Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems

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Abstract

Tundra ecosystems are widely recognized as precious areas and globally important carbon (C) sinks, yet our understanding of potential threats to these habitats and their large soil C store is limited. Land-use changes and conservation measures in temperate regions have led to a dramatic expansion of arctic-breeding geese, making them important herbivores of high-latitude systems. In field experiments conducted in high-Arctic Spitsbergen, Svalbard, we demonstrate that a brief period of early season belowground foraging by pink-footed geese is sufficient to strongly reduce C sink strength and soil C stocks of arctic tundra. Mechanisms are suggested whereby vegetation disruption due to repeated use of grubbed areas opens the soil organic layer to erosion and will thus lead to progressive C loss. Our study shows, for the first time, that increases in goose abundance through land-use change and conservation measures in temperate climes can dramatically affect the C balance of arctic tundra.

Keywords: belowground herbivory, C sink, C source, ecosystem respiration, goose grubbing, high arctic, land-use change, net ecosystem exchange, Spitsbergen

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Introduction

Tundra ecosystems are considered to be globally important carbon (C) sinks (Callaghan *et al.*, 2004), yet our understanding of potential threats to the large soil C store is limited. For example, climatic change has resulted in a net release of CO_2 in recent warmer years, transforming arctic tundra from a C sink into a source (Billings *et al.*, 1982; Oechel *et al.*, 1993; Callaghan *et al.*, 2004). Meanwhile, vertebrate grazers have become increasingly abundant in many of these northern systems, and it is important to understand how this affects ecosystem C balance. Geese are among the most prevalent of arctic tundra herbivores (Van der Wal, 2005). In recent years, land-use change throughout the northern hemisphere, notably increased agricultural production and implementation of conservation mea-

sures, have dramatically improved the ability of geese to survive the winter and their northerly migration to arrive in their arctic-breeding grounds in good physical condition (Abraham *et al.*, 2005; Van Eerden *et al.*, 2005). Arctic ecosystems are vulnerable to overgrazing as evidenced in low-Arctic Canada, where enhanced grazing and grubbing by lesser snow geese (*Anser caerulescens caerulescens*) along the Hudson Bay coast has led to large-scale destruction of salt marshes (Jefferies, 1988; Walker *et al.*, 2003). Here, we investigate, for the first time, whether increase in goose abundance can affect the C balance of arctic tundra. Increasing numbers of pink-footed geese *Anser brachyrhynchus* arrive in Spitsbergen in early spring before there is sufficient aboveground forage. They, thus, feed initially on belowground plant parts (Fox *et al.*, 2006) and we ask the question whether this brief period of early season belowground foraging is sufficient to reduce soil C stocks and C sink strength of arctic tundra.

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Materials and methods

Field site

Field experiments were performed in Adventdalen (78°10′N, 16°07′N), a well-vegetated valley on the west coast of high-Arctic Spitsbergen, Svalbard. The vegetation is tundra moss heath interspersed with vascular plants. The soil and moss layers are frozen for most of the year, restricting vascular plant growth to June–August when increased solar radiation during 24 h of daylight causes progressive thawing of the active layer to a depth of up to 70 cm. Annual precipitation is low (190 mm, 1988–2000 average) and soil moisture is largely determined by snow lie and subsurface water flow. As a consequence, small differences in topography or position in the landscape have a disproportionate effect on moisture and resultant vegetation composition. Our study sites ranged from mesic to wet and were located on the outermost part of an alluvial fan with continuous summer water supply from melting of the Foxfønna glacier. The soils have a shallow organic horizon (5 cm depth) that overlays fluvial silt deposits.

