

University of New Hampshire University of New Hampshire Scholars' Repository

Faculty Publications

6-15-2016

Longer thaw seasons increase nitrogen availability for leaching during fall in tundra soils

Claire C. Treat

University of New Hampshire, Durham

Wilfred M. Wollheim

University of New Hampshire, Durham, wil.wollheim@unh.edu

Ruth K. Varner

University of New Hampshire, Durham, ruth.varner@unh.edu

William B. Bowden

University of Vermont

Follow this and additional works at: https://scholars.unh.edu/faculty_pubs

Recommended Citation

Treat, C., W. Wollheim, R.K. Varner, and W.B. Bowden (2016) Longer thaw seasons increase nitrogen availability for leaching during fall in tundra soils, *Environ. Res. Lett.*, 11, doi: 10.1088/1748-9326/11/6/064013.

This Article is brought to you for free and open access by University of New Hampshire Scholars' Repository. It has been accepted for inclusion in Faculty Publications by an authorized administrator of University of New Hampshire Scholars' Repository. For more information, please contact nicole.hentz@unh.edu.

LETTER • OPEN ACCESS

Longer thaw seasons increase nitrogen availability for leaching during fall in tundra soils

To cite this article: Claire C Treat *et al* 2016 *Environ. Res. Lett.* **11** 064013

View the [article online](#) for updates and enhancements.

Related content

- [Amino acid production exceeds plant nitrogen demand in Siberian tundra](#)
Birgit Wild, Ricardo J Eloy Alves, Jii Bárta *et al.*
- [The impacts of recent permafrost thaw on land-atmosphere greenhouse gas exchange](#)
Daniel J Hayes, David W Kicklighter, A David McGuire *et al.*
- [21st century tundra shrubification could enhance net carbon uptake of North America Arctic tundra under an RCP8.5 climate trajectory](#)
Zelalem A Mekonnen, William J Riley and Robert F Grant

Recent citations

- [Spatially-explicit estimate of soil nitrogen stock and its implication for land model across Tibetan alpine permafrost region](#)
Dan Kou *et al*
- [Linking permafrost thaw to shifting biogeochemistry and food web resources in an arctic river](#)
Michael R. Kendrick *et al*
- [Below-ground plant traits influence tundra plant acquisition of newly thawed permafrost nitrogen](#)
Rebecca E. Hewitt *et al*

Environmental Research Letters



LETTER

Longer thaw seasons increase nitrogen availability for leaching during fall in tundra soils

OPEN ACCESS

RECEIVED

6 October 2015

REVISED

13 May 2016

ACCEPTED FOR PUBLICATION

20 May 2016

PUBLISHED

15 June 2016

Claire C Treat^{1,5}, Wilfred M Wollheim^{1,2}, Ruth K Varner^{1,3} and William B Bowden⁴¹ Earth Systems Research Center, Institute for the Study of Earth, Oceans & Space, University of New Hampshire, Durham, NH, USA² Department of Natural Resources & Environment, University of New Hampshire, Durham, NH, USA³ Department of Earth Sciences, University of New Hampshire, Durham, NH, USA⁴ Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, Vermont, USA⁵ Now at University of Alaska Fairbanks, Fairbanks, AK, USA.E-mail: claire.treat@unh.edu**Keywords:** nitrogen, carbon, permafrost thaw, tundra soils, changing seasonalitySupplementary material for this article is available [online](#)

Original content from this work may be used under the terms of the [Creative Commons Attribution 3.0 licence](#).

Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.

**Abstract**

Climate change has resulted in warmer soil temperatures, earlier spring thaw and later fall freeze-up, resulting in warmer soil temperatures and thawing of permafrost in tundra regions. While these changes in temperature metrics tend to lengthen the growing season for plants, light levels, especially in the fall, will continue to limit plant growth and nutrient uptake. We conducted a laboratory experiment using intact soil cores with and without vegetation from a tundra peatland to measure the effects of late freeze and early spring thaw on carbon dioxide (CO₂) exchange, methane (CH₄) emissions, dissolved organic carbon (DOC) and nitrogen (N) leaching from soils. We compared soil C exchange and N production with a 30 day longer seasonal thaw during a simulated annual cycle from spring thaw through freeze-up and thaw. Across all cores, fall N leaching accounted for ~33% of total annual N loss despite significant increases in microbial biomass during this period. Nitrate (NO₃⁻) leaching was highest during the fall ($5.33 \pm 1.45 \text{ mg N m}^{-2} \text{ d}^{-1}$) following plant senescence and lowest during the summer ($0.43 \pm 0.22 \text{ mg N m}^{-2} \text{ d}^{-1}$). In the late freeze and early thaw treatment, we found 25% higher total annual ecosystem respiration but no significant change in CH₄ emissions or DOC loss due to high variability among samples. The late freeze period magnified N leaching and likely was derived from root turnover and microbial mineralization of soil organic matter coupled with little demand from plants or microbes. Large N leaching during the fall will affect N cycling in low-lying areas and streams and may alter terrestrial and aquatic ecosystem nitrogen budgets in the arctic.

Introduction

Permafrost soil store an estimated 1035 Pg carbon (C), more than is currently stored in the atmosphere (Hugelius *et al* 2014). Warmer air temperatures, soil temperatures and the resulting permafrost thaw can result in large losses of soil organic matter due to increased decomposition (Natali *et al* 2011, Schuur *et al* 2015). Even in tundra soils that remain very cold throughout the year, periods outside of the traditional 'growing season' can be important controls of annual carbon and nitrogen budgets (Hobbie and Chapin 1996, Natali *et al* 2011). While C gas fluxes have

been quantified at a number of sites for periods outside of the traditional growing season, few studies have explicitly investigated C and N leaching outside of the growing season and prior to fall freeze-up, especially from tundra soils (Harms and Jones 2012). In sub-arctic streams and rivers, higher inorganic N concentrations have been measured during the late growing season and fall (Petroni *et al* 2006, Cai *et al* 2008), suggesting that nutrient cycling and leaching during these periods potentially play an important role in annual nutrient export.

