mycorrhizal symbionts, and due to fractionation during transfer of N from fungi to host plant (Michelsen et al. 1998; Craine et al. 2009; Yano et al. 2010). Hence, as multiple reasons may explain ^{15}N natural abundance patterns, studies with ^{15}N enrichment may often provide clearer information on N transfers within ecosystem compartments and exchange with the environment. For instance, by injection of ^{15}N-enriched compounds separately in soil and in root-free soil compartments with mycorrhizal fungal access solely, it has been shown that ectomycorrhizal dwarf birch (*Betula nana*) roots showed highest preference for ammonium while the fungal component showed low nitrate uptake (Clemmensen et al. 2008). Furthermore, ecto- and ericoid mycorrhizal plants show higher N uptake than non-mycorrhizal plants in long-term studies, with uptake of N in both inorganic and organic form, as amino acids (Andresen et al. 2008).

Microbes generally immobilize more than half and even up to 90 % of pulse-added ^{15}N after a few days, while plants typically access less than 5 % (Andresen et al. 2008; Sorensen et al. 2008a, b). Low plant species diversity in some ecosystem types may imply that the plant community potentially could be less efficient in retaining N, which, consequently, may be leached from the ecosystem, for instance, during freeze–thaw in autumn and spring when plant N uptake still may take place but lysis of soil microbes is high (Larsen et al. 2007a). However, in most subarctic heath and forest understory systems, plants seem efficient in taking up N released from dying microbes. For instance, when adding low amounts of ^{15}N to a species-rich subarctic heath, and to a more species-poor birch forest understory, the N cycling in both ecosystems was dominated by a substantial turnover of ^{15}N recently acquired by microbes that coincided with a significant increase in plant ^{15}N uptake (Grogan and Jonasson 2003; Andresen et al. 2008).

Strong demand for N led to high plant retention of ^{15}N in the species-rich mesic heath (Fig. 1b) even 1 year after ^{15}N pulse-addition (Sorensen et al. 2008a, b), but ^{15}N export could potentially be higher in the species-poor ecosystem type with less diversified niches of plant functional types, which remain to be investigated. At the mesic heath, microbes harbored 90 % of the added ^{15}N one day after addition, but less than 30 % after 1 year, when more than 40 % of the total ^{15}N was strongly bound in recalcitrant non-microbial soil organic matter fractions, to which plants without ericoid mycorrhiza have limited or no access.

Interestingly, 14 years of summer climate manipulations at the mesic heath had little or no effect on the partitioning of added ^{15}N between plant, microbial and soil pools (Sorensen et al. 2008a, b). However, in the short term, environmental factors affect plant nutrient and C acquisition. For instance, light attenuation similar to an enhanced cloud cover led to reduced photosynthesis and allocation to mycorrhizal fungi, but mycorrhizal uptake of ^{15}N^{13}C-labeled amino acid was still high, demonstrating that plants prioritize N uptake in nutrient deficient subarctic tundra types (Olsrud and Michelsen 2009).

SOIL MICROBIAL COMMUNITY RESPONSES TO MANIPULATIONS

Because microbial activity governs the processing of soil C and because the microbial pool of N and P equals or even exceeds the amount stored in vegetation (Jonasson et al. 1999; Schmidt et al. 2002), it is vital to know how environmental factors affect the microbial biomass. The fumigation-extraction technique has been used to follow effects of experimental manipulations on microbial biomass over 15 years (Fig. 4).