Adventdalen becomes snow-free relatively early and is increasingly used by pink-footed geese as prebreeding staging area. In 2004, 2000–3000 birds arrived at the onset of snow melt around mid May and left early June for their respective breeding sites (Fox *et al.*, 2006; Glahder *et al.*, 2006). Following snow melt when the soil is still frozen, pink-footed geese feed largely upon the standing dead grass from the previous year. However, they grub for carbohydrate-rich belowground plant parts as soon as the moss and soil layer starts thawing (Fig. 1). Analyses of goose droppings revealed that initially, shallow roots of horsetail *Equisetum arvensis* are taken, followed by rhizomes of the forb *Bistorta vivipara*, stem bases of the sedge *Eriophorum scheuchzeri* and roots and rhizomes of *Dupontia* grasses (Fox & Bergersen, 2005; Fox *et al.*, 2006; D. Kuijper, unpublished data). In early June, when aboveground growth starts, the relative contribution of belowground food items to the diet declines and the birds become predominantly grazers. Areas that are used by geese to grub for graminoid stem bases and rhizomes are clearly recognizable from the high density of dislodged moss tufts remaining on the surface, while grubbing for *Bistorta* rhizomes leaves small distinct holes in the moss and soil. Such signs of disruption are also observed in the breeding grounds of pink-footed geese throughout Svalbard.

Three areas with contrasting vegetation and moisture regimes that had been utilized to an increasing extent by pink-footed geese during the previous three springs (R. van der Wal, personal observation) were selected for
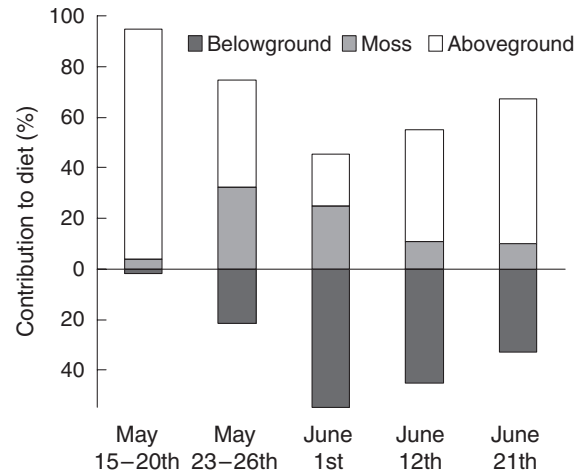

Fig. 1 Relative contribution of above- and belowground vascular plant parts and mosses to the diet of pink-footed geese during the short period of prebreeding spring staging, 2004. Aboveground material taken before June is dead grass. The proportion of birds grubbing for belowground plant parts increased steeply after 20th May as soil thawed. Diet composition was determined through microhistological inspection of fecal material collected from staging birds in Adventdalen (first three periods) and from breeding birds (last two periods) in the nearby side valley Foxdalen as most geese departed to their breeding sites in early June. Data from D. Kuijper, unpublished; Fox *et al.* (2006) and Fox & Bergersen (2005).

this study. Impacts of the geese on the vegetation were investigated in a wet meadow (60 m × 140 m), and in areas of moist and mesic tundra (each 10 m × 20 m). The wet meadow was also the main experimental site, used to determine the impact of goose grubbing on the ability of arctic tundra to sequester C. The vegetation at the wet site was dominated by *E. scheuchzeri* and *Dupontia* spp. growing in a loose moss mat composed of largely *Calliergon richardsonii*. The vascular plant community at the moist site was composed of *Dupontia* spp., *E. scheuchzeri*, *Salix polaris*, *Saxifraga cernua* and *B. vivipara* and the bryophytes *Philonotis tomentella*, *Distichium capillaceum* and *Campylium* spp. while at the mesic site the most abundant vascular plants were *S. polaris*, *Alopecurus borealis*, *B. vivipara* and *S. cernua* and the bryophyte layer was largely composed of *Tomentypnum nitens*, *Orthothecium chryson* and *Sanonia uncinata*. Nomenclature followed Elvebakk & Prestrud (1996).

