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Temporal variability in plant and soil nitrogen pools in a high-Arctic ecosystem

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Abstract

This study determined temporal variability in N pools, both aboveground and belowground, across two contrasting plant communities in high-Arctic Spitsbergen, Svalbard (78°N). We measured N pools in plant material, soil microbial biomass and soil organic matter in moist (*Alopecurus borealis* dominated) and dry (*Dryas octopetala* dominated) meadow communities at four times during the growing season. We found that plant, microbial and dissolved inorganic and organic N pools were subject to significant, but surprisingly low, temporal variation that was controlled primarily by changes in temperature and moisture availability over the short growing season. This temporal variability is much less than that experienced in other seasonally cold ecosystems such as alpine tundra where strong seasonal partitioning of N occurs between plant and soil microbial pools. While only a small proportion of the total ecosystem N, the microbial biomass represented the single largest of the dynamic N pools in both moist and dry meadow communities (3.4% and 4.6% of the total ecosystem N pool, respectively). This points to the importance of soil microbial community dynamics for N cycling in high-Arctic ecosystems. Microbial N was strongly and positively related to soil temperature in the dry meadow, but this relationship did not hold true in the wet meadow where other factors such as wetter soil conditions might constrain biological activity. Vascular live belowground plant parts represented the single largest plant N pool in both dry and moist meadow, constituting an average of 1.6% of the total N pool in both systems; this value did not vary across the growing season or between plant communities. Overall, our data illustrate a surprisingly low growing season variability in labile N pools in high-Arctic ecosystems, which we propose is controlled primarily by temperature and moisture.

Keywords: High Arctic; Nitrogen cycling; Temporal variation; Soil microbial biomass; Nitrogen mineralisation; Moss; Dry and moist meadows

1. Introduction

It is widely recognised that soil microbes act as a major nitrogen (N) pool in terrestrial ecosystems (Fisk and Schmidt, 1996; Zogg et al., 2000; Bardgett et al., 2003; Phoenix et al., 2004). This is especially the case in strongly N-limited ecosystems, such as Arctic and alpine tundra, where soil microbes compete effectively with plants for N (Schimel and Chapin, 1996; Nordin et al., 2004) leading, in some cases, to similar quantities of N being found in the microbial and plant pool (Jonasson et al., 1999; Bardgett et al., 2002). Understanding the dynamics of microbial N and the factors that influence the ability of microbes to act as a N sink in terrestrial ecosystems is of great importance for nutrient cycling; not only does microbial uptake of N influence the availability of N to plants (Schimel and Chapin, 1996; Jaeger et al., 1999; Schimel and Bennett, 2004; Bardgett et al., 2005) but it can also act as a buffer limiting the export of N to adjacent ecosystems (Brooks et al., 1998).

To understand the significance of microbial N for ecosystem properties, knowledge is required of the spatial and temporal variability of this and other plant and soil N

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pools. The importance of spatial factors related to topographical position and regional climate for microbial properties and N cycling is widely recognised (Barrett et al., 2002; Wardle, 2002; McCulley and Burke, 2004; Bardgett, 2005). A number of studies also point to the importance of seasonal dynamics in soil microbial communities for N cycling. In particular, studies of alpine ecosystems reveal a strong seasonality in environmental conditions, leading to temporal partitioning of N between plants and soil microbes. This was shown by Jaeger et al. (1999), who found that the dominant plant species of an alpine meadow in the Colorado Rocky Mountains took up N maximally after snowmelt, when soils had warmed, but were still moist, whereas soil microbes immobilised N maximally in the autumn, after plant senescence. Similar patterns have been found in montane heath communities in Scotland, where microbial N was greater in autumn, after plant senescence, than early in the growing season when microbes were strongly N limited (Bardgett et al., 2002). Studies in low Arctic tundra (Toolik Lake, Alaska) also reveal that temporal patterns in microbial and plant demand for soil N play a major role in regulating N pool dynamics (Weintraub and Schimel, 2005). Collectively, what these studies suggest is that both microbial and plant N pools show strong seasonality with important implications for ecosystem N cycling.

