

LETTER

Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes

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Abstract

Whether climate change will turn cold biomes from large long-term carbon sinks into sources is hotly debated because of the great potential for ecosystem-mediated feedbacks to global climate. Critical are the direction, magnitude and generality of climate responses of plant litter decomposition. Here, we present the first quantitative analysis of the major climate-change-related drivers of litter decomposition rates in cold northern biomes worldwide. Leaf litters collected from the predominant species in 33 global change manipulation experiments in circum-arctic-alpine ecosystems were incubated simultaneously in two contrasting arctic life zones. We demonstrate that longer-term, large-scale changes to leaf litter decomposition will be driven primarily by both direct warming effects and concomitant shifts in plant growth form composition, with a much smaller role for changes in litter quality within species. Specifically, the ongoing warming-induced expansion of shrubs with recalcitrant leaf litter across cold biomes would constitute a negative feedback to global warming. Depending on the strength of other (previously reported) positive feedbacks of shrub expansion on soil carbon turnover, this may partly counteract direct warming enhancement of litter decomposition.

Keywords

Alpine, carbon, circum-arctic, global change, growth form, litter turnover, mass loss, vegetation change.

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INTRODUCTION

Cold northern biomes have been globally important accumulators of plant litter and soil organic carbon (ACIA 2005). Global warming and associated environmental changes are predicted to affect most regions of the northern hemisphere and will be particularly pronounced at high northern latitudes this century (IPCC 2001; ACIA 2005). Changes in the rate of decomposition and associated CO₂ release from dead plant material as a consequence of global warming could have profound repercussions for terrestrial carbon sequestration vs. losses in cold regions, feeding back to atmospheric CO₂ concentrations and the global climate (Gorham 1991; Callaghan *et al.* 2004a; Mack *et al.* 2004; Welker *et al.* 2004; Knorr *et al.* 2005). Not only do deeper and older carbon pools contribute importantly to such feedbacks, but also recently formed labile carbon pools, particularly litter (Christensen *et al.* 1998; Grogan *et al.* 2001). The litter feedback to climate will depend principally on the balance between litter accumulation vs. decomposition. Litter decomposition rates may change owing to direct effects of climate change on microbial activity and/or to indirect effects on microbial activity through changing litter quality (Hobbie 1996; Wardle 2002; Parton *et al.* 2007). Climate warming, or the elevated atmospheric CO₂ concentrations partly causing it (IPCC 2001), as well as increased UV-B radiation in the Arctic, may alter the litter quality of extant species via their 'afterlife' effects on foliage quality (Norby *et al.* 2001; Tolvanen & Henry 2001; ACIA 2005; Aerts 2006). In the long-term, however, shifts in vegetation composition, particularly in terms of the predominant plant functional types or growth forms, may also result in overall shifts in litter quality and decomposability (Hobbie *et al.* 2001; Saleska *et al.* 2002; Quedsted *et al.* 2003).

Recent climate warming has already caused drastic recent changes to vegetation abundance and composition of arctic and alpine life zones of the northern hemisphere, including the widespread appearance and expansion of shrubs in low plant communities (Myeni *et al.* 1997; Kullman 2002; Sanz-Elorza *et al.* 2003; ACIA 2005; Chapin *et al.* 2005; Sturm *et al.* 2005; Tape *et al.* 2006). Models predict further dramatic increases of woody plant biomass and vegetation productivity in response to further warming of cold biomes during the 21st century (Epstein *et al.* 2000; Kittel *et al.* 2000; Cramer *et al.* 2001; Saleska *et al.* 2002; Callaghan *et al.* 2004a). Increased productivity will probably increase litter production, leaves being the predominant source of annual aboveground litter production. The degree to which this litter will accumulate or disappear, and thereby feed back to climate, will depend on its rate of decomposition. In order to predict future large-scale changes to terrestrial litter turnover in the cold northern biomes of the world, it is important to simultaneously assess the relative contributions to the rate of decomposition of: (1) direct climate effects, (2) climate-induced changes to litter quality of a given species, (3) climate-induced changes to litter quality through changes to plant species and growth form composition and of (4) variation in litter quality of given species in relation to site characteristics. Here we present the results of a circum-arctic-alpine study that, for the first time, disentangles and quantifies the contributions and main interactions of each of these factors on litter decomposition rates directly and comprehensively in one large *in-situ* experiment.