Climate warming has resulted in both shorter winters and longer thawed periods due to an earlier spring

onset and later fall freeze-up (Serreze *et al* 2000, Euskirchen *et al* 2006, Barichivich *et al* 2012), extending the time in which heterotrophic respiration can occur. Unlike an earlier spring thaw, extending the thawed period into the fall has little effect on timing of plant senescence (Oberbauer *et al* 1998) or rates of photosynthesis (Starr *et al* 2008) because of the limited daylight hours. However, in other nutrient-limited ecosystems, such as moist acidic tundra and boreal peatlands, increased heterotrophic activity associated with later onset of freezing and warmer soil temperatures resulted in both greater soil C losses and greater N mineralization (Clein and Schimel 1995, Hobbie and Chapin 1996, Michaelson and Ping 2003, Aerts *et al* 2006). In both alpine and arctic tundra sites, N mineralized during the spring and early summer is assimilated into plants, while N mineralized in the fall is more likely to be assimilated into microbial biomass, and less likely to be taken up by plants due to senescence (Jaeger *et al* 1999, Schmidt *et al* 1999, Edwards and Jefferies 2013). N mineralized during the fall can also be leached from the soils during precipitation events (Harms and Jones 2012). However, little data is available specifically addressing N fluxes between soil pools, plants pools, and soil microbial pools after plant senescence and prior to spring green-up in low arctic tundra, especially from wet sedge tundra.

The mineralization of N during fall has important implications for soil N retention versus leaching to aquatic ecosystems, especially given the likelihood of the increased duration of microbial activity due to later freeze-up and earlier spring thaw in the future. We hypothesized that a longer thaw season with a later fall freeze and earlier spring thaw would increase microbial respiration resulting in increased C and N mineralization and subsequent ecosystem leaching loss with precipitation events. However, nutrient assimilation into microbial biomass has been found to offset nutrient losses during the winter in other sites; no data is available from riparian tundra regions.

Riparian areas are an important place for biogeochemical transformations prior to terrestrial export to aquatic ecosystems. This study focuses on a riparian area that is classified as non-tussock sedge, dwarf shrub, moss tundra, which covers an estimated 569 000 km² of the arctic and is one of the most common types of tundra (Walker *et al* 2005). However, nutrient cycling in this type of tundra is poorly understood. While the plant species composition in these riparian non-tussock sedge, dwarf shrub, moss tundra is relatively similar to the more well-studied areas of moist acidic tundra, these riparian sites are poorly drained with mire-forming vegetation and receive some hydrologic inputs from the surrounding areas. Changes in C and N cycling due to decoupling of plant-microbe interactions either within these ecosystems or in the adjacent, well-drained tundra areas could alter the long-term ecosystem productivity in both the riparian areas and downstream ecosystems.

To assess the effects of longer thaw seasons on soil C and N losses, we used a laboratory mesocosm experiment to manipulate the length of the soil thaw period by extending the date of fall freeze-up and inducing an earlier spring thaw. Our research questions were:

- (1) Does an extended thaw lead to greater ecosystem losses of C and N because plants do not take up nutrients mineralized by microbes?
- (2) If an extended thaw leads to greater ecosystem losses of C and N, does microbial biomass C and N increase due to assimilation of these additional nutrients?

We conducted a laboratory experiment to determine the effects of longer thaw duration on ecosystem respiration (ER) and leaching of C and N by leaching using soil mesocosms that contained intact active layer organic soils (typic hemistel) from tundra with and without living vegetation. We measured seasonal variations in net carbon dioxide (CO₂) exchange, methane (CH₄) emissions, microbial biomass C and N, and leaching of dissolved organic carbon (DOC) and N forms (total dissolved nitrogen (TDN), NO₃⁻, NH₄⁺, and dissolved organic nitrogen (DON)) from tundra organic soils over the course of a simulated growing season and late freeze treatment.

Methods

Site description

Soil cores were taken from a wet sedge tundra mire (non-tussock sedge, dwarf-shrub, moss tundra) (Walker *et al* 2005) near Toolik Field Station, Alaska, USA in September 2011 (68.607 °N, 149.594 °W). The mean annual air temperature is -10 °C and the mean annual precipitation ranges from 200 to 400 mm, including snow water equivalents. The snow covered season generally lasts from September or October through early June, with green-up occurring after snowmelt and plant senescence occurring in mid- to late-August (Environmental Data Center Team 2016). The riparian site is adjacent to a beaded stream ('Peat Inlet') and has been previously described (Treat *et al* 2014). The soils used in this experiment have histic epipedons, permafrost, pH ranging from 4.8 to 7.1 (table S2), C contents that ranged from 22% to 54% (table S3), and were classified mainly as typic hemistels (Soil Survey Staff 1999). Two cores were classified as fluvaquentic historthels because layers within the top 30 cm had slightly lower C content (17%–18%) and some evidence of iron oxidation. Mean soil C/N ratios were 21 ± 10, and ranged from 15 to 61 (table S3).

Eighteen 10 cm diameter soil cores were sampled within a 50 m × 100 m area that was dominated by vascular vegetation and mosses including *Carex* spp.,

Table 1. Summary of experimental setup, including number of days per season, hours of daylight, mean seasonal soil temperatures at 10 cm depth, thaw depth, day when leaching occurred, and number of cores harvested for destructive sampling over the course of the experiment for both the ambient and late freeze/early thaw treatment. Mean values across cores with (standard error).

Season	Days	Daylight (h d ⁻¹)	Soil temperature (°C)		Thaw depth (cm)			No. cores harvested	
			Ambient	Late/early	Ambient	Late/early	Day leached	Ambient	Late/early
Spring ^a	1–42	0–12	4.7 (0.3)		11 (0)		50		0
Summer ^a	43–102	18–24	8.6 (0.2)		24 (1)		94		3
Fall	103–129	0–12	3.8 (0.5)	6.7 (0.3)	21 (1)	24 (1)	113	2	2
Late freeze	130–157	0	−10.4 (0.9)	5.2 (0.4)	0 (0)	26 (1)	140	0	2
Winter	158–176	0	−11.4 (0.1)	−11.6 (0.0)	0 (0)	0 (0)	NA	0	0
Early thaw	177–182	0	−12.1 (0.9)	−5.0 (1.5)	4 (1)	1 (1)	NA	0	0
Final spring	183–188	0	2.9 (0.4)	2.9 (0.4)	30 (1)	26 (1)	189	5	6

^a Growing conditions were the same for both seasonality treatments (ambient and late/early thaw).

