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Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization

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Global warming is predicted to be most pronounced at high latitudes, and observational evidence over the past 25 years suggests that this warming is already under way¹. One-third of the global soil carbon pool is stored in northern latitudes², so there is considerable interest in understanding how the carbon balance of northern ecosystems will respond to climate warming^{3,4}. Observations of controls over plant productivity in tundra and boreal ecosystems^{5,6} have been used to build a conceptual model of response to warming, where warmer soils and increased decomposition of plant litter increase nutrient availability, which, in turn, stimulates plant production and increases ecosystem carbon storage^{6,7}. Here we present the results of a long-term fertilization experiment in Alaskan tundra, in which increased nutrient availability caused a net ecosystem loss of almost 2,000 grams of carbon per square meter over 20 years. We found that annual aboveground plant production doubled during the experiment. Losses of carbon and nitrogen from

deep soil layers, however, were substantial and more than offset the increased carbon and nitrogen storage in plant biomass and litter. Our study suggests that projected release of soil nutrients associated with high-latitude warming may further amplify carbon release from soils, causing a net loss of ecosystem carbon and a positive feedback to climate warming.

The effects of climate warming on ecosystem carbon (C) storage remain uncertain. Despite the low temperatures at high latitudes, C storage in tundra and boreal ecosystems is thought to be constrained ultimately by carbon–nutrient interactions because plant production is usually nitrogen (N)-limited^{6,7}. As soils warm in response to climate change, nutrient mineralization from soil organic matter is expected to increase^{8,9}, which should, in turn, increase plant production. Total ecosystem C storage, however, depends on the balance between production and decomposition, and the relationship between nutrient availability and decomposition remains uncertain.

In ecosystems at lower latitudes, natural and manipulated nutrient concentrations have had a positive, a negative, or no effect on the decomposition of litter and soil organic C (SOC)^{10–13}. This variable response probably reflects ecosystem differences in form and quality of litter and SOC, but the regulatory mechanism for this is poorly understood¹³. High-latitude ecosystems are unusual because they store a larger proportion of total ecosystem C in soil compared with temperate and tropical ecosystems¹⁴. In arctic tundra, as much as 90% of the total ecosystem C resides in organic horizons and frozen mineral soils¹⁵. Thus, the response of SOC to changes in nutrient availability will play a critical role in determining net ecosystem C balance in a changing climate.

Previous results from nutrient manipulations suggested that increased nutrient availability should increase the total C storage in tundra ecosystems^{2,9,15,16}. Nutrient addition greatly increases C stored aboveground by stimulating plant productivity and by shifting species composition from slow-growing species to more productive shrubs that accumulate C in long-lived woody biomass^{4,17–19}. In addition, leaf, root and stem litter from shrubs decomposes more slowly than the graminoid-dominated litter they replace⁹, so conversion to shrub tundra was thought to slow decomposition and increase ecosystem C accumulation¹⁹. However, these inferences were based on aboveground and surface soil measurements only. The lack of soil-profile measurements reflects the expectation that the large heterogeneous belowground C pool