METHODS

Experimental sites of litter origin and species

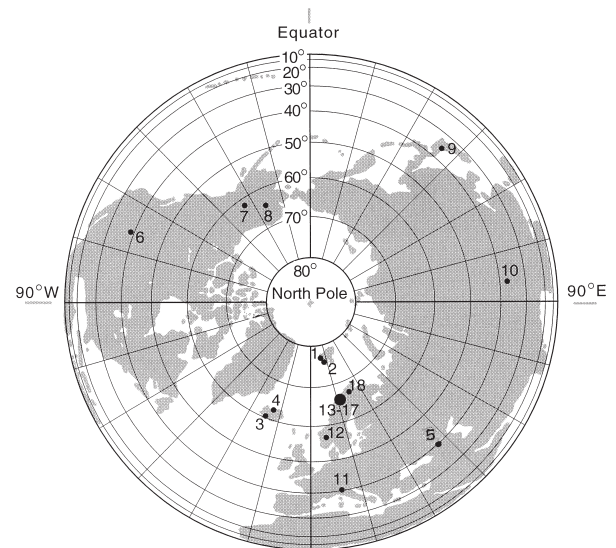
We formed the Meeting of Litters consortium, involving scientists representing a total of 33 experiments with

medium-term *in-situ* ecosystem climate manipulations in diverse tundra, heath, fell-field and meadow ecosystems above or on the natural climatic tree-line, in 18 geographically widespread sites in 10 northern hemisphere countries (Fig. 1). There were 3 experiments in high-arctic sites (Svalbard); 13 in sub-arctic and boreal sites at low altitude (Alaska, N Sweden, N Finland, Iceland); 7 in sub-arctic and boreal alpine (> 900 m alt.) sites (Canada, N Sweden, Norway); 10 in lower latitude alpine (> 1800 m alt.) sites (Tibetan Plateau, Japan, Caucasus, Western USA, Italy). The experiments comprised both single factors and factorial combinations of treatments (Fig. 1) as well as ambient (control) treatments. The majority of the experiments involved warming treatments (1–4 °C air warming) mimicking warming scenarios for this century (IPCC 2001), and/or fertilization treatments thought to mimic the greater mineral nutrient availability that is likely to be induced by warming (Rustad *et al.* 2001; Mack *et al.* 2004). Further global change treatments (Fig. 1) included growing season watering (mimicking an increased precipitation scenario), increased ultraviolet-B light irradiance (mimicking the ‘ozone hole’), elevated atmospheric CO₂ concentration and increased shading (mimicking effects of a new overstorey canopy and/or increased cloudiness). These latter treatments were relatively poorly represented here, as they are also sparsely represented in *in-situ* global change experiments in cold biomes. Details of the experimental sites and of all treatments in the different experiments (e.g. method, treatment levels, duration) are given in Appendix S1.

We collected fresh leaf litter of the predominant species in each experiment. These species represented the dominant vascular growth forms (Chapin *et al.* 1996) in their sites: deciduous dwarf shrubs (11 species; 35 species by experiment combinations), evergreen dwarf shrubs (4 species; 19 combinations); grasses (7 species; 13 combinations); sedges (6 species; 14 combinations) and forbs (herbaceous dicots, 14 species, 35 combinations) (further details in Appendix S1). We additionally included two mosses.

Litter processing

Each experimental plot of each global change manipulation treatment in each site provided one litter sample for a given species. This way we could retain the original replication in these experiments in the blocked design of the litter incubations (see below). Most samples were collected between August and October 2000, but litter from Toolik Lake (Alaska) was from August 2001, while *Cassiope tetragona* litter from the Paddus and Slättatjåkka sites (both Abisko, N Sweden) was collected in 1996 and frozen until processing in September 2000.