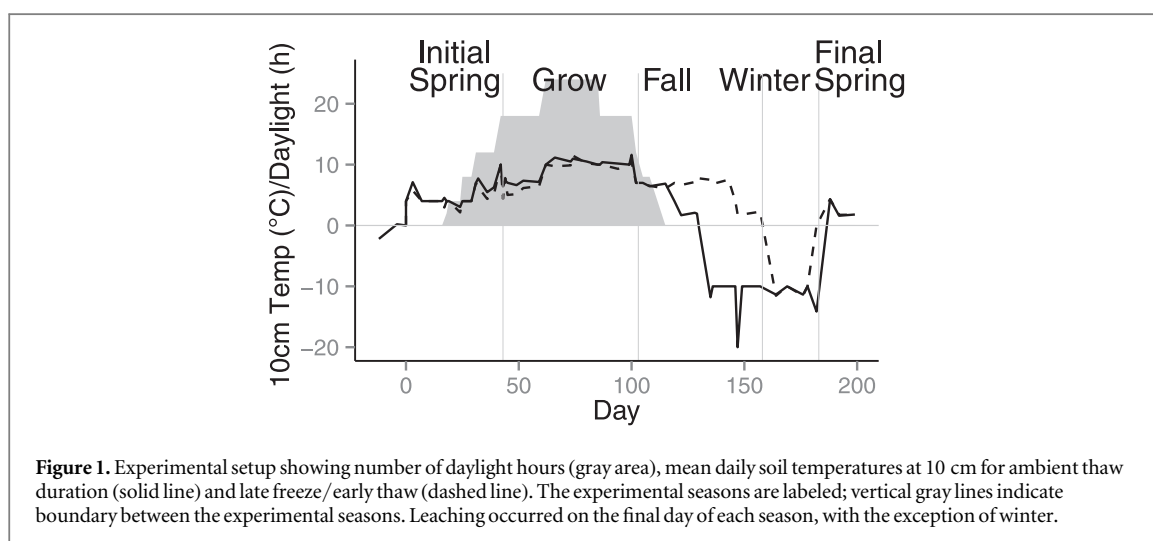


Figure 1. Experimental setup showing number of daylight hours (gray area), mean daily soil temperatures at 10 cm for ambient thaw duration (solid line) and late freeze/early thaw (dashed line). The experimental seasons are labeled; vertical gray lines indicate boundary between the experimental seasons. Leaching occurred on the final day of each season, with the exception of winter.

Eriophorum spp., *Sphagnum* spp., scattered *Betula nana* and *Hylocomium* species. Intact soil cores, including surface vegetation of *Carex* spp. and *Eriophorum* spp., were taken in September 2011 after plant senescence to capture the maximum extent of thaw depth (~30 cm) using a 10 cm diameter beveled PVC corer. Sampling was conducted in the fall to minimize disturbance; care was taken while sampling to avoid compaction of the upper soil layers. After sampling, the cores were frozen to -10°C over two days to simulate winter conditions, shipped and stored frozen at the University of New Hampshire until the experiment was begun.

Laboratory setup

We conducted a laboratory experiment to determine differences in C and N cycling due to longer thaw durations using 18 replicate intact soil cores from tundra. Soil cores were assigned to the ambient treatment (normal thaw period of 129 days, $n = 5$), to the late freeze treatment that had later soil freezing in the fall and earlier thaw in the spring (table 1, $n = 6$), or to be destructively harvested during the experiment prior to starting the late freeze/early thaw treatment ($n = 7$). For the late freeze treatment, we simulated an additional 23 days of thaw at 5°C during the fall and 7

days of thaw during the spring based on recent observations (Barichivich *et al* 2012) by using an incubation chamber to regulate soil temperature and light levels. During the spring, soil temperature and daylight hours were increased in gradual steps from -10°C and 0 h to 10°C and 18 h, kept at a plateau of 10°C and 18–24 h during the summer and were decreased in gradual steps at the end of the experimental growing season to 2°C – 5°C and 0–6 h (table 1, figure 1). The winter season was the same for all cores with a mean temperature of $\sim -11.5^{\circ}\text{C}$ at 10 cm (table 1) and was similar to winter soil temperatures in the Toolik area (Oechel *et al* 1997) despite the lack of snow cover in this experiment that would have insulated the soils from even colder air temperatures and been a source of melt water during the spring. The final spring period saw soil temperatures gradually increase to 4°C although the timing was 7 days earlier in the late freeze/early thaw treatment than the ambient treatment. All cores received the same amount of daylight and were held at field soil capacity. Due to disturbance effects, vegetation regeneration occurred in only $\sim 50\%$ of cores during the first experimental spring. We included vegetation presence/absence as an additional

treatment and used stratified random sampling when assigning the cores to the late freeze treatments.

We measured above-ground plant biomass, soil C and N pools, microbial biomass C and N pools, CO₂ and CH₄ fluxes, and DIN (NH₄⁺, NO₃⁻), DON, and DOC leaching seasonally throughout the experiment with the exception of the end of winter. Net ecosystem exchange (NEE) and ER were measured weekly. Measurements of DOC, DIN, and DON leaching were made before each seasonal transition using an extraction of soil porewater with a stainless steel porewater sampler attached to a syringe following a simulated precipitation (rainfall) event (table 1). Destructive harvests of a subset of cores followed the seasonal transitions for determination of soil carbon stocks, nitrogen stocks, and microbial biomass (table 1). Soil temperatures at 2 cm, 10 cm were measured simultaneously using type T thermocouples and data collected on a datalogger (CR1000, Campbell Scientific, Logan, Utah, USA). Thaw depth within the cores was measured concurrently with weekly flux measurements (table 1).

Measurements of CO₂ and CH₄ fluxes were made weekly using static chamber techniques (Carroll and Crill 1997). NEE and ER used light and dark chamber measurements of CO₂ flux; gross primary productivity (GPP) was calculated as the difference between the measurements due to plant CO₂ uptake. Concentrations of CO₂ in the chamber headspace were measured using an infrared gas analyzer (Li-Cor Biosciences, Lincoln, Nebraska). Methane fluxes were measured using dark chambers for a period of ten minutes; CH₄ concentrations were measured using a gas chromatograph equipped with a flame ionization detector (Treat *et al* 2007).