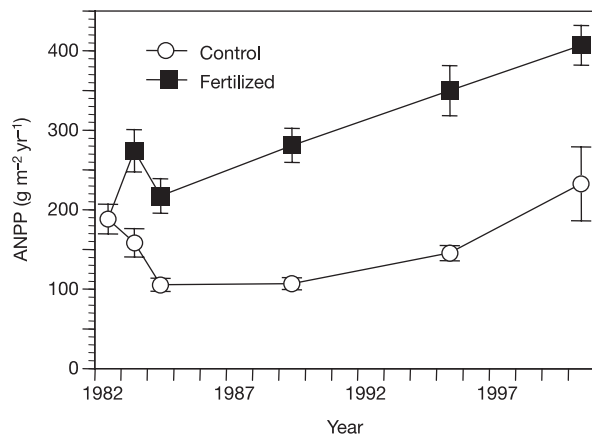


Figure 1 Effect of fertilization on vascular plant aboveground net primary production (ANPP) in tundra. Fertilized plots in moist acidic tundra near Toolik Lake, Alaska, have received 10 g N m⁻² yr⁻¹ and 5 g P m⁻² yr⁻¹ since 1981. Values are means (±1 standard error, s.e.); means from 1982–95 are reported in ref. 19; the year-2000 data are from this study (*n* = 4). Components of ANPP (new leaves and reproductive parts, new stems and secondary growth) are shown in Supplementary Fig. 1.

would respond to changes in plant inputs too slowly to be detected in short-term experimental manipulations.

To investigate the effects of nutrient availability on whole-ecosystem C balance, we examined C and N pools in a long-term fertilization experiment at the arctic Long-Term Ecological Research site near Toolik Lake, Alaska. To our knowledge, this is the longest-running nutrient-addition experiment in arctic tundra. Fertilized plots in moist acidic tundra (MAT) have received 10 g N and 5 g P m⁻² year⁻¹ since 1981 (ref. 19). This is approximately 5 to 8 times the annual soil N uptake requirement for aboveground production in MAT, and similar to the N uptake requirement in nearby shrub tundra characteristic of warmer sites^{5,20}. Two decades of fertilization greatly increased aboveground net primary productivity (ANPP; Fig. 1); over this time about 1,500 g m⁻² of additional C entered fertilized plots as ANPP, which had shifted from graminoid tundra dominated by the tussock-forming sedge, *Eriophorum vaginatum*, to shrub tundra dominated by *Betula nana*¹⁹. Because of the unique long-term nature of this experiment, changes in belowground C pools and total ecosystem C balance are now detectable.

In our experiment, increased nutrient availability had a larger effect on decomposition than on plant production, resulting in a net loss of almost 2,000 g C m⁻² from this ecosystem over 20 yr (Fig. 2a; *P* = 0.04). Carbon storage increased aboveground (*P* < 0.001) because of the accumulation of woody shrub biomass and litter, but this was offset by a larger decrease of C in belowground pools (*P* = 0.02) due to a pronounced decrease in the C contained in deep organic (>5 cm depth) and upper mineral soil layers (Fig. 2b). The decrease in the deep organic layer C pool was the result of a reduction in the thickness of the layer, because neither %C nor bulk density was affected by fertilization (Supplementary Information). In the upper mineral soil, fertilization reduced %C by 50% (*P* = 0.04), whereas the depth to the frozen soil surface and mineral

soil bulk density did not change (Supplementary Information).

Decreased C storage in the fertilized treatment does not appear to be caused by decreased plant production. As expected, ANPP of vascular plants was higher in fertilized plots (Fig. 1). Root C pools were not different between treatments (Fig. 2b), and in a related study, root productivity tended to be higher in fertilized plots²¹. The productivity of mosses and lichens was not measured in this harvest, but their production has been estimated as 25–60 g C m⁻² in unmanipulated MAT^{5,20,22}. Although they were mostly absent from fertilized plots in both 1995 and 2000, the loss of their productivity would be insufficient to offset the large increases in vascular productivity. Because plant production increased total C inputs, the net loss of C from the fertilized plots could only have been caused by accelerated decomposition of C.

Several mechanisms could have contributed to the nutrient-induced acceleration of decomposition. First, nutrient additions could have altered the decomposability of fresh plant litter through changes in the species composition or tissue quality of the plant community. However, the increased C in biomass, litter and surface soils of fertilized plots (1,311 g m⁻²) was similar to increased ANPP inputs over the past 20 yr (~1,500 g m⁻²), indicating relatively little decomposition of the increased litter inputs. Furthermore, *B. nana* leaves, stems and roots are relatively less decomposable than those of the community they replace⁹, making it unlikely that litter decomposed more quickly in the fertilized treatment owing to changes in tissue quality alone. These observations argue against changes in litter decomposability having a major role in increased decomposition in fertilized plots.