Experimental design

In the wet meadow, eight separate locations where grubbing was evident were selected on June 9/10, 2004, just after which most pink-footed geese had left the study site. At each location a 40 cm × 75 cm plot was

marked to represent naturally grubbed vegetation, along with two additional plots of similar size and as close as possible to the grubbed area to represent undisturbed but otherwise comparable vegetation. Of these, one served as an ungrubbed control, while the other was subject to a manual grubbing treatment (on June 9/10, 2004) to determine whether there were confounding factors that would invalidate the comparison of naturally grubbed and ungrubbed vegetation. At the moist and mesic sites, six grubbed and six ungrubbed plots (1 m × 1 m) were selected and staked out.

The design of the artificial grubbing treatment at the wet site was based on close inspection of naturally grubbed locations within the experimental area of 60 m × 140 m, in which 100 randomly located grubbing points (i.e. single holes in the moss mat created by geese) were examined for remains of plant species extracted by pink-footed geese. Belowground parts of *Dupontia* spp. (38%) and *E. scheuchzeri* (29%) had been targeted most frequently, while damage to roots of *S. polaris* (7%), *A. borealis* (5%) and *Equisetum arvense* (4%) was infrequent. Although traces of *B. vivipara* were hardly ever observed (2%), we suspect that in many cases the whole rhizome had been removed and that this probably accounted for many of the 15% of grubbing points where no damage to plants could be established. On the basis of these data, manual grubbing was done by pulling out appropriately sized tufts of moss between index finger and thumb, and removing all visible *Dupontia*, *Eriophorum* and *Bistorta* tissue within each resulting hole with pliers the size of a pink-footed goose bill. Moss was pulled out in a checker-board fashion, with the aim of removing ca. one-third of the moss cover in all eight artificial grubbing plots, and vascular plants were extracted to a depth comparable with the adjacent naturally grubbed plots. All biomass removed from the plot was sorted in the laboratory into moss (green and brown combined), the different vascular plant species and vascular plant litter, dried for 72 h at 70 °C and weighed.

Goose grubbing impact on early season plant biomass

To determine differences in plant biomass between naturally grubbed and ungrubbed vegetation at the onset of the experiment, three 10 cm × 10 cm turfs per plot were cut out down to the moss–soil interface on June 13, 2004 and all plant material was sorted, dried and weighed as described before. Biomass in artificially grubbed plots was calculated by subtracting the amount of plant tissue removed from a plot from that present in the appropriate control. This showed goose grubbing to result in a sizeable (59%) reduction of

Table 1 Differences in total plant biomass (means ± SE in g m^{-2}) between intact wet tundra vegetation (control), adjacent goose-grubbed and experimentally grubbed areas directly after visitation by pink-footed geese in early June

Parameter	Control	Grubbed	Experimentally grubbed
Moss	1110 (251)	995 (193)	762 (260)
Dupontia spp.	86 (30)	40 (14)	45 (20)
Eriophorum scheuchzeri	80 (17)	22 (6)	64 (15)
Total vascular plants	191 (45)	78 (20)	126 (36)

vascular plant biomass in particular (Table 1). The impact of our artificial grubbing treatment on plant biomass (with the exception *E. scheuchzeri* biomass) was of a similar magnitude, justifying the use of this manipulation to evaluate the ecosystem implications of goose grubbing.

Goose grubbing impact on plant cover

The impact of goose grubbing on plant abundance at the three tundra sites was determined by visual estimates of the cover of bryophytes and vascular plants (two-dimensional projection of their total cover) within each of the plots. Estimates were made at around peak standing crop, on July 21, 2004 at the mesic and moist sites, and on August 14, 2004 at the wet meadow site. Owing to a mid season flooding event at the wet site, two of the eight experimental blocks had been lost and vegetation cover estimates therefore made on the remaining six blocks.