To date, work on seasonal variability of plant and soil N pools has focussed largely on alpine ecosystems. There is limited understanding of whether similar variability occurs in other strongly N-limited ecosystems, such as those found in the high Arctic. To redress this, we examined temporal variability in N pools, both plant and soil, in two contrasting high-Arctic plant communities, Spitsbergen, Svalbard (78°N), where environmental conditions strongly constrain biological processes of N cycling (Van der Wal and Brooker, 2004; Van der Wal et al., 2004). This allowed us to explicitly test whether patterns of seasonal variation in N pools differed between two widespread and contrasting plant communities. The two plant communities were a moist meadow, dominated by the grass *Alopecurus borealis*, typically located in wetter areas that receive drainage waters, and a dry meadow, dominated by the rush *Luzula confusa* and the dwarf shrub *Dryas octopetala*, typically found on elevated ridges with relatively free-draining soil. Our overarching goal was to quantify temporal patterns in the size of plant and soil N pools in these plant communities and provide insights into the factors that control these patterns in Arctic ecosystems.

2. Materials and methods

2.1. Study sites and sampling

The study was conducted in 2001 in Adventdalen, which is approximately 10 km east of Longyearbyen, Svalbard (78°13′N). Adventdalen is a wide valley approximately 30 km long and 2–3 km wide, with most of the valley floor and sides consisting of extensive tundra vegetation, which is within the bioclimatic Arctic sub-zone C (CAVM Team, 2003). We selected two widespread and contrasting plant communities. One of the communities was a moist meadow, which occurred in locations receiving drainage waters and was dominated by the grass *A. borealis*, the dwarf shrub *Salix polaris* and the mosses *Sanionia uncinata* and *Hylocomium splendens* which form a continuous layer of 38 ± 1 mm depth overlaying an organic soil horizon of 80 ± 4 mm depth. The second habitat, a dry meadow, was found on a series of elevated ridges and was predominantly vegetated by the rush *L. confusa* and the dwarf shrub *D. octopetala*, with low, but characteristic, occurrence of the sedge *Carex rupestris* and a *Tomentypnum nitens* dominated moss layer of 31 ± 1 mm overlaying an organic soil horizon of 63 ± 2 mm depth. These sites are referred to as moist and dry meadow herewith. Within each site, 10 discreet sampling patches (5 m × 5 m) were randomly selected, and within each sampling patch four plots were randomly chosen and marked out using bamboo canes (plots were 20 cm × 30 cm). All moist sites were located within a 140 m × 300 m area, while dry sites were all within an 80 m × 300 m area. The individual sampling patches within each of the two plant communities were therefore considered statistically independent.

At four dates, spanning the short growing season, the sites were visited to retrieve soil turves and cores for further analysis. The first sampling was on 10 June, immediately after snowmelt; the second and third were on 24 June and 17 July, to represent periods of active plant growth; the final sampling was on August 18th during the period of plant senescence. Each sampling patch was visited and a plot was chosen at random. Two turves (each with dimensions of 100 mm × 100 mm) were cut from each plot to a depth of 2 cm into the mineral soil and a single intact core was also taken for bulk density assessment and measurement of soil moisture content (36 mm diameter × 50 mm length). Moss depth and soil temperature beneath the moss layer (at approximately 5 cm depth) were determined for each plot separately. Turves and cores were stored in a cold room at 5 °C prior to measurement.

2.2. Measurement of vegetation biomass and N content

Live above- and belowground vascular plant biomass, as well as live moss, decaying moss and detritus were collected as separate components from one of the turves. The live aboveground vascular plant material occurring in the live moss layer was kept separately from that occurring above the moss layer. Similarly, belowground material in the decomposing moss layer was kept separately from that occurring in the organic or mineral soil horizons. All material was dried at 65 °C for 3 days and weighed. The dried vegetation was shipped back to Lancaster for quantification of N content. This was done by first grinding plant material, using a Retsch mixer ball mill, and then

determining N content of this using a Leco FP428 combustion system to yield percentage dry matter N.