Second, the loss of deep-rooted graminoid species from the fertilized plots¹⁹ could have altered environmental controls over root decomposition by changing the depth at which root litter was deposited. Although total root biomass C was not different between treatments, fertilization did shift the distribution of root biomass

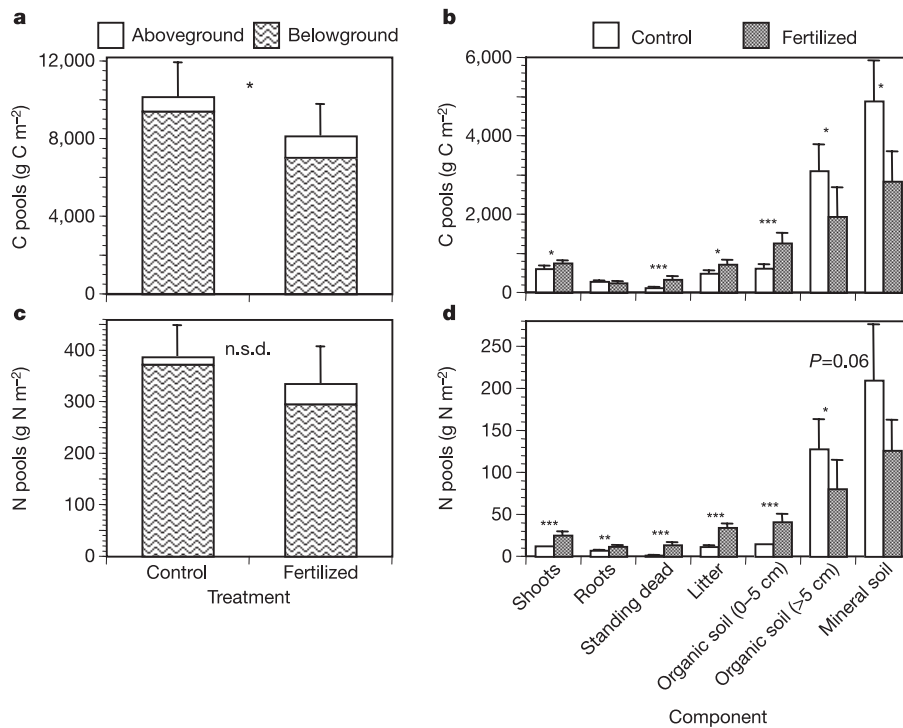


Figure 2 Effects of fertilization on tundra carbon and nitrogen pools after 20 yr of fertilization. **a, c**, Mean (± 1 s.e.) above- and belowground carbon (**a**) and nitrogen (**c**) pools in unmanipulated control and fertilized treatments of moist acidic tundra near Toolik Lake, Alaska. Aboveground pools include shoots, standing dead plant material, and rhizomes. Belowground pools include surface litter, roots, and organic and mineral soil.

b, d, Mean (± 1 s.e.) carbon (**b**) and nitrogen (**d**) pools in plant and soil compartments. Pool treatment means were compared with nested ANOVA (*n* = 4). Means that are significantly different are indicated with asterisks: **P* < 0.05; ***P* < 0.01; ****P* < 0.001. n.s.d., not significantly different.

towards the soil surface. Seventy percent of root biomass was in litter and surface organic soils (0–5 cm) in the fertilized plots, whereas only 30% of root biomass was in these layers in the control plots ($P < 0.05$). Furthermore, there was 50% less root biomass in the mineral soil layer of fertilized plots than in control plots ($P < 0.01$). Because of the large gradients in temperature and moisture in soils overlaying permafrost, this upward shift of root biomass in the fertilized plots may have placed root inputs into a warmer, drier environment where decomposition was more rapid. However, even if root decomposition rates doubled in the fertilized plots, root production ($\sim 34 \text{ g C m}^{-2} \text{ yr}^{-1}$; ref. 21) would constrain the amount of C available for decomposition. At most, increased root decomposition could explain 17% of the C missing from the fertilized plots.