33 Arctic and Alpine Field Experiments in the Meeting of Litters:

- | | |
|---|--|
| 1. Ny Ålesund, Svalbard, Norway (F,I) | 10. Qinghai, China (4 exp., W) |
| 2. Adventdalen, Svalbard (2 exp.; UV,W) | 11. M. Rondinaio, Italy (2 exp., F) |
| 3. Thingvellir, Iceland (W) | 12. Finse, Norway (2 exp.; W,F) |
| 4. Audkuluheidi, Iceland (W) | 13. Latnjajaure, Sweden (3 exp.: W,F) |
| 5. Caucasus, Russia (F,I) | 14. Abisko, Sweden (4 exp.: W,F,I,CO ₂ ,SH) |
| 6. Medicine Bow, USA (2 exp.: W) | 15. Paddus, Sweden (2 exp.; W,F,SH) |
| 7. Ruby Range, Canada (W,F) | 16. Slättatjåkka (Abisko), Sweden (W,F,SH) |
| 8. Toolik Lake, Alaska, USA (W,F,SH) | 17. Stordalen, Sweden (2 exp.; W,CO ₂ ,F) |
| 9. Tateyama, Japan (W) | 18. Kilpisjärvi, Finland (2 exp.; W,F) |

Treatments: W, warming; F, fertilising; I, irrigation; CO₂, elevated CO₂ concentration; UV, elevated UVB irradiance; SH, shading

Figure 1 The Northern Hemisphere with sites and *in situ* global change experiments (exp.) from which leaf litter was collected and incubated. The total number of experiments in which each treatment is represented equals: 24 W, 17 F, 4 I, 2 CO₂, 4 UV, 3 SH, 8 W*F^d, 3 F*I, 1 W*CO₂, 1 W*UV, 1 CO₂*UV, 1 CO₂*I, 1 UV*I, 1 CO₂*UV*I (*combination of treatments). All 33 experiments had a control or ambient treatment. For details about the experiments see Appendix S1.

We collected fresh, undecomposed leaf litter of the predominant species in each of these sites according to a standard project protocol based on Quedstedt *et al.* (2003). For species that retain dead leaves on the plant (e.g. graminoids, evergreens, mosses) these were cut off. Petioles that remained attached to the leaf blades were not removed. We avoided collecting partly eaten or diseased leaves. All leaf litter was stored air-dried in the dark. We assembled all litter collections in Amsterdam, where we processed each of the litter samples into two similar, preweighed subsamples sealed into litterbags. A third representative subsample was used for analysis of moisture percentage (70 °C, 48 h) in order to calculate oven-dry mass of the litterbag subsamples. We used 1 mm nylon mesh voile as the standard litterbag material, but for some very small-leaved or narrow-leaved species we had to use 0.3 mm mesh (see Control experiments below). The standard amount

of air-dried sample per bag was *c.* 500 mg where enough litter was available, but we used *c.* 300 mg or *c.* 100 mg (in correspondingly smaller bags) for those species by site by treatment combinations that yielded insufficient amounts of litter (see Control experiments below).

We then transferred all litterbags to North Sweden, where we remoistened them with very low-mineral water before 2-year incubation commenced on 30/31 August 2001. Each of the two litterbag subsets, containing samples from the 33 sites, was then incubated simultaneously in one of two *in situ* 'litter beds' *sensu* Cornelissen (1996), each representing a contrasting Litter incubation life zone (LILZ). The colder site (Latnjajaure, alt. 980 m a.s.l., 68°21.5' N, 18°29.5' E) was a snow bed meadow with a subarctic-alpine climate, akin to a mid-arctic climate at lower altitudes: *c.* 87 snow-free days with mean temperature > 0 °C annually, growing season mean air temperature of 5.8 °C, and 572 thawing degree days (sum of daily temperatures > 0 °C). The milder site (Abisko, alt. 380 m a.s.l., 68°21' N, 18°49' E) was a birch heath tundra with a subarctic climate: *c.* 167 snow-free days with mean temperature > 0 °C annually, growing season mean air temperature 9.5 °C, and 1164 thawing degree days (data from meteorological stations at Latnjajaure and Abisko). Soil water availability appears to be non-limiting in both sites during the frost-free season. The difference in climate between these sites (3.7 °C warmer during a much longer season of thawed soil in Abisko) is within the predicted range of warming at high northern latitudes this century (IPCC 2001), while the different incubation mediums used at each site (see below) could represent realistic future shifts in litter composition from colder to milder life zones (zono-biomes or oro-biomes *sensu* Walter 1984) at given locations.