Seasonal measurements of DOC and N leaching were made before each seasonal transition (table 1) by simulating a precipitation event, with the exception of winter as the soil was still frozen. The total leaching approximated annual precipitation for the site (~300 mm). We slowly added ~60 mm runoff (DI water) over a period of 4–6 h and extracted the soil pore water ('leachate') from the bottom of the active layer 12 h later (Judd and Kling 2002). Soils could not always drain freely due to presence of frozen layer at the bottom of the core, so the leachate was extracted until soils either stopped draining freely and no more leachate was extractable, or an equal volume of leachate was extracted. Leachate was filtered using a 0.77 μm GF/F filter and frozen until analysis for DOC, TDN, nitrate (NO₃⁻ + NO₂), and ammonium (NH₄⁺). NO₃⁻ and NH₄⁺ were measured using colorimetric methods using a Smartchem Chemistry Analyzer, and DOC and TDN were measured with using a TOC/TN analysis system at the Water Quality Analysis Lab at the University of New Hampshire, Durham, NH, USA. DON was estimated by subtracting DIN (NO₃⁻ and NH₄⁺) concentrations from TDN. All leaching values were converted to milligrams

per m⁻² based on the amount of leachate volume, leachate concentration, and core area. Total leaching was calculated by summing seasonal nutrient leaching.

Destructive harvests of soils and vegetation were used to determine seasonal changes in above-ground vegetation biomass, microbial biomass C and N, and soil C and N stocks. Entire soil cores were harvested seasonally throughout the experiment both prior to and after the thaw-season length treatments were established (table 1). The remaining soil cores were harvested at the end of the experiment and compared to determine experimental differences. Green above-ground vegetation was removed, dried and weighed. Soil cores were sectioned into 5 cm increments and analyzed for bulk density, soil moisture, and C and N content. Carbon and N content of bulk soils were measured using an elemental analyzer (Costech Inc., Valencia, CA, USA). Total microbial biomass C and N was measured in surface soils (0–15 cm) seasonally throughout the experiment and concurrently with the destructive harvests, using chloroform fumigation and K₂SO₄ extraction (Vance *et al* 1987) and an extraction efficiency for arctic soils of $k_{EC} = 0.35$ and $k_{EN} = 0.4$ (Jonasson *et al* 1996).

Statistical analysis

We tested for treatment effects and seasonal differences using mixed effects modeling. When testing for seasonal treatment differences, we used mixed effects modeling to account for repeated sampling using the same cores, and included core as a random effect. Correlations among variables in the mixed effects models were fit using restricted maximum likelihood and including core as a random effect. We used Tukey's Honest Significant Difference (HSD) post-hoc tests to identify significant pair-wise differences among means for seasons and vegetation treatments. When testing for the seasonal effects, the vegetation differences were considered a continuous variable that was covariate among the cores, and thus were implicit in the model structure and accounted for by the random 'core' effect. We explicitly tested for vegetation treatment differences (with and without living vegetation) within each season using an analysis of variance and Tukey's HSD post-hoc test. All statistical analysis were done using R (R Development Core Team 2008); mixed effects modeling was done using the R package lme4 (Bates *et al* 2015).

Results and discussion

Nitrogen leaching was largest during the fall and late freeze periods of the experiment for both treatments. TDN leaching was >70% higher during the fall and late freeze periods than during the summer and spring, mostly due to elevated NO₃⁻ and NH₄⁺ losses compared to the earlier seasons (figure 2, table 2). The late freeze was an important contributor to the overall