2.3. Measurement of soil N pools

At each sampling date, a second turf was destructively harvested, and soil was passed through a 5 mm sieve, to make a range of measures of soil N pools, including total soil N, microbial biomass C and N, and dissolved organic (DON) and inorganic N (DIN). Because no seasonal change in total soil N was expected, this measure was determined only at the first sampling, using the Leco FP428 combustion system described earlier. Microbial biomass C and N were measured using the fumigation-extraction technique of Vance et al. (1987). Briefly, soil samples (5 g fresh weight) were fumigated with ethanol-free $CHCl_3$ for 24 h at 25 °C. After removal of the $CHCl_3$, soluble C was extracted from fumigated and un-fumigated samples with 0.5 M K_2SO_4 for 30 min on an orbital shaker (soil:solution 1:4 w/v). Total organic C in filtered extracts (Whatman No. 1) was determined using a Shimadzu 5000A TOC analyser. Microbial C flush (difference between extractable C from fumigated and un-fumigated samples) was converted to microbial biomass C using a k_{EC} factor of 0.35 (Sparling et al., 1990). Extractable N in the above extracts was determined by oxidation with $K_2S_2O_8$, using the methodology of Ross (1992), and measurement of the resultant NO_3^--N and NH_4^+-N was done by auto-analyser procedures. The microbial N flush was converted to microbial biomass N using a K_{EN} factor of 0.54 (Brookes et al., 1985).

Soil concentration of mineral N (DIN) was determined by shaking 5 g fresh soil with 25 ml 1 M KCl for 30 min on an orbital shaker. The resulting suspension was filtered through Whatman No. 1 paper. The concentration of NH_4^+-N and NO_3^--N in the extracts was determined by auto-analyser procedures. DON was measured by adding 70 ml distilled water to 10 g moist soil samples, which were shaken on an orbital shaker for 10 min prior to being filtered through Whatman No. 1 paper. DON in the extract was determined by oxidation with potassium persulphate ($K_2S_2O_8$), and measurement of the resultant NO_3^--N and NH_4^+-N was done by auto-analyser procedures.

2.4. Data analyses

All values were expressed on a unit area basis ($g\,m^{-2}$), calculated using bulk density values recorded for each plot. Data were analysed using generalised linear mixed models (GLMM) with replicate nested within site as the random effect. The models were fitted by the method of residual maximum likelihood (REML) in SAS for Windows v.8.2. Denominator degrees of freedom were estimated using Satterthwaite's approximation (Littell et al., 1996). Autocorrelation between observations within plots was modelled as a first-order auto-regressive (AR1) process. For each parameter under investigation, we first ran a model with Date, Site and Date × Site as fixed effects using type 1 hypothesis testing. Subsequently, models were run for the moist and dry site separately. Additionally, for DIN, soil moisture was fitted as a covariate. Similarly, microbial biomass N was modelled with DON (log-transformed) as a covariate. Data are presented as means ± S.E.

3. Results

3.1. Abiotic factors

Environmental site conditions (i.e., soil temperature and moisture) changed rapidly during the early part of the growing season at both the dry and moist meadow sites (Fig. 1a and b). As a consequence, seasonal variability in environmental conditions generally exceeded those that occurred between sites. At both sites, soils were typically very wet at the first sampling, which was soon after snowmelt, and were considerably drier afterwards (Fig. 1a, Table 1). Whereas moist meadows dried out gradually over time, soil moisture in dry meadows dropped more dramatically and rewetted later in the season due to subsurface water transport from higher slopes. Soil temperature increased rapidly up to late July, after which soils cooled down again (Fig. 1b, Table 1). Importantly, seasonal variability in both soil moisture and temperature differed between sites, being stronger in dry than in moist meadows (Table 1).