The Latnjajaure litter bed consisted of six 0.18 m tall wooden frames (sunk 30 mm into the soil partly onto the rocky matrix) filled with a litter incubation matrix consisting of multiple high altitude species (with high proportions of *Eriophorum* spp., *Carex* spp., *Calamagrostis lapponica*, *Vaccinium uliginosum*, *Betula nana*). The litter bags were laid out flat, without overlap, on top of the very low and sparse vegetation (any plants taller than 20 mm were cut), then covered with a 10 mm layer of the incubation medium (which declined to 5 mm for most of the incubation after initial compaction). The pre-existing Abisko litter bed (details in Quedsted *et al.* 2003) consisted of three wooden frames with several compartments each, divided into a total of six sections for the current experiment. The composition of the litter medium in this litter bed (predominantly *Betula pubescens*, dwarf shrubs, some forbs and graminoids), collected from predominant lower-altitude ecosystems, followed Quedsted *et al.* (2003). Here the litterbags were laid

out inside the litter medium, with *c.* 20 mm of litter on top. The litter incubation medium was held in place in both litter beds by stretching very large-mesh nylon netting across, after which the litter beds were made mammal-proof by stapling chicken-wire onto the frames. Each of the six frames or sections in each litter bed served statistically as a block hosting a litter sample of one of the replicate plots of each site by species by treatment combination. On 30/31 August 2003 all litterbags were retrieved and transported to Amsterdam. The litter samples were cleaned up and dried (70 °C, 48 h). Litter mass loss % over 2 years was expressed on the basis of initial dry mass.

Control experiments

We checked for the effects of mesh size on litter mass loss % by including additionally 36 pairs of subsamples (18 pairs for each litter incubation site) with both 1 and 0.3 mm mesh representing a wide range of species by site combinations and all vascular growth forms (deciduous and evergreen shrubs, graminoids, forbs). We found no significant mesh size effect in two-tailed paired *t*-tests, and a strong relationship between mass loss in the two mesh sizes (milder site Abisko: $t = 1.98$, $P = 0.064$, $R^2 = 0.91$; colder site Latnjajaure: $t = 1.85$, $P = 0.081$, $R^2 = 0.95$). We also checked for the effects of initial litter amount on mass loss % by including additional samples of 55 different species by site by treatment combinations, for which we employed two or three subsamples with different litter amounts (100, 300, 500 mg), again with all vascular growth forms represented. In analyses of covariance on arcsine-square-root-transformed data (see below), with combination as the fixed factor and litter amount as the covariate, we found no significant effects of initial litter amount (milder site Abisko: 55 combinations $F = 0.3$, $P < 0.001$, initial amount $F = 2.48$, $P = 0.12$; colder site Latnjajaure: 55 combinations $F = 15.4$, $P < 0.001$, initial amount $F = 1.90$, $P = 0.17$). Similar ANCOVAs within each of the vascular growth forms revealed no trends for initial litter amount either (data not shown). In all subsequent analyses, we took the average litter mass loss % for any sample represented by more than one subsample for mesh size or initial amount.

The litter from the Caucasus experiment was only incubated in the milder Abisko site (for 1 year) and was added to the big experiment on 31 August 2002. Based on a previous study in the same incubation bed (Quedsted *et al.* 2003) we knew that the ranking of mass losses among species was robust to incubation duration. Using linear regressions, data for Caucasus samples (herbaceous species only) could therefore be transformed from 1-year (X) to

2-year values (Y) from that study (forbs: $Y = 42.4 \ln(X) - 99$, $R^2 = 0.87$, $N = 32$ species; monocots: $Y = 44.5 \ln(X) - 103$, $R^2 = 0.84$, $N = 12$ species).

Data analysis

All litter mass loss % data were arcsine-square-root transformed prior to any subsequent analysis so as to approach normal distributions and homogeneity of variance as indicated by visual inspection of percentile and residual plots (see also Quasted *et al.* 2003). Initial ANOVAs with factors Site of litter origin (SLO) by Species by Block including the data for ambient (control) plots only, revealed no significant Block effects on litter mass loss, or interactions of Blocks with Species and/or SLO, for either of the litter incubation beds (details not shown here). Therefore, Blocks were excluded from further analyses. SLO by Species by GCT combinations with one litter sample only were removed. We first ran an ANOVA on transformed mass loss % with the following main independent variables: SLO (df = 34) (GCT, excluding interaction treatments occurring in only one experiment, df = 9), LILZ (df = 1), Growth form (GF, df = 5), and Species nested within GF (df = 36). This analysis revealed that the variance due to nested Species (MS = 0.254, $F = 56.2$, $P < 0.001$) explained only 11% of the variance due to GF (MS = 2.281, $F = 503.7$, $P < 0.001$), while GF and LILZ climate together explained 79% of the total variance due to the main effects plus two-way interactions. Based on these findings, we carried out a subsequent four-way ANOVA as above without the nested Species, the results of which are summarized in Fig. 2. For a subsequent two-way ANOVA to