For the remainder of the missing C, we hypothesize that increased nutrient availability stimulated the decomposition of old litter and/or SOC in deep soil layers, leading to loss via mineralization or leaching of dissolved organic C. Other experiments in tundra have also detected increased decomposition rates with increased N availability for fresh leaf litter²³ and for SOC fractions¹³, or have inferred N limitation of decomposer activity²⁴. These results may have been caused directly by nutrient stimulation of decomposer activity, which occurs in systems where litter C quality is low and C:N ratios are high¹². Alternatively, indirect effects of nutrient addition on plant–microbe interactions and soil food-web dynamics may have caused these results. Decreased C:N ratios are expected to shift microbial community composition from fungal to bacterial dominance, resulting in greater energy flow to higher trophic levels and more rapid decomposition²⁵. Regardless of the specific mechanism, the clear result of this study is that increased nutrient availability enhanced decomposition of belowground C pools in deep soil layers more than it increased primary production, leading to a substantial net loss of C from this ecosystem. As an increasing number of ecosystems are subjected to human-driven change in climate and N inputs, the sensitivity of decomposition to nutrient availability may be important for determining ecosystem C balance worldwide.

Even though a total of 200 g N m^{-2} was added to fertilized plots over 20 yr, our results show that fertilization had no net effect on total N pools (Fig. 2c). Increased N storage in aboveground biomass ($P < 0.001$) was balanced by a trend towards decreased N storage belowground ($P = 0.14$). As with C pools, N pools in the fertilized treatment were significantly smaller in deep organic soils and tended to be smaller in mineral soil (Fig. 2d). Concentrations of NH_4^+ and NO_3^- were an order of magnitude higher in the fertilized than in the control plots at all soil depths (Supplementary Information), suggesting that fertilizer N penetrated to deeper soil layers.

Net loss of N from deep soil despite penetration of fertilizer N shows that decomposers in these layers were unable to immobilize N, perhaps owing to C limitation caused by the low soil C:N ratio and the high respiratory demands of cold soils. Furthermore, decreased root biomass at depth probably reduced plant competition for organic and mineral N, leading to increased potential for nitrification and leaching losses of dissolved organic N and nitrate to downslope and aquatic ecosystems²⁶. High concentrations of NO_3^- in the fertilized plots indicate that denitrification may be an important loss pathway as well. These results show that the fertilized ecosystem had almost no capacity for net retention of increased N inputs despite 20 yr of sustained increase in plant production (Fig. 1).

Although it remains to be seen how this response to fertilization will compare with the effects of climate warming on tundra ecosystems, several lines of evidence suggest that a nutrient-mediated positive feedback could occur, amplifying the predicted temperature response of decomposition. First, the amount of N released by warming is likely to be similar in magnitude to our fertilizer addition, ranging from the release of 7 to $9.4 \text{ g N m}^{-2} \text{ yr}^{-1}$

for a 3- to 7-degree increase in mean annual temperature, respectively (see Methods). Second, naturally occurring shrub tundra characteristic of warmer sites has less soil C storage than tussock tundra²⁷ despite its greater nitrogen availability⁸ and ANPP⁷, suggesting that environmental shifts to increased shrub abundance will lead to decreased ecosystem C storage. Finally, we observed the effects of nutrient availability on C storage in the absence of other effects of climate warming, such as increased soil temperature, decreased soil moisture, and increased depth of thaw. Each of these changes is predicted to have a positive effect on decomposition⁷. The observed sensitivity of deep soil C decomposition to increased nutrient availability could amplify these effects and further stimulate C losses from high-latitude systems.