3.2. Plant biomass and N pool sizes

Live aboveground vascular plant biomass, both above and within the live moss layer, varied significantly across the season; this seasonal variation was most obvious in the moist meadow (Fig. 2). Such seasonality was not observed in any of the belowground plant biomass components in either site. However, belowground vascular plant biomass in both the soil and decomposing moss layer differed significantly between sites, being greatest in the moist meadow. The amount of aboveground vascular plant biomass in the live moss layer was greatest in the dry meadow. Although seasonally variable, the aboveground live vascular plant components were very small, representing on average only 9% and 13% of total live vascular plant biomass for moist and dry meadows, respectively, or 5% vs. 6% when considering live biomass above the moss layer alone. In sum, the seasonal build-up of aboveground biomass at both sites was significantly and positively related to the seasonal pattern in soil temperature ($F_{1,6} = 10.30$, $P < 0.05$). The majority of belowground vascular plant biomass was located in the decomposing moss layer rather than in the soil. Biomass of live moss was seasonally invariable, while moss and vascular plant litter combined was present in greater quantities in early June than in mid July. Live and decomposing moss together (including relatively small amounts of vascular plant litter)

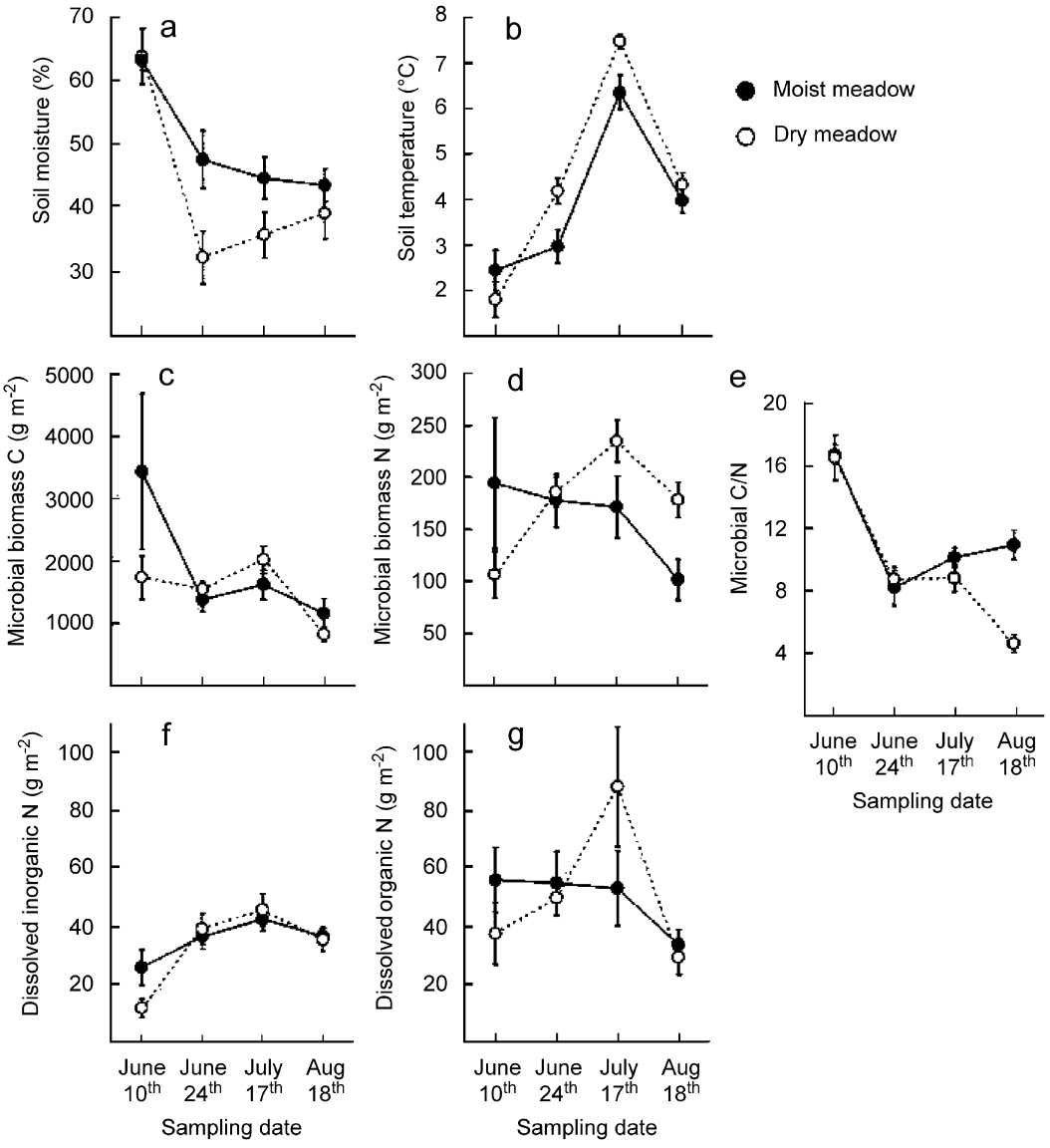