The warming had not significantly affected microbial biomass C, N, or P in the mesic heath soils until after 15 manipulation years (Jonasson et al. 1999; Ruess et al. 1999; Rinnan et al. 2008), when the microbial biomass C concentration was 17 % lower in the warmed than in the control soil of the mesic heath (Rinnan et al. 2007a; Fig. 4). The reduction was not expected because the same treatment led to increased shrub biomass (Table 1) (Sorensen et al. 2008a, b, 2012). One of the reasons for the unchanged or even reduced microbial biomass could be top-down regulation caused by grazing by fungal and bacterial feeding nematodes, which doubled in abundance after 8 treatment years (Ruess et al. 1999). More specific analyses of the microbial community support the finding of reduced microbial biomass. Bacterial community growth rate was significantly decreased by warming, by as much as 73 % after 17 treatment years (Rinnan et al. 2011a). As microbial community composition had been little affected by warming (Rinnan et al. 2007b, 2008), the reduced growth rate appears to be due to lower substrate quality in the warmed soil. Changes were more distinct at the mesic heath with 15 manipulation years (Rinnan et al. 2007a) than in the wet heath site with 7 manipulation years (Rinnan et al. 2008). While the fungal biomass was unchanged (Table 1), it is likely that bacterial growth was limited by substrate availability, since the mainly N-limited bacterial communities had shifted towards limitation by C and P in response to 7 years of warming (Rinnan et al. 2007b).

In the long term, warming is expected to lead to higher soil nutrient availability following stimulated nutrient mineralization in soil (Callaghan et al. 2004). However, in situ buried bag studies suggest that the soil temperature increase by 1–2 °C as in the passive warming (Michelsen et al. 1996; Ruess et al. 1999) does not significantly increase the microbial net N mineralization (Robinson et al. 1995; Schmidt et al. 2002; Jonasson et al. 2006; Rinnan et al. 2007b). When soil warming by 5 °C was accomplished by heating cables buried 5 cm below the soil surface, seasonal net mineralization was transiently doubled after 2 years, but the difference disappeared after 5 years (Hartley et al. 1999). Hence, fertilization treatments at high doses, intended to mimic the expected higher soil nutrient availability in response to warming, do not therefore reflect long-term effects of climate warming but rather they serve as a means to study effects of alleviated nutrient limitation.

Effects of fertilization, a much more dramatic treatment than warming, have developed over long time: in the mesic heath, microbial biomass was marginally affected by fertilization after 5 (Jonasson et al. 1999) and 6 (Ruess et al. 1999) years but not after 10 treatment years (S. Jonasson and A. Michelsen, unpublished data). After 12 treatment years,