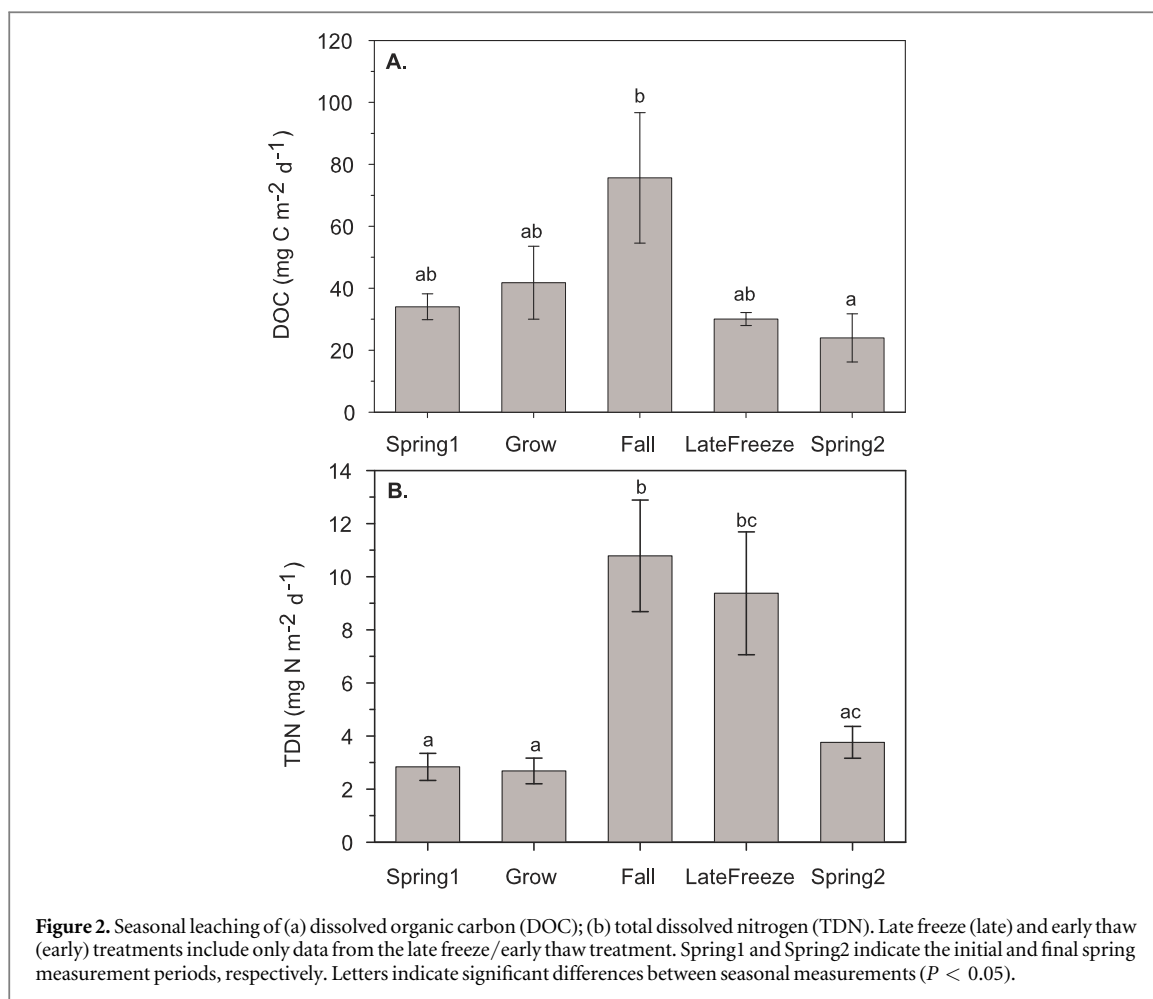


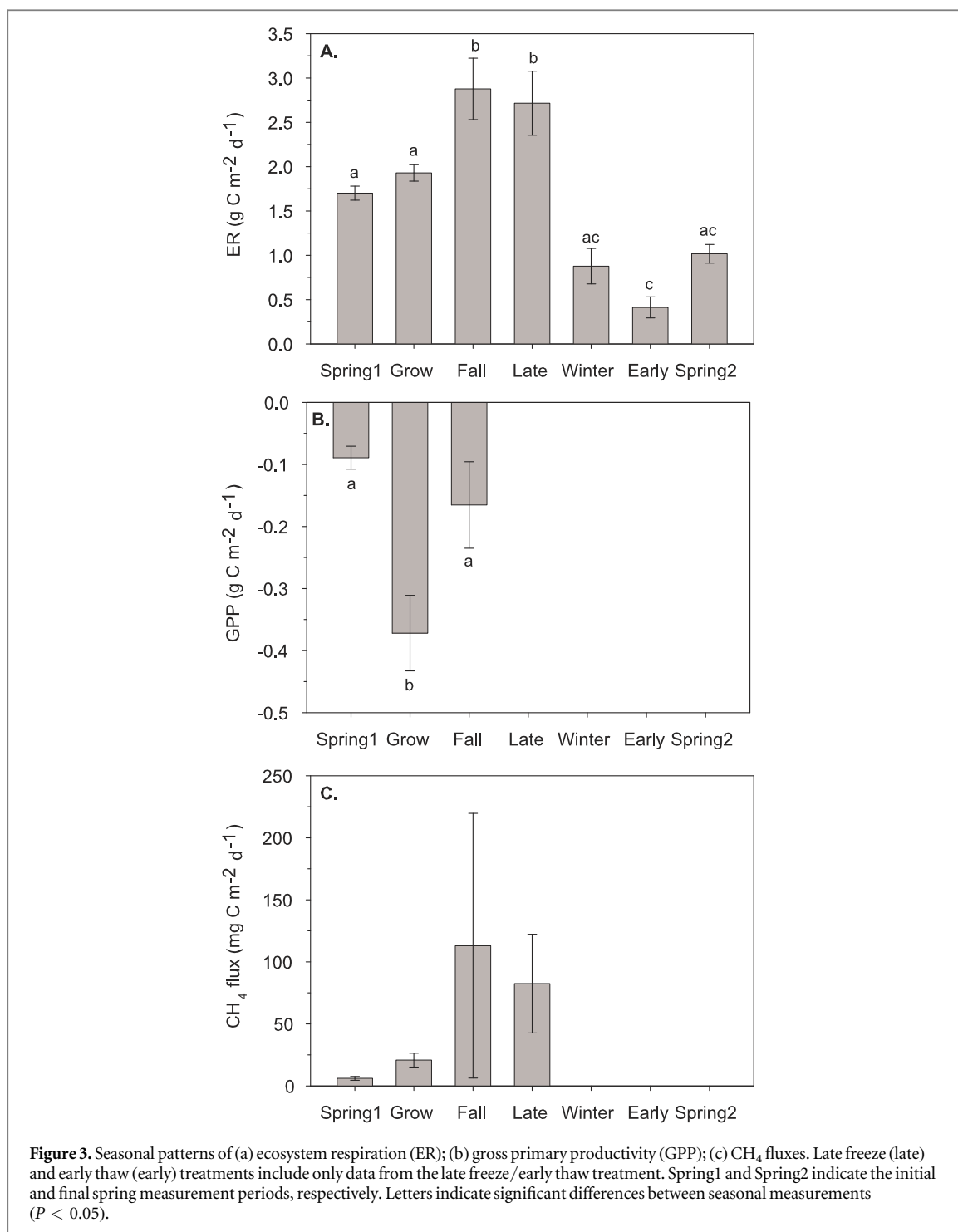
Table 2. Mean daily production of leaching constituents for the thaw duration treatments over entire 189 day experiment. Late freeze values include only late freeze/early thaw treatment; other seasons represent both treatments. In other seasons, differences between treatments were not significant ($P > 0.10$; table S1). Superscript letters indicate significant differences ($P < 0.05$) among seasonal means.

Season	DOC ($\text{mg C m}^{-2} \text{d}^{-1}$)		DIN ($\text{mg N m}^{-2} \text{d}^{-1}$)		DON ($\text{mg N m}^{-2} \text{d}^{-1}$)		NO_3^- ($\text{mg N m}^{-2} \text{d}^{-1}$)		NH_4^+ ($\text{mg N m}^{-2} \text{d}^{-1}$)	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Spring	34.0	(4.2) ^{ab}	1.4	(0.4) ^a	1.5	(0.2) ^{ab}	0.7	(0.2) ^a	0.8	(0.3)
Summer	41.8	(11.8) ^{ab}	1.3	(0.3) ^a	1.4	(0.3) ^{ab}	0.4	(0.2) ^a	0.8	(0.3)
Fall	75.6	(21.1) ^a	7.8	(1.9) ^b	2.9	(0.7) ^a	5.3	(1.4) ^b	2.5	(1.0)
Late Freeze	30.1	(2.1) ^{ab}	8.2	(2.3) ^b	1.2	(0.4) ^{ab}	5.6	(1.9) ^b	2.6	(1.3)
Final spring	24.0	(7.8) ^b	3.0	(0.7) ^{ab}	0.8	(0.3) ^b	1.7	(0.6) ^{ab}	1.3	(0.2)

N budgets. Over half (53%) of total annual NO_3^- leaching and 50% of total annual NH_4^+ leaching occurred during the late freeze period. Nitrate was the largest component of N leaching during the fall period ($43.0 \pm 9.5\%$) and accounted for 50% of total N leaching for the season (table 2). However, differences in cumulative N leaching were not significantly different between the ambient and late freeze/early thaw treatment due to high variability (table 3; $P > 0.25$). Field studies in sub-arctic and high arctic streams have observed peaks in inorganic N concentrations in stream water during late summer and fall (Petrone *et al* 2006, Cai *et al* 2008), as well as late

growing season NO_3^- soil leachate from high arctic tundra (Schaeffer *et al* 2013), highlighting the importance of late summer and fall for understanding annual nitrogen budgets.