Fig. 1. Seasonal patterns in soil abiotic conditions (a, b), soil biological properties (c, d, e) and soil nitrogen concentrations (f, g) at two contrasting high-Arctic plant communities across the plant growing season. Individual panels are (a) average (±S.E.) gravimetric soil moisture, (b) soil temperature at 5 cm depth, (c) microbial carbon, (d) microbial nitrogen, (e) microbial C to N ratio, (f) dissolved inorganic nitrogen (NH_4^+-N and NO_3^--N combined) and (g) dissolved organic nitrogen. Connecting lines are provided for clarity. Summary statistics for these data are given in Table 1.

Table 1
Summary GLMM statistics for seasonal patterns in soil abiotic conditions, soil biological properties and soil nitrogen concentrations at two contrasting high-Arctic plant communities across the plant growing season

	Date			Site			Site × Date		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
Soil moisture	*3,35*	*28.00*	*<0.0001*	1,19	4.06	0.06	*3,35*	*2.95*	*<0.05*
Soil temperature	*3,30*	*138.60*	*<0.0001*	1,18	2.23	>0.15	*3,30*	*5.80*	*<0.01*
Microbial biomass C	*3,29*	*3.62*	*<0.05*	1,14	1.81	>0.19	3,29	1.94	>0.14
Microbial biomass N	3,41	1.83	>0.15	1,17	1.23	>0.28	*3,41*	*2.98*	*<0.05*
Microbial C to N ratio	*3,32*	*43.91*	*<0.0001*	*1,18*	*6.71*	*<0.05*	*3,32*	*6.54*	*>0.005*
Dissolved inorganic N	*3,42*	*11.86*	*<0.0001*	1,18	0.41	>0.5	3,42	1.65	>0.19
Dissolved organic N	*3,44*	*3.78*	*<0.05*	1,17	0.06	>0.8	3,44	1.86	>0.14

Data given are degrees of freedom (d.f.) and *F* and *P*-values for main and interactive effects. Significant effects in italics.