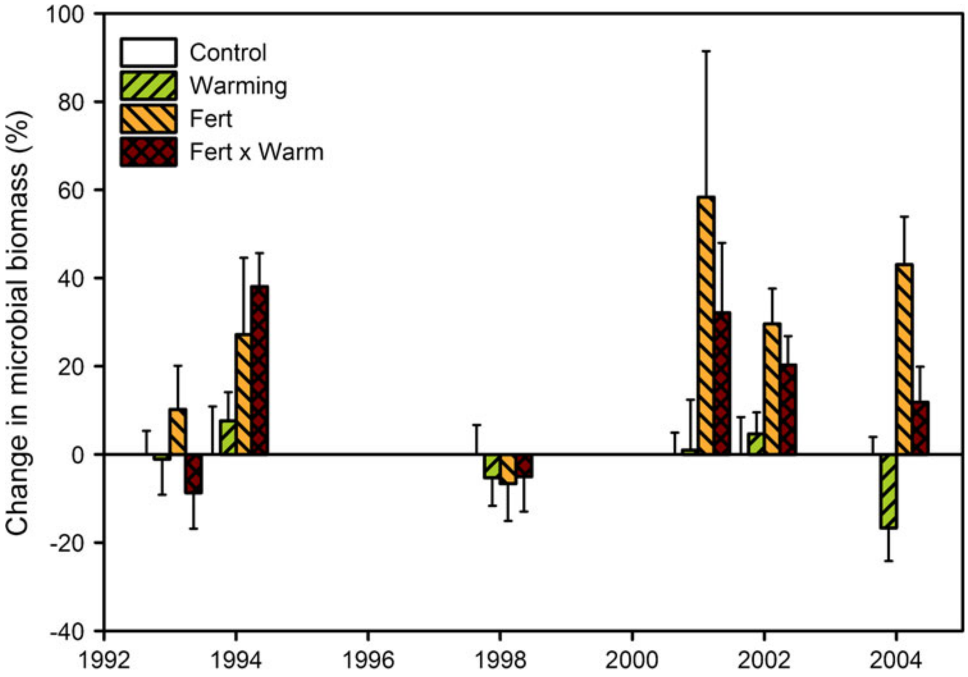

Fig. 4 Microbial biomass C in mesic shrub heath with open-top chambers and fertilizer addition plots in a fully factorial design. Treatments were initiated in 1989. The figure shows the relative change in microbial biomass C compared to control plots (± SE, $n = 6$). Data modified from Jonasson et al. (1999), Ruess et al. (1999), S. Jonasson and A. Michelsen (unpublished), Rinnan et al. (2007a) and Sorensen et al. (2008a, b). Microbial biomass C differed between years ($P < 0.001$; repeated measures two-way ANOVA) and was generally significantly higher in fertilized plots ($P < 0.01$) but with a tendency towards interaction between year and fertilizer treatment ($P < 0.1$)

there was 58 % more microbial biomass C in the fertilized soil as compared to unfertilized soil (Sorensen et al. 2008a), and this increase remained at 43 % with 3 more years of manipulation treatment (Rinnan et al. 2007a) (Fig. 4). At the alpine fellfield, which had been fertilized for 10 years, however, the microbial biomass was unchanged 6 years after the treatment ceased, except if labile C in the form of sugar also had been added, in which case microbial biomass C, N, and P was still higher than in control plots (Haugwitz et al. 2011). An analysis of the microbial community composition at the lower altitude heaths using lipid biomarkers has shown that the fertilization-induced increase in microbial biomass is mainly due to an increase in the amount of soil fungi (Rinnan et al. 2007a). Tracking incorporation of isotopic signature from different C substrates to microbial biomarker lipids has further revealed that fertilization stimulates fungal uptake of simple organic substrates and the breakdown of more complex substrates, as, e.g., vanillin (Rinnan et al., unpublished data).

The treatment with mountain birch litter addition, used to mimic the natural fertilization effect of the increasing leaf litter deposition following the ongoing deciduous shrub expansion, has not altered the N concentrations or pools in soil or microbial biomass, but it has increased the concentrations of inorganic and microbial biomass P (Rinnan et al. 2008). While the total microbial biomass was unaffected by this treatment, the relative proportion of Gram-positive bacteria in the microbial community increased (Rinnan et al. 2008). When combined with warming, litter addition significantly increased the bacterial growth rate and altered the chemical quality of the soil (Rinnan et al. 2007b).

Most manipulation treatments suffer from unwanted side effects. For soil microbial communities, the most critical of these is probably drying of soils in warming treatments, as water availability is one of the most important factors affecting microbial activity. It has been suggested that litter decomposition is limited by water availability in plots warmed by OTCs (Aerts 2006). The warming treatment of the mesic heath reduced the soil water content in the uppermost 5 cm by 37 % (Rinnan et al. 2007a) despite the access of rainwater to the plots both from the open top of the greenhouses and from surface runoff on the sloping terrain. Here and in the combined warming and litter addition treatment (Rinnan et al. 2007b), higher evaporation and transpiration from a higher plant biomass may partly explain the drying. Hence, drying of the soil surface may accompany warming, also under natural field conditions.

The warming-induced changes in microbial activity may influence the soil C stores, because microbial activity is one of the most important drivers determining the C balance of arctic soils under climate change. The responses in warming experiments described above have all been measured during the growing season, when the microbial biomass in these types of soils is largely constant (Jonasson et al. 1999). However, major fluctuations take place during winter and early spring, when the snowmelt water and repeated freeze–thaw cycles perturb the soil environment (Larsen et al. 2007a).

EXCHANGE OF GREENHOUSE GASES IN SUBARCTIC HEATH ECOSYSTEMS

Arctic soils harbor such a large amount of C so that its release to the atmosphere would seriously alter the atmospheric C concentrations. Carbon dioxide is taken up from the atmosphere by photosynthetic activity and released by respiration of plants, animals and microorganisms. The balance between uptake and release determines whether an ecosystem is a sink or source of CO_2, and this C balance can be altered by environmental perturbations and climate change. In general, it is expected that climate change stimulates plant biomass production and photosynthetic uptake of CO_2, but increases loss of C from soils (Mack et al. 2004).