Goose grubbing impact on C flux

Ecosystem CO_2 fluxes in the wet meadow were estimated twice during the growing season, in the first week of July 2004 on all eight blocks, and in the last week of July 2004 on the six blocks remaining after the flood (averages between dates were used in analysis). All measurements within a block were made simultaneously between 10:00 and 16:00 hours. Ecosystem CO_2 fluxes were measured with an open system composed of custom-built cuvettes 30 cm in diameter attached to EGM-4 Infra Red Gas Analysers (IRGAs; PP Systems, Hitchin, UK, see Sjögersten et al., 2006 for details). Both net ecosystem exchange (NEE) and ecosystem respiration (R_e) were measured at each plot in the following sequence: subsequent to placement of the basal rim and cuvette the system was allowed to settle effectively for 5–10 min; NEE data were collected over the next 20 min; a hood was placed over the cuvette to exclude light and

stop photosynthesis; the system was allowed 5–10 min to settle, and then R_e was measured for 15 min. Negative flux numbers imply C uptake, whereas positive numbers imply losses from the system. Consequently, an indication of gross ecosystem photosynthesis (GEP) was obtained by adding NEE and R_e fluxes.

Goose grubbing impact on C stocks

The impact of goose grubbing on C stocks was determined for the naturally grubbed and ungrubbed control plots at the wet site. Vegetation turfs had already been sampled, sorted, dried and weighed. A soil sample (22 mm diameter, 5 cm into the mineral soil) was taken on June 17, 2004 from the center of each of the three vegetation sample pits per plot, dried for 48 h at 105 °C and weighed. C content of mineral soil, organic soil, moss and vascular plant biomass (above- and below-ground combined) was analyzed on pooled samples from each plot on a Carlo Erba NA1500 (Carlo Erba, Milano, Italy) elemental analyzer and C pool size was calculated by multiplying C content with weight of the respective component.

Statistical analysis

Data were analyzed in SAS for Windows V. 8.2 using generalized linear mixed models (GLMM) with 'experimental block' as the random effect. The models were fitted by the method of residual maximum likelihood (REML). Denominator degrees of freedom were estimated using Satterthwaite's approximation (Littell *et al.*, 1996) and the residual variances were modeled as constant to the mean using PROC MIXED. Differences between individual treatments were inspected on the basis of *post hoc* contrasts within the appropriate model structure. We used GLM to determine the impact of grubbing on plant cover in moist and mesic sites.

Results

Grubbing strongly influenced NEE thereby reducing C sink strength (Fig. 2). NEE is determined by the balance of GEP and ecosystem respiration (R_e). Both GEP and R_e were suppressed by grubbing, but the impact on GEP exceeded that on R_e. The reduction in R_e, therefore, did not offset the large negative impact on GEP and consequently, grubbing by pink-footed geese reduced C sink strength of wet tundra. Artificial grubbing influenced NEE, GEP and R_e in a similar way to natural goose grubbing, indicating that findings were not due to initial differences between the naturally grubbed and ungrubbed areas.
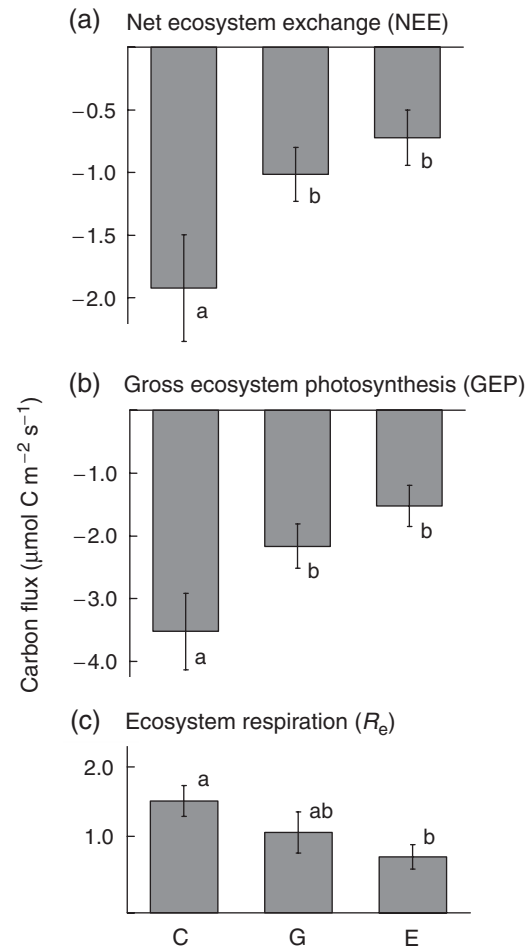