test the effects of GF and LILZ, we used only mass loss data for litters from ambient plots of each experiment. Within each GF and LILZ combination, the mean for each Species*SLO combination was considered as a replicate observation.

RESULTS

To tease apart the relative contributions of different factors to litter decomposition rate, we examined four primary variables and their interactions: (1) the direct climate effect as measured in a colder vs. a milder LILZ; (2) climate effects as measured by experimental global change treatment effects on litter quality (GCT); (3) differences in litter quality among different plant growth forms (GF), and (4) differences in litter quality of given species from sites with different climate and soil characteristics (SLO). A four-way analysis of variance (total df = 1766) revealed that both direct climate effects (LILZ) and plant growth form effects (GF) were the principal drivers of variation in 2-year leaf litter mass loss, together accounting for 80.4% of the explained variance (Fig. 2). Subsequent analysis of the ambient (control) plots from all sites revealed there were significant, non-interactive effects of both LILZ and plant growth form (two-way ANOVA: GF, $F = 84.7$, $P < 0.001$; LILZ, $F = 50.0$, $P < 0.001$; GF by LILZ interaction, $F = 0.98$, $P = 0.43$; a similar two-way ANOVA excluding mosses gave similar results, data not shown). Litter mass loss was 42% faster in the warmer than in the colder LILZ, reflecting differences of 3.7 °C in soil temperature and nearly twice as long a season of thawed soil. This range of difference in litter mass loss was similar to that among growth forms within each of the incubation sites; on average grass and sedge litters were decomposed 40% faster than shrub litter (Fig. 3). Forbs decomposed consistently faster than grasses or sedges (herbaceous monocots), and all three herbaceous growth forms decomposed consistently faster than both shrub types (Fig. 3). Given the broad representation of these predominant growth forms across so many contrasting sites, we believe these relationships of decomposition rate to LILZ and GF to apply throughout cold biomes.

Site of litter origin contributed 7.4% to the explained variance in litter mass loss. This effect was due primarily to variability within each species between sites rather than to a species-by-site interaction indicating that our results are not biased by species selection (four-way ANOVA using six species with litter collected from at least three distant sites, with factors SPECIES, SLO, LILZ and GCT; total df = 681; SLO, $F = 10.0$, $P < 0.001$; SPECIES by SLO interaction, $F = 2.77$, $P = 0.064$). Which site factors contributed most strongly to litter quality and mass loss is presently unknown. Surprisingly, variation in litter decomposability due to experimental global change treatments

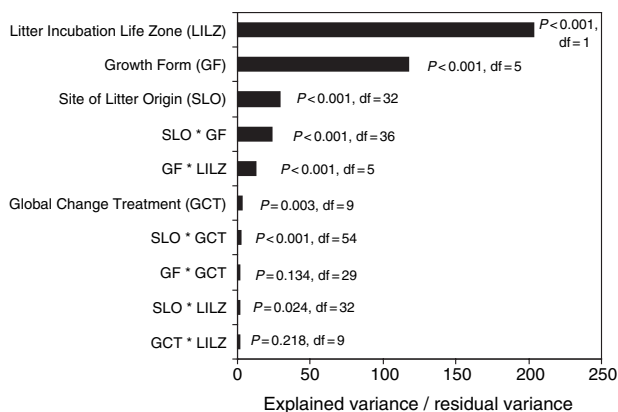


Figure 2 Results of a four-way analysis of variance unravelling the key biotic and abiotic effects on % mass loss of leaf litters, based on the predominant plant species in 33 experiments in arctic and alpine sites in the Northern Hemisphere (see Fig. 1). Mass loss % data were arcsine(square-root(100/x)) transformed prior to analysis. Total df = 1766. Explained variance/residual variance corresponds with the F values of the ANOVA.