Most research into effects of climate change on C balance of subarctic ecosystems has focused on wet peaty ecosystems with CH_4 emission comprising a significant part of the ecosystem gas exchange. Here, we concentrate on heaths, which are considered a small sink of CO_2 and CH_4 from the atmosphere. In the Torneträsk catchment area in Northern Sweden, the average CO_2 uptake by heaths is estimated to be 3 g C m^{-2} $year^{-1}$ (Christensen et al. 2007). However, spatial variation in CO_2 exchange is high (Fox et al. 2008), and the same site can be a sink in some years and a source of CO_2 in other years (Christensen et al. 2007).

After a decade of experimental manipulations at the mesic heath in Abisko (Fig. 1a), a chamber technique was used for in situ measurements of ecosystem CO_2 fluxes over the growing season (Illeris et al. 2004). Fertilization increased both ecosystem respiration and gross ecosystem production, while warming had no significant effects (Illeris et al. 2004). In contrast, summer warming by OTCs in tundra in Alaska and Canada, and in other tundra types in Scandinavia has been shown to increase annual CO_2 efflux (Welker et al. 2000, 2004; Sjögersten and Wookey 2009). The contrasting responses to warming may be due to differences in soil moisture conditions, which strongly control ecosystem respiration, especially in mesic-dry heath systems.

The wet heath site (Fig. 1b) was a net sink for CO_2 during the growing season, but both warming and litter addition treatments reduced net ecosystem CO_2 exchange so that the system shifted into a net source of CO_2 when the treatments were combined (Tiiva et al. 2008). The elevated temperature increased the decomposition of the added leaf litter and possibly also enhanced the release of previously accumulated C from the peaty soil, leading to higher CO_2 release than the photosynthetic CO_2 uptake by the increased plant biomass (Rinnan et al. 2008; Tiiva et al. 2008). Although respiration derived from recently photosynthesized C is more temperature-sensitive than respiration from soil organic matter C, climate warming can also accelerate respiration of deeper soil C (Dorrepaal et al. 2009).

Wintertime C losses can account to a significant part of the annual C budget (Fahnestock et al. 1999), and the C efflux is likely to increase if the snow depth increases (Welker et al. 2000; Larsen et al. 2007a). In the mesic heath, cold-season (October–May) respiration accounted for 22 % of the annual respiratory CO_2 release, and rather surprisingly, photosynthetic activity outside the growing season accounted for 19 % of the annual gross CO_2 uptake, partly compensating for the respiratory C losses (Larsen et al. 2007b). Freeze–thaw cycles appear to have few if any effects on CO_2 release (Larsen et al. 2007b).

The heath ecosystems are in general small net sinks for the greenhouse gas methane, which is consumed by methanotrophic bacteria in the aerobic soil. Inorganic N additions have been observed both to stimulate (Christensen et al. 1997) and inhibit (Christensen et al. 1999) methane consumption in subarctic heaths. Emission of another strong greenhouse gas, N_2O, from subarctic heath soils is minimal, and is stimulated by inorganic N additions (Christensen et al. 1999).

EMISSION OF BIOGENIC VOLATILE ORGANIC COMPOUNDS (BVOCS)

The subarctic heath and forest ecosystems are sources for a plethora of reactive trace gases called biogenic volatile organic compounds (BVOCs), which are emitted from plants both constitutively and in response to biotic and abiotic stresses. As an example of the emitted compounds, willow (*Salix*) species, mosses and sedges emit isoprene (Ekberg et al. 2009, 2011; Rinnan et al. 2011b), the crowberry (*Empetrum hermaphroditum*) sesquiterpenes (Faubert et al. 2012), *Vaccinium* species monoterpenes (Faubert et al. 2012), and the dwarf birch (*Betula nana* L.) and the mountain birch (*Betula pubescens* ssp. *czerepanovii*) emit many monoterpenes and sesquiterpenes (Haapanala et al. 2009; Rinnan et al. 2011b). Although the BVOCs are mainly released from vegetation, soils and microbial processes also contribute to the total ecosystem BVOC emissions (Faubert et al. 2012).