These results from the Toolik Lake fertilization experiment confound predictions of how nutrient-limited northern ecosystems will respond to climate warming. Previous predictions have suggested that warmer soils should stimulate decomposition and increase nutrient availability, which, in turn, will stimulate plant production more than decomposition and increase ecosystem C storage^{6,7}. Our results show the opposite response to increased nutrient availability. Decomposition was stimulated more than plant production, leading to a net loss of C from the ecosystem. Furthermore, the system had no capacity for net retention of increased N inputs. These results suggest that a new conceptual model for the response of tundra to climate warming is required, one in which decomposition is more sensitive than production to changes in nutrient availability and N is susceptible to loss. □

Methods

Site description

The experimental plots were located in moist acidic tundra near Toolik Lake, Alaska, at the Arctic Tundra Long Term Ecological Research site in the northern foothills of the Brooks Range. The soil is a histic pergelic cryaquept, with a $\sim 20 \text{ cm}$ peat layer over silty mineral soil and permafrost. Mean air temperature during the June–August growing season is $\sim 9.3^\circ \text{C}$ and total precipitation is $\sim 180 \text{ mm}$. The vegetation in the experimental plots is similar to moist acidic tundra across the Alaskan North Slope, northern Canada, and eastern Siberia²⁸.

Experimental design

This experiment was established in 1981 as described in detail elsewhere⁴. The design consisted of four replicate blocks of moist acidic tundra; each block contained four $5 \text{ m} \times 20 \text{ m}$ plots. Treatments, including control and fertilization, were randomly assigned. The fertilized treatment has received $10 \text{ g m}^{-2} \text{ N}$ as $\text{NH}_4\text{-NO}_3$ and $5 \text{ g m}^{-2} \text{ P}$ as P_2O_5 each spring immediately following snowmelt since 1981.

Harvest and analyses of ecosystem C and N pools

In late July 2000, we destructively harvested five $20 \text{ cm} \times 20 \text{ cm}$ quadrats from each plot. Quadrats were randomly arrayed along 20-m transects located 1 m from the eastern edge of the plot. Shoots, litter, belowground stems and rhizomes were collected by sawing the organic soil down to the surface of the mineral soil with a knife. Quadrats were returned to the lab and sorted using the methods of previous harvests^{5,19}.

Organic soil was harvested volumetrically from $5 \text{ cm} \times 5 \text{ cm}$ monoliths taken from the side of the hole where the $20 \text{ cm} \times 20 \text{ cm}$ quadrat was removed. Mineral soil was sampled with a 2.5-cm-diameter corer beneath each monolith, from the surface of the mineral soil to the permafrost. Organic soil monoliths were separated into depth increments in the field, including litter (recognizable dead plant material), 0–5 cm organic, 5–15 cm organic, and $>15 \text{ cm}$ organic. Soil samples were returned to the laboratory, where live roots were removed by hand and sorted into coarse ($>2 \text{ mm}$) and fine ($<2 \text{ mm}$) size fractions. Root volume and mass were determined and subtracted from soil volume and mass. The remaining soil was subsampled for gravimetric water content and C and N concentration.

All plant and soil samples were dried to a constant mass at 65°C and weighed. As in previous harvests from this experiment^{5,19}, samples from individual quadrats were composited by plot for analyses of C and N content (that is, $n = 4$). Plant shoots, belowground stems, and rhizomes were analysed for C and N concentration on a Perkin-Elmer CHN analyser (Norwalk, Connecticut, USA). Root and soil C and N concentrations were determined on a Carlo Erba CHN analyser (Milan, Italy). Soil %C is reported for bulk soil.

Carbon and N pools were estimated for shoots (aboveground parts, belowground stems and rhizomes), aboveground litter, roots (>5 and $<5 \text{ mm}$ in diameter), and soils for each quadrat by multiplying biomass or soil mass by the plot element concentration for that pool. Total ecosystem C and N pools were estimated by summing all pools. Treatment effects were analysed using nested analyses of variance²⁹, with blocks nested within treatments. Aboveground NPP was estimated as the sum of measured apical and estimated secondary growth¹⁸.