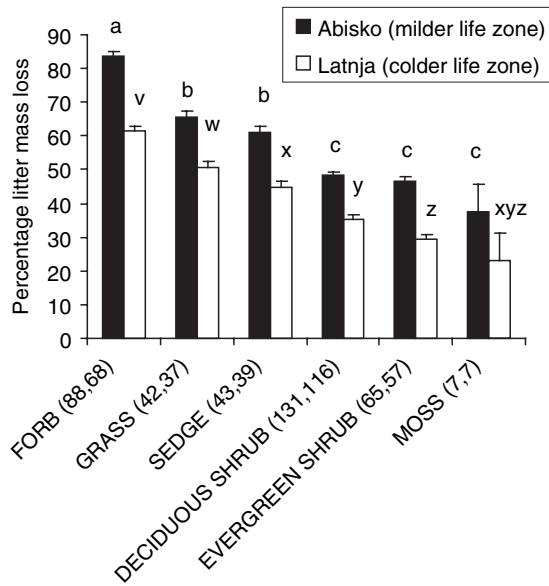


Figure 3 Mean mass loss % of leaf litters from predominant plants of six growth forms collected from ambient plots in circum-arctic-alpine sites, after 2 years of outdoor incubation in two contrasting Litter incubation life zones (LILZ). Numbers in parentheses refer to replication in the milder LILZ (Abisko) and the colder LILZ (Latnja), respectively. ANOVA output: Growth Form $F = 84.7$, $P < 0.001$; LILZ $F = 50.0$, $P < 0.001$; GF by LILZ interaction $F = 0.98$, $P = 0.43$. Standard errors are shown one-sided. Within each LILZ, growth forms with the same letter are not significantly different in *post-hoc* Games–Howell tests.

contributed only 0.71% to the explained variance in mass loss (or only 1.2% if species was used instead of GF in an alternative four-way ANOVA, data not shown).

DISCUSSION

Our results on the proportional contributions of different drivers of leaf litter decomposition rate may have important implications for predictions about future contributions of cold northern biomes to carbon dynamics worldwide. Shrub expansion into low-stature communities has occurred in many cold regions of the world (Tape *et al.* 2006). In the Arctic, for instance, shrubs have expanded in recent decades and caused substantial greening of the tundra (Myeni *et al.* 1997; Sturm *et al.* 2005; Tape *et al.* 2006), while low stature alpine ecosystems in Europe have also seen substantial recent shrub invasions (Theurillat & Guisan 2001; Kullman 2002; Sanz-Elorza *et al.* 2003). Field climate manipulation experiments have revealed similar shrub expansion in response to warming in arctic (Arft *et al.* 1999; Dormann & Woodin 2002; van Wijk *et al.* 2004; Walker *et al.* 2006) and alpine sites (Harte & Shaw 1995; Jónsdóttir *et al.* 2005; Klein *et al.* 2007). Moreover, models predict not only strong shrub

expansion in lower and high arctic tundra on a century time-scale, but also relative shifts from sedges to shrubs (Epstein *et al.* 2000, 2004). What will happen to the increasing absolute and relative leaf litter mass produced and shed by these shrubs in warming cold biomes? Our results suggest that the factors driving decomposition in the northern cold biomes will result in both a positive and a negative feedback to warming. The positive feedback will result from direct temperature effects on decomposition whereby warming enhances decomposition rates and, hence, increases the leaf litter carbon released into the atmosphere in response to further warming this century (Hobbie *et al.* 2001). There is also, however, a negative feedback that results from the warming-induced shifts in plant growth-form composition. Here, the higher quality, faster decomposing graminoid and forb litter is replaced with the lower quality, slower decomposing shrub leaf litter; this reduces the amount of carbon released to the atmosphere, and nutrients released in the soil to support plant production (Shaver *et al.* 2000). This negative feedback could partly offset the direct warming-induced acceleration of litter decomposition and should be incorporated into large-scale climate and carbon cycling models (Cramer *et al.* 2001; Stith *et al.* 2003).