The fall seasons were also important for C dynamics. ER was significantly higher in both the fall and the late freeze periods than the spring and summer periods for both treatments (figure 3(a)), while GPP was highest in the summer (figure 3(b)). However, the magnitude of GPP was much smaller in this study than field observations, likely a result of disturbance effects resulting from the mesocosm approach, including potential damage to the root system. Low rates of GPP



may have contributed to slightly lower net above-ground primary productivity in this study ($60 \text{ g m}^{-2} \text{ y}^{-1}$) than in other wet tundra sites in Alaska ($81 \text{ g m}^{-2} \text{ y}^{-1}$) (Shaver and Chapin 1991). Methane and DOC losses were highest during the fall season for both treatments (figures 2(a) and 3(c)).

High N leaching during the fall may have resulted from increased microbial decomposition of soil organic matter due to warmer soils and deeper active layer depths, increased root mortality, reduced microbial uptake and immobilization of N, or some combination of the above. Decomposition of soil organic

matter in tundra soils is strongly positively correlated with temperature (Hamdi *et al* 2013). Therefore, we would expect the highest rates of the decomposition of soil organic matter to occur during the warmest period of summer (table 1), which has been observed in previous field studies in nearby sites (Grogan and Chapin 1999, 2000). In this study, however, rates of ER were highest during the fall for both treatments despite cooler temperatures (figure 3). Similarly, if the thawing of N-rich soils at the interface of the active layer and permafrost was the source of N leached from the soils (figure S2; e.g. Petrone *et al* 2006, Harden

Table 3. Mean cumulative total gaseous C, DOC, and N leaching for both the ambient and late freeze/early thaw treatments. Standard error is given in parentheses. Results of mixed-effects models used to test for treatment differences (F -statistics and p -values) are also shown here.

Constituent	Ambient		Late freeze/ early thaw		$F_{(1,9)}$	P
	Mean	SE	Mean	SE		
ER (g C m ⁻²)	271	(15)	339	(31)	3.46	0.10
GPP (g C m ⁻²)	30	(12)	37	(10)	0.26	0.62
CH ₄ (g C m ⁻²)	0.33	(0.22)	3.67	(2.28)	1.74	0.22
DOC (g C m ⁻²)	7.18	(3.02)	4.21	(0.30)	1.17	0.31
TDN (mg N m ⁻²)	542	(95)	654	(129)	0.45	0.52
NO ₃ ⁻ (mg N m ⁻²)	256	(125)	307	(118)	0.09	0.77
NH ₄ ⁺ (mg N m ⁻²)	113	(36)	166	(26)	1.52	0.25
DON (mg N m ⁻²)	174	(94)	173	(21)	0	0.99

et al 2012, Harms and Jones 2012, Keuper *et al* 2012), we would expect that highest rates of N leaching would coincided with the initial thaw during the early part of the summer. While total TDN leaching was positively correlated with thaw depth for all seasons using data from the individual cores ($r = 0.27$, $F_{1,64} = 4.95$, $P = 0.03$), the greatest seasonal leaching of TDN occurred during the fall when thaw depths were shallower than the summer (figure 2; table 1), indicating that the source of N released during the fall was not from deeper soils at the interface between the permafrost and the active layer. Results from both ER and nitrogen leaching suggest that the decomposition of soil organic matter is unlikely to be the sole source of C respired and N leached during the fall period from either the warm and shallow soils or recently thawed, deep active layer soils.

The decomposition of plant roots and subsequent leaching likely contributed to high N leaching during the fall in this experiment. In this experiment, root mortality and decomposition likely occurred throughout the measurement period due to disturbance effects of the initial sampling in comparison to field conditions, especially in cores without vegetation. During the summer season when GPP was highest, NO₃⁻ leaching was 11 times larger from cores without plants than with plants (1.2 ± 0.5 and 0.1 ± 0.05 mg N m⁻² d⁻¹, respectively; $F_{1,13} = 13.8$, $P < 0.01$). Higher NO₃⁻ leaching from these cores is likely a combination of decomposition of roots that release NO₃⁻ (e.g. Varner *et al* 2003) and the absence of NO₃⁻ uptake by plants in these collars. However, NO₃⁻ leaching from cores with plants equaled and exceeded cores without vegetation during the fall and late freeze period. During the fall, NO₃⁻ leaching was similar (plants: 3.9 ± 1.2 ; no plants: 3.5 ± 3.1 mg N m⁻² d⁻¹) and greater during the late freeze (plants: 3.6 ± 1.6 ; no plants: 2.6 ± 1.3 mg N m⁻² d⁻¹) from cores with plants than without plants, respectively. The pulse of NO₃⁻ leaching following senescence in cores with plants also suggests root turnover at the end of the growing season as the largest source of NO₃⁻ in this experiment, which has also been found in boreal forest ecosystems (Kieland *et al* 2006). Additional decomposition of roots

from other vegetation types or additional mineralization of soil organic matter due to priming by root exudates may have also occurred.

During the fall, field studies in other tundra types have observed that available N from bulk soils is assimilated into microbial biomass, which buffers soil N loss after plant senescence (Jaeger *et al* 1999, Schmidt *et al* 1999, Edwards and Jefferies 2013). In this study, microbial biomass C increased throughout the fall, late freeze and final spring seasons (table 4), as previously observed in organic soils from other tundra sites (Buckridge *et al* 2013, Sistla and Schimel 2013). Microbial biomass C was significantly larger in the final spring than during the previous summer (table 4). Microbial biomass N was not significantly different among the seasons (table 4; $P > 0.26$) but microbial C/N ratios were largest during the fall and late freeze periods, likely due to a transition to fungal dominated communities during the winter (e.g. Buckridge *et al* 2013). In this experiment, leaching of N was highest during the fall but increases in microbial biomass N were not observed. In these organic soils with a relatively low C/N ratio (21 ± 10), the C limitations on microbial growth, especially for fungal communities, likely also contributed to high rates of ammonification and subsequent leaching of NH₄⁺ from the mineralization of organic matter (Chapin *et al* 2002). While the microbial biomass was likely not a direct source of N leached from soils, the microbial mineralization of organic matter and the transition to fungal communities did not immobilize N during the fall and late freeze periods.