Estimating N release from climate warming

Assuming that (1) annual heterotrophic respiration in unmanipulated tundra is roughly equal to total plant production ($150 \text{ g C m}^{-2} \text{ yr}^{-1}$) as it is in many mature ecosystems, (2) that soil respiration responds to temperature change with a Q_{10} of 2, and (3) the depth-weighted average C:N ratio of SOM is 26 (Supplementary Information), then the projected 3°C temperature increase¹ should result in the mineralization of $7 \text{ g N m}^{-2} \text{ yr}^{-1}$. A 7°C temperature increase should result in the mineralization of $9.4 \text{ g N m}^{-2} \text{ yr}^{-1}$. This is a conservative estimate of temperature stimulation of N release because respiration in soils from cold regions tends to be highly sensitive to temperature, often responding to temperature change with Q_{10} values greater than 2 (ref. 30). Nevertheless, these simple calculations show that our rate of N addition is similar in magnitude to potential N release from climate warming.

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Environmental predictors of pre-European deforestation on Pacific islands

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Some Pacific island societies, such as those of Easter Island and Mangareva, inadvertently contributed to their own collapse by causing massive deforestation^{1–7}. Others retained forest cover and survived^{3,8,9}. How can those fateful differences be explained? Although the answers undoubtedly involve both different cultural responses of peoples and different susceptibilities of environments, how can one determine which environmental factors predispose towards deforestation and which towards replacement of native trees with useful introduced tree species? Here we code European-contact conditions and nine environmental variables for 81 sites on 69 Pacific islands from Yap in the west to Easter in the east, and from Hawaii in the north to New Zealand in the south. We thereby detect statistical decreases in deforestation and/or forest replacement with island rainfall, elevation, area, volcanic ash fallout, Asian dust transport and makatea terrain (uplifted reef), and increases with latitude, age and isolation. Comparative analyses of deforestation therefore lend themselves to much more detailed interpretations than previously possible. These results might be relevant to similar deforestation-associated collapses (for example, Fertile Crescent, Maya and Anasazi) or the lack thereof (Japan and highland New Guinea) elsewhere in the world.

All Pacific islands suitable for agriculture were occupied before European arrival by colonists originating ultimately from Asia, mostly in a wave of Polynesians and their Lapita ancestors from 1200 BC to AD 1200 (refs 2, 10, 11). They cleared land and cut trees, especially for agriculture, timber and fuel. Early European visitors observed that forest cover varied greatly between islands, from totally deforested with almost all original tree species extinct (Easter, Necker and Nihoa) to extensive forests (Samoa, Taveuni and Bismarck Archipelago). Forests seen by early Europeans also varied greatly in composition, from ones still dominated by native species to others whose native species had been largely replaced by introduced species valuable for arboriculture.

From accounts of early European visitors, we coded five-point scales for deforestation (in which 1 represented virtually no deforestation and 5 complete deforestation) and for forest replacement (in which 1 represented virtually no replacement and 5 complete replacement) (see Methods and Supplementary Table S1 for details). Deforestation and replacement proved to be correlated, but they measure different things and the correlation is not tight (Spearman correlation $r = 0.43$, $p < 0.001$, in our data set of 81 entries). For 12 of our 69 islands we coded two different locations on the island (usually windward and leeward coasts) because of very different rainfall values often associated with different degrees of deforestation. Thus, our full data set had $69 + 12 = 81$ entries. We also analysed a reduced data set of 69 entries, which excluded 12 large islands of northern Melanesia and New Zealand, because we wondered whether those 12 islands might be driving some conclusions, but results were similar.

We performed four types of statistical analysis (see Methods) for both data sets, relating our two outcome variables (deforestation and replacement) to nine independent variables discussed below.