Other shifts in growth-form abundance could also be important with respect to large-scale changes in litter decomposition rate. A relative shift from forbs to graminoids in response to warming and/or fertilization has been reported for several high-alpine and high-arctic herbaceous communities (Zhang & Welker 1996; Soudzilovskaia *et al.* 2005; Walker *et al.* 2006; but see Klein *et al.* 2007 for a counter example). Such a shift could lead to similar negative feedback due to reduced leaf litter decomposition rates. In contrast, global-change impacts on bryophytes have been little studied so far and have not yet revealed any consistent large-scale abundance or productivity responses as yet, although there may be a slight negative trend (Weltzin *et al.* 2001; van Wijk *et al.* 2004; Walker *et al.* 2006). Given the high abundance of mosses in many cold biomes, any consistent global change effects on the relative abundance of mosses are likely to feed back to carbon cycling, partly through their low litter quality and decomposability (Ross-wall *et al.* 1975; Hobbie *et al.* 2001; Dorrepaal *et al.* 2005; Fig. 3).

Our data have revealed the potential of increasing shrub leaf litter accumulation to reduce accelerated carbon losses due to the direct warming effects on litter decomposition rates. The next question is to which extent this litter feedback will affect large-scale soil carbon stocks (Saleska *et al.* 2002; Sturm *et al.* 2005). To answer this question, other reported feedbacks on the carbon cycle arising from increasing shrub abundance should be considered. First, graminoids at least in Alaskan tundra tend to have relatively deep root systems. The more shallow root systems of shrubs

are deposited generally in the drier, warmer upper soil layers, where decomposition rates will generally be higher (Mack *et al.* 2004). Also, belowground carbon inputs tend to be reduced in moist, graminoid-dominated ecosystems with shrub invasion, both in the Arctic and in warmer regions of the world (Jackson *et al.* 2002; Sturm *et al.* 2005). Second, increased litter accumulation resulting from increased productivity and associated litter production of shrubs (Shaver *et al.* 2001), combined with their lower rates of decomposition, may increase fuel loads and the flammability of the litter layer. Stems and branches of woody plants generally decompose more slowly than leaves (Preston *et al.* 2000; Hobbie *et al.* 2001), presumably further adding to litter accumulation (Weintraub & Schimel 2005) and fuel load. An increase in the flammability of the litter layer might promote fire-induced carbon release to the atmosphere in cold biomes, although the magnitude of increase will depend on precipitation and soil hydrology trends (Chapin & Starfield 1997; Hobbie *et al.* 2001; Thonicke *et al.* 2001). Third, increasing shrub canopy cover could at the same time induce negative feedback to soil carbon sequestration due to soil cooling below a shrub canopy in summer (Callaghan *et al.* 2004b), and positive feedback from insulating effects of increased snow captured and held by the shrub cover (Callaghan *et al.* 2004a; Sturm *et al.* 2005). Together with positive feedback of shrub expansion due to reductions in surface albedo, particularly in spring, this is likely to result in net soil warming and accelerated carbon and nutrient mineralization, at least in arctic Alaska (Chapin *et al.* 2005). Furthermore, the relative strengths of these various feedbacks due to growth form shifts should be considered in the context of longer-term warming effects on deeper, soil organic carbon dynamics, and of positive feedbacks from severe disturbances other than fire, e.g. pest outbreaks, human exploitative land-use and thermokarst (Chapin & Starfield 1997; Hobbie *et al.* 2001; Thonicke *et al.* 2001; Callaghan *et al.* 2004a; Chapin *et al.* 2005; Weintraub & Schimel 2005). As warming and associated vegetation shifts can affect soil carbon stocks even over decadal time scales (Saleska *et al.* 2002; Mack *et al.* 2004), the long-term warming treatments that supplied the litter for this experiment could provide an excellent opportunity to test the net effect on soil carbon of the growth form feedbacks presented here.

We conclude that not only direct climate warming effects, but also broad shifts in vegetation composition have the potential to be important drivers of future patterns of litter accumulation vs. decomposition in cold northern biomes. A next challenge will be to quantify the importance of possible negative feedback on carbon cycling due to growth form shifts, particularly the expansion of shrubs. Such quantification will have to be done by linking such feedback quantitatively to the other

important feedbacks on carbon cycling operating simultaneously.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Details of litter collection sites, species and experiments.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01051.x>

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