It seems that the subarctic BVOC emissions increase more per unit temperature increase than the emissions from vegetation at lower latitudes (Holst et al. 2010; Faubert et al. 2010). Warming of the wet heath (Fig. 1b) has been shown to double the emissions of monoterpenes and sesquiterpenes (Faubert et al. 2010) and to increase the isoprene emissions by 50–80 % (Tiiva et al. 2008; Fig. 5). Furthermore, especially when combined with mountain birch litter addition, warming increased the relative emission of the highly reactive sesquiterpenes (Fig. 5). The warming-induced increase in BVOC emission could be due to direct stimulation of BVOC production or release by higher air temperature, or due to indirect effects via long-term changes in vegetation composition or biomass in response to warming. The first explanation is most likely, because the warming effect was not significant when the open-top greenhouses were removed (Tiiva et al. 2008; Faubert et al. 2010).

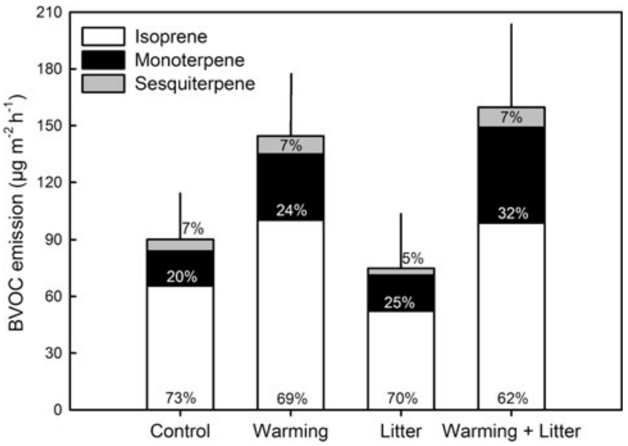

Fig. 5 Volatile organic compound emissions from mixed, wet dwarf shrub heath with warming by open-top chambers and litter addition plots. The figure shows average emissions (± SE, $n = 6$) from July 2006 and 2007, after 8–9 years of treatment. Data modified from Tiiva et al. (2008), and Faubert et al. (2010). Percentage of isoprene, monoterpene and sesquiterpene emissions of the total BVOC emission in each treatment is shown

Increased BVOC emissions in response to warming may influence climate via complex atmospheric processes (Peñuelas and Staudt 2010). In the arctic areas free of anthropogenic pollutants, the most relevant process is probably the formation of secondary organic aerosols with further effects on radiation scatter and cloud formation.

LONG-TERM FATE OF SUBARCTIC TUNDRA ECOSYSTEMS

Subarctic heath ecosystems are experiencing rapidly advancing climatic warming, which is shaping the vegetation cover of the tundra landscape with, e.g., mountain birch spreading to higher elevation and further north. The long-term experiments suggest that deciduous and evergreen shrubs will expand their cover at the expense of mosses and lichens. This affects the C and nutrient cycling in heath ecosystems, with consequences for C pools and greenhouse gas emissions. Warming will probably lead to enhanced emission of CO_2 and a whole range of reactive volatile organic compounds, which affects atmospheric environment. It is important to evaluate the consequences of climate change for the soil C stocks, because the large amount of C stored in the high latitude soils has a potential to intensify global warming if released to the atmosphere. The long-term field experiments also suggest that warming leads to reduced microbial biomass C, which may be due to top-down regulation by microbivores, and possibly lower organic matter quality due to progressive N limitation. Mycorrhizal fungi play an important role in the tight nutrient cycling, organic matter turnover and plant nutrient uptake in these inherently N deficient systems. Warming might increase soil nutrient availability, which leads to higher biomass of dwarf shrubs, but as mosses and lichens are strongly reduced when the plant canopy closes, associated N_2 fixation diminishes, which will moderate the rate of expansion of canopy forming shrubs in the longer run. As both vegetation and organic matter turnover in subarctic ecosystems respond slowly to changes and experimental results from the first and second decade of long-lasting field experiments may differ, it is essential to continue climate change related experiments over a long time span to be able to make reliable predictions of the truly long-term effects of climatic warming.

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