Fig. 2 Impact of goose grubbing on carbon flux between the atmosphere and the plant/soil system. Means ± SE are given for intact control (C), goose grubbed (G) and experimental grubbed (E) wet tundra. Negative numbers imply carbon uptake and positive numbers imply carbon losses from the system. Negative impact of grubbing treatments was evident in both NEE (a; $F_{2,10} = 7.73$, $P < 0.01$) and GEP (b; $F_{2,10} = 8.81$, $P < 0.01$). The impact of grubbing on R_e (c; $F_{2,10} = 2.77$, $P = 0.11$) was strongly influenced by a single extreme value in a goose-grubbed plot. After removal of this outlier treatment differences were significant ($F_{2,9} = 6.75$, $P < 0.02$) with R_e being higher in intact swards than in both grubbing treatments. Values with different letters are significantly different at the $P < 0.05$ level.

In wet tundra, grubbing led to a severe reduction in the cover of bryophytes ($F_{2,10} = 11.42$, $P < 0.01$; Fig. 3a) and vascular plant cover was also significantly reduced ($F_{2,10} = 8.11$, $P < 0.01$; Fig. 3b). Again, no statistically significant differences were observed between natural and artificial goose grubbing, confirming that it was grubbing by the pink-footed geese, and not initial site differences, that resulted in the reduction in plant cover. Goose grubbing also reduced live bryophyte and vascular plant cover in the nearby moist and mesic areas
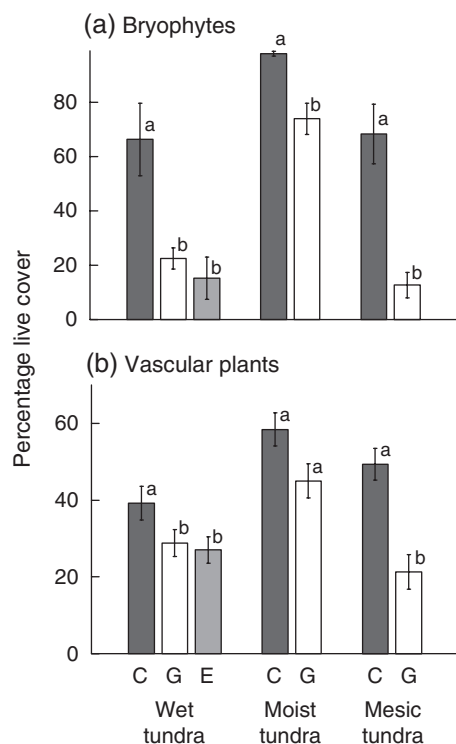
(a) Bryophytes

(b) Vascular plants

C G E   C G   C G
Wet tundra   Moist tundra   Mesic tundra

Percentage live cover

Fig. 3 Negative impact of goose grubbing on the cover of bryophytes (a) and vascular plants (b). Means ± SE are given for intact control (C), goose grubbed (G) and experimentally grubbed (E) swards for wet tundra, while a comparison between intact and goose-grubbed swards only is made for both moist and mesic tundra. Values with different letters within a habitat are significantly different at the $P < 0.05$ level. The difference in vascular plant cover between intact and goose-grubbed moist tundra was marginally significant ($P = 0.06$).

(Fig. 3), demonstrating that goose grubbing can severely impact plant abundance across a range of habitats.