Measurements of fall N dynamics (leaching, mineralization, and denitrification) in tundra ecosystems are rare. In this study, TDN leaching during fall period was an important component of the annual budget and was 120% higher than spring and summer period N leaching combined for both treatments (figure 2(b)), which made the fall period measurements important for accurately calculating the annual N budget. Two factors in this experiment may have led to an overestimation of leaching from these riparian tundra systems compared with field conditions. First, N may have been flushed from the soils during the simulated precipitation events (60 mm rainfall, ~ 15 mm h⁻¹), which is a relatively

Table 4. Mean season microbial biomass (standard error) per gram dry weight of soil. Mean values represent a minimum of three separate depth increments per core ($n > 6$). Microbial biomass C differed significantly among seasons ($\text{Chi}^2 = 14.4$, d.f. = 3, $P < 0.01$); superscript letters indicate significant differences between means. Seasonal differences in microbial biomass N and C/N were not statistically significant.

Season	Microbial biomass C (mg C g ⁻¹)	Microbial biomass N (mg N g ⁻¹)	Microbial biomass C/N
Summer	6.24 (2.64) ^a	1.02 (0.41)	13 (2)
Fall	15.95 (2.04) ^{ab}	0.92 (0.38)	41 (11)
Late freeze	15.82 (2.90) ^{ab}	0.78 (0.43)	49 (19)
Final spring	23.52 (1.50) ^b	1.51 (0.21)	22 (2)

high intensity storm. Second, disturbance effects from using intact soil mesocosms resulted in root turnover throughout the experiment which likely also enhanced N leaching, especially during the summer in cores without vegetation. While the magnitude of N leaching measured in this study must be interpreted with caution because of the differences between experimental mesocosm approach and field conditions, the consistent seasonal trends and differences between soil cores with and without plants point to the importance of root turnover in controlling the size of extractable N pools and fall N dynamics, both factors that also likely occur in the field.

Nitrogen mineralized during the fall period has three potential fates that depend on soil biology and hydrology: (1) retention in soil microbial N pools; (2) loss as gaseous NO, N₂O, or N₂ via denitrification; and (3) leaching to other landscape positions, including streams. While nitrogen is not assimilated into plant biomass during the fall, it can be assimilated into microbial biomass in the fall and retained until the spring for plant or microbial growth (Jaeger *et al* 1999, Lipson *et al* 1999, Schmidt *et al* 2007, Edwards and Jefferies 2013). In this study, microbial biomass increased during the fall and into the final spring (table 4), indicating the retention of N by incorporation into microbial biomass. However, net N leaching remained high during the fall. Net N leaching decreased in the final spring and did not differ significantly between the first and second spring seasons (table 2), which, combined with the increased microbial biomass, suggests that net N immobilization occurred during the fall period. However, N mineralization during the fall in this study outpaced the microbial immobilization in the soil and still resulted in large net leaching.

In conclusion, we found large leaching of N species following the growing season from this riparian tundra site despite increases in microbial biomass. During the period following the growing season, the mineralization of soil organic matter and plant litter exceeded the microbial immobilization of N, likely due to microbial C limitation, and resulted in elevated N leaching losses. If N leaching is sustained *in situ* during the non-growing season, progressive N limitation

could develop as thaw season lengthens. In an already nutrient limited system, long-term changes in N leaching during the fall in arctic ecosystems, such as the riparian tundra in this study, may result in changes to terrestrial and aquatic N cycling, including changes in vegetation composition, ecosystem productivity, N₂O emissions, and stream food web dynamics.

Acknowledgments

This research was from a thesis submitted to the Graduate School at the University of New Hampshire as part of the requirements for completion of a doctoral degree. C T was supported by the DOE-SCGF Fellowship (administered by ORISE-ORAU under contract no. DE-AC05-06OR23100) and a University of New Hampshire Dissertation Year Fellowship. We also thank NSF ARC-0902106 and the Iola K Hubbard Grant for Climate Change Research from to the Institute for the Studies of Earth, Oceans and Space at UNH for funding. We thank K Merrill and G Waldvogel for field assistance, Toolik Field Station for logistical support, A Marquis, A Perry, A Price and S Werner for lab assistance, and J Harden for helpful discussion.

References

- Aerts R, Cornelissen J H C and Dorrepaal E 2006 Plant performance in a warmer world: general responses of plants from cold, northern biomes and the importance of winter and spring events *Plant Ecology* **182** 65–77
- Barichivich J, Briffa K R, Osborn T J, Melvin T M and Caesar J 2012 Thermal growing season and timing of biospheric carbon uptake across the Northern Hemisphere *Glob. Biogeochem. Cycles* **26** GB4015
- Bates D, Maechler M, Bolker B and Walker S 2015 Fitting linear mixed-effects models using lme4 *J. Stat. Software* **67** 1–48
- Buckeridge K M, Banerjee S, Siciliano S D and Grogan P 2013 The seasonal pattern of soil microbial community structure in mesic low arctic tundra *Soil Biol. Biochem.* **65** 338–47
- Cai Y H, Guo L D, Douglas T A and Whitledge T E 2008 Seasonal variations in nutrient concentrations and speciation in the Chena River, Alaska *J. Geophys. Res.-Biogeosci.* **113** G03035
- Carroll P and Crill P 1997 Carbon balance of a temperate poor fen *Glob. Biogeochem. Cycles* **11** 349–56
- Chapin F S III, Matson P A and Mooney H A 2002 *Principles of Terrestrial Ecosystem Ecology* (New York: Springer)
- Clein J S and Schimel J P 1995 Microbial activity of tundra and taiga soils at subzero temperatures *Soil Biol. Biochem.* **27** 1231–4
- Environmental Data Center Team 2016 *Meteorological Monitoring Program (Toolik, Alaska)* (http://toolik.alaska.edu/edc/abiotic_monitoring/data_query.php)
- Edwards K A and Jefferies R L 2013 Inter-annual and seasonal dynamics of soil microbial biomass and nutrients in wet and dry low-Arctic sedge meadows *Soil Biol. Biochem.* **57** 83–90
- Euskirchen E S *et al* 2006 Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems *Glob. Change Biol.* **12** 731–50
- Grogan P and Chapin F S 1999 Arctic soil respiration: effects of climate and vegetation depend on season *Ecosystems* **2** 451–9
- Grogan P and Chapin F S 2000 Initial effects of experimental warming on above- and belowground components of net ecosystem CO₂ exchange in arctic tundra *Oecologia* **125** 512–20