NEE was strongly and linearly related to total plant cover, with greatest C sink strength where live plant cover was high (Fig. 4). Both bryophytes ($F_{1,14} = 13.28$, $P < 0.01$) and vascular plants ($F_{1,14} = 29.98$, $P < 0.0001$) contributed to this relationship, and separate analysis of the data from each of the C measuring dates showed that the relationship was evident in both early and late July ($P < 0.01$). Importantly, the grubbing treatments did not explain any of the remaining variation ($P > 0.8$). Early season thaw depth, and thus soil temperature, differed among treatments ($F_{2,10} = 14.6$, $P < 0.01$) at the onset of the experiment and was $12.1 ± 0.6$ cm in naturally grubbed sites while only $8.2 ± 1.1$ and $8.8 ± 1.2$ cm in experimentally grubbed and untreated controls, respectively. However, there was no evidence that abiotic factors, such as soil temperature and thaw depth, explained the observed treatment effect on NEE. From this we conclude that pink-footed geese, via the reduc-
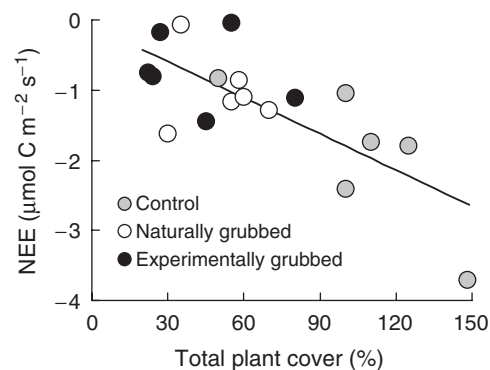

Fig. 4 Relationship between net ecosystem exchange (NEE) of carbon and live plant cover. NEE in wet tundra was directly related to the combined cover of bryophytes and vascular plants ($F_{1,14} = 22.18$, $P < 0.001$) and all experimental treatments follow a common slope.
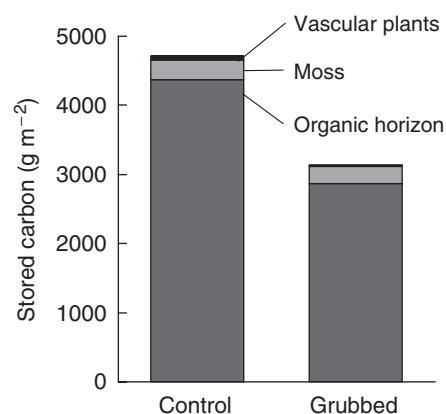

Fig. 5 Impact of goose grubbing on carbon stocks. The amount of stored carbon in the organic horizon in particular was reduced by goose grubbing. Carbon pool size in the underlying mineral layer was $4597 ± 571$ and $3492 ± 564$ g C m^{-2} of control and goose-grubbed soils, respectively.

tion in live plant cover, directly influenced the C sink strength of arctic tundra.

Goose grubbing influenced not only short-term C fluxes, but also the total amount of C stored in the soil ($F_{1,14} = 5.26$, $P < 0.05$). C stock in the organic soil horizon (mean depth 7 cm) and plant biomass combined were 33% lower in the naturally grubbed plots than the intact wet tundra (Fig. 5), this being due to loss of mass from the system rather than to a reduction in C concentration.

Discussion

We have demonstrated that a brief period of disturbance from belowground herbivory by geese was sufficient to strongly reduce both C stocks and C sink

strength of arctic tundra. This feeding mode is typical for larger-billed arctic-breeding geese (notably species of the genera *Anser* and *Chen*) early in the season, when insufficient fresh green leaf material is available for efficient aboveground grazing. Goose grubbing occurs in a range of habitats but most extensively in wet tundra. As these areas have the strongest C sink function (Sjögersten *et al.*, 2006), the negative impact of geese on the ability of arctic tundra to sequester C is likely to be disproportional to their overall occurrence.