- Hamdi S, Moyano F, Sall S, Bernoux M and Chevallier T 2013 Synthesis analysis of the temperature sensitivity of soil respiration from laboratory studies in relation to incubation methods and soil conditions *Soil Biol. Biochem.* **58** 115–26
- Harden J W *et al* 2012 Field information links permafrost carbon to physical vulnerabilities of thawing *Geophys. Res. Lett.* **39** L15704
- Harms T K and Jones J B 2012 Thaw depth determines reaction and transport of inorganic nitrogen in valley bottom permafrost soils *Glob. Change Biol.* **18** 2958–68
- Hobbie S E and Chapin F S 1996 Winter regulation of tundra litter carbon and nitrogen dynamics *Biogeochemistry* **35** 327–38
- Hugelius G *et al* 2014 Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps *Biogeosciences* **11** 6573–93
- Jaeger C H, Monson R K, Fisk M C and Schmidt S K 1999 Seasonal partitioning of nitrogen by plants and soil microorganisms in an alpine ecosystem *Ecology* **80** 1883–91
- Jonasson S, Michelsen A, Schmidt I K, Nielsen E V and Callaghan T V 1996 Microbial biomass C, N and P in two arctic soils and responses to addition of NPK fertilizer and sugar: implications for plant nutrient uptake *Oecologia* **106** 507–15
- Judd K E and Kling G W 2002 Production and export of dissolved C in arctic tundra mesocosms: the roles of vegetation and water flow *Biogeochemistry* **60** 213–34
- Keuper F, van Bodegom P M, Dorrepaal E, Weedon J T, van Hal J, van Logtestijn R S P and Aerts R 2012 A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands *Glob. Change Biol.* **18** 1998–2007
- Kielland K, Olson K, Ruess R W and Boone R D 2006 Contribution of winter processes to soil nitrogen flux in taiga forest ecosystems *Biogeochemistry* **81** 349–60
- Lipson D A, Schmidt S K and Monson R K 1999 Links between microbial population dynamics and nitrogen availability in an alpine ecosystem *Ecology* **80** 1623–31
- Michaelson G J and Ping C L 2003 Soil organic carbon and CO₂ respiration at subzero temperature in soils of Arctic Alaska *J. Geophys. Res.* **108** 8164
- Natali S M, Schuur E A G, Trucco C, Pries C E H, Crummer K G and Lopez A F B 2011 Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra *Glob. Change Biol.* **17** 1394–407
- Oberbauer S F, Starr G and Pop E W 1998 Effects of extended growing season and soil warming on carbon dioxide and methane exchange of tussock tundra in Alaska *J. Geophys. Res.* **103** 29075–82
- Oechel W C, Vourlitis G and Hastings S J 1997 Cold season CO₂ emission from arctic soils *Glob. Biogeochem. Cycles* **11** 163–72
- Petrone K C, Jones J B, Hinzman L D and Boone R D 2006 Seasonal export of carbon, nitrogen, and major solutes from Alaskan catchments with discontinuous permafrost *J. Geophys. Res.: Biogeosci.* **111** G02020
- R Development Core Team 2008 *R: A Language and Environment for Statistical Computing* (Vienna, Austria: R Foundation for Statistical Computing)
- Schaeffer S M, Sharp E, Schimel J P and Welker J M 2013 Soil-plant N processes in a High Arctic ecosystem, NW Greenland are altered by long-term experimental warming and higher rainfall *Glob. Change Biol.* **19** 3529–39
- Schmidt I K, Jonasson S and Michelsen A 1999 Mineralization and microbial immobilization of N and P in arctic soils in relation to season, temperature and nutrient amendment *Appl. Soil Ecology* **11** 147–60
- Schmidt S K, Costello E K, Nemergut D R, Cleveland C C, Reed S C, Weintraub M N, Meyer A F and Martin A M 2007 Biogeochemical consequences of rapid microbial turnover and seasonal succession in soil *Ecology* **88** 1379–85
- Schuur E A G *et al* 2015 Climate change and the permafrost carbon feedback *Nature* **520** 171–9
- Serreze M C, Walsh J E, Chapin F S, Osterkamp T, Dyrugerov M, Romanovsky V, Oechel W C, Morison J, Zhang T and Barry R G 2000 Observational evidence of recent change in the northern high-latitude environment *Clim. Change* **46** 159–207
- Shaver G R and Chapin F S 1991 Production: biomass relationships and element cycling in contrasting arctic vegetation types *Ecological Monographs* **61** 1–31
- Sistla S A and Schimel J P 2013 Seasonal patterns of microbial extracellular enzyme activities in an arctic tundra soil: identifying direct and indirect effects of long-term summer warming *Soil Biol. Biochem.* **66** 119–29
- Soil Survey Staff 1999 Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys *US Department of Agriculture Handbook* 2nd edn (Washington, DC: Natural Resources Conservation Service) p 886
- Starr G, Oberbauer S F and Ahlquist L E 2008 The photosynthetic response of Alaskan tundra plants to increased season length and soil warming *Arctic Antarct. Alpine Res.* **40** 181–91
- Treat C C, Bubier J L, Varner R K and Crill P M 2007 Timescale dependence of environmental and plant-mediated controls on CH₄ flux in a temperate fen *J. Geophys. Res.-Biogeosci.* **112** G01014
- Treat C C, Wollheim W M, Varner R K, Grandy A S, Talbot J and Frolking S 2014 Temperature and peat type control CO₂ and CH₄ production in Alaskan permafrost peats *Glob. Change Biol.* **20** 2674–86
- Vance E D, Brooks P C and Jenkinson D S 1987 Microbial biomass measurements in forest soils: the use of the chloroform fumigation-incubation method in strongly acid soils *Soil Biol. Biochem.* **19** 697–702
- Varner R K, Keller M, Robertson J R, Dias J D, Silva H, Crill P M, McGroddy M and Silver W L 2003 Experimentally induced root mortality increased nitrous oxide emission from tropical forest soils *Geophys. Res. Lett.* **30** 1144
- Walker D A *et al* 2005 The circumpolar arctic vegetation map *J. Vegetation Sci.* **16** 267–82