Goose grubbing reduces the differential between short-term C gain and loss because it results in a reduction in moss and vascular plant photosynthetic tissue. Thus, the GEP, and so sink strength, of the tundra is reduced by this belowground herbivory. This is in line with the handful of existing studies on aboveground grazing and C fluxes, suggesting that herbivory in general diverts plant C away from soils (Bremer *et al.*, 1998; Sankaran & Augustine, 2004; Welker *et al.*, 2004; Nieveen *et al.*, 2005). Our study suggests that, in the Arctic, belowground herbivory also has longer-term consequences as it results in reduction of soil C stocks. Grubbing opens up the vegetation mat, exposing the organic layer to erosion by both flooding and wind, which leads to a loss of stored C. This loss was considerably greater than the grubbing impact on short-term C dynamics via suppression of GEP rates.

We predict that, at the local level, goose grubbing will trigger events which will cause progressive mobilization of C from arctic tundra. When soils begin to thaw out in spring, pink-footed geese, like any other large-billed goose species, switch to feeding on belowground storage organs (Fox *et al.*, 2006), and in so doing disrupt the moss mat. The moss mat strongly influences the rate of soil thaw, acting as an insulatory blanket keeping the soil cool (van der Wal & Brooker, 2004). Geese preferentially grub in areas where soil thaw is advanced (Fox *et al.*, 2006). This likely affects the pattern of soil thaw in subsequent years as disruption to the moss mat allows faster soil warming. We have observed that geese prefer to revisit previously grubbed areas than utilize intact tundra. All of the wet meadow plots that were either experimentally or naturally grubbed in 2004 were extensively used by geese in the subsequent year, leaving very little moss, whereas only one of the six control plots was grubbed and another partially (30%) utilized. Geese similarly revisited grubbed plots in mesic and moist tundra, all of which suggests that disruption of the moss mat renders grubbed areas profitable, at least in the short term, because of earlier thaw.

The appearance within our study sites of small areas that are completely denuded suggests that disruption to the vegetation by repeated grubbing, in combination with water and wind erosion, may eventually lead to very significant loss of the soil organic layer. On a local scale, the loss of C and associated nutrients in organic matter will lead to instability of fragile, nutrient-limited tundra ecosystems. Consequences for wider arctic ecosystem C balance depend on the fate of the mobilized organic matter. Clearly, there is a net loss of C from the tundra store, and the most likely scenario for our tundra site is that this C enters the freshwater and then marine system. Organic C of terrestrial origin contributes significantly to both heterotrophic metabolism and C burial in sediments in the Arctic Ocean (e.g. Goni *et al.*, 2005). Increased understanding of the marine transport and fate of the terrigenous organic C pool, and indeed of how sources of this organic C may respond to environmental change, is critical to our ability to predict potential climate change feedbacks within the Arctic (Guo *et al.*, 2004; Goni *et al.*, 2005).

Our study illustrates the vulnerability of arctic ecosystems to disturbance from belowground herbivory in spring. Economic, policy and legislative changes in temperate regions, leading to large-scale land-use changes, have allowed dramatic population growth of many goose species through substantially increased winter survival (Abraham *et al.*, 2005) and enhanced reproductive success (Fox *et al.*, 2005). Along the Hudson Bay coast, Canada, such population increases have resulted in large-scale disturbance of subarctic salt marsh habitat from early season grubbing. Here, the development of hypersaline conditions arrests the system in a denuded state in which re-establishment via seeds or fragments is highly compromised (Srivastava & Jefferies, 1996; Handa & Jefferies, 2000). Although grubbing by pink-footed geese in Spitsbergen clearly demonstrates how C cycling is under strong herbivore control, we currently have no evidence for severe herbivore-driven habitat degradation on the Canadian scale in the European Arctic. Yet, our study does demonstrate that a further increase in the numbers of large-billed arctic-breeding geese is likely to reduce C sequestration by arctic tundra. Whether this has implications for climate forcing will depend on the extent of goose grubbing at the landscape scale. Research has, therefore, been initiated to reveal the spatial extent and magnitude of goose grubbing and to determine the role played by abiotic factors in amplifying the impacts of belowground herbivory on critical ecosystem services including C sequestration.

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