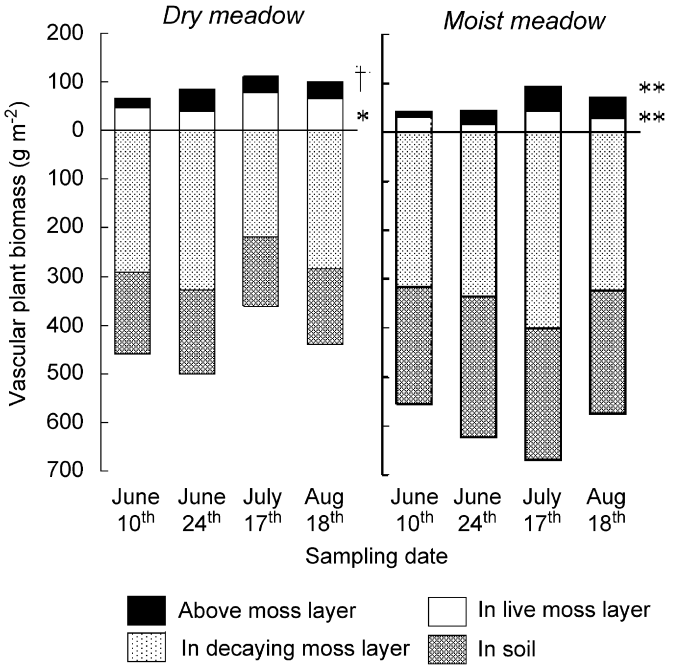

Fig. 2. Patterns in components of live vascular plant biomass at two contrasting high-Arctic plant communities across the plant growing season. Symbols indicate habitat-specific significant seasonal differences for the respective component ($^{\dagger}0.10 > P > 0.05$, $^{*}P < 0.05$, $^{**}P < 0.01$). Summary GLMM statistics with significant effects in italics for Live above moss layer: *Date* $F_{3,41} = 6.32$, $P < 0.005$, *Site* $F_{1,18} = 0.04$, $P > 0.8$, Date × Site $F_{3,41} = 2.79$, $P = 0.05$; Aboveground in live moss layer: $F_{3,47} = 6.26$, $P < 0.05$, *Site* $F_{1,18} = 19.11$, $P < 0.001$, Date × Site $F_{3,47} = 0.91$, $P > 0.4$; Belowground biomass in decomposing moss layer: $F_{3,36} = 0.19$, $P > 0.9$, *Site* $F_{1,18} = 7.88$, $P < 0.05$, Date × Site $F_{3,36} = 1.71$, $P > 0.18$; Belowground biomass in soil: $F_{3,45} = 0.28$, $P > 0.8$, *Site* $F_{1,17} = 22.78$, $P < 0.001$, Date × Site $F_{3,45} = 0.24$, $P > 0.8$.

was comparable to total live vascular plant biomass for both sites (Table 2).

Of all plant N pools, only the aboveground vascular plant pool varied significantly across season, most noticeably in the moist meadow (Table 2). Live vascular plant belowground parts represented the single largest plant N pool. Mosses and detritus together, however, held either similar (moist meadows) or only slightly smaller amounts of N than all live vascular plant tissue together.

3.3. Soil N pools

Analysis of the relative contribution of different soil components to the total N pool size for the two contrasting sites revealed that most pools varied seasonally more than they did between the two sites (Table 3). To further explore seasonal and site-specific patterns in individual soil N pool sizes, we concentrated on absolute rather than relative amounts of N. Soil microbes represented a sizeable and seasonally dynamic N pool; seasonality of microbial biomass N was evident predominantly in dry meadow rather than in moist meadow (Table 2, Fig. 1d), which appeared to be related to soil temperature (Fig. 3). Microbial biomass C and its C:N ratio also showed strong seasonal variability (Tables 1 and 2), and for the latter this was also most pronounced in dry meadow (Fig. 1c and e). Microbial biomass C and N, and microbial C:N, tended to decline over the season in moist meadow, whereas microbial biomass N peaked in late July in dry meadow.

Soil concentrations of DON and DIN also showed clear seasonal patterns (Fig. 1f and g); as with the soil microbial measures, seasonality was most pronounced in dry meadow (Tables 1 and 2). DIN (and the individual

Table 2
Plant biomass and nitrogen pool sizes of different ecosystem components for two contrasting plant communities

	Plant biomass ($g\,m^{-2}$)				Nitrogen pool size ($g\,m^{-2}$)			
	Dry ridge		Moist meadow		Dry ridge		Moist meadow	
	Mean (S.E.)	Seasonal variability	Mean (S.E.)	Seasonal variability	Mean (S.E.)	Seasonal variability	Mean (S.E.)	Seasonal variability
Live aboveground vascular[a]	33.7 (3.5)	<0.1	*32.8 (3.9)*	*<0.05*	0.52 (0.08)	ns	*0.54 (0.06)*	*<0.001*
Live belowground vascular[b]	496.9 (28.6)	ns	636.4 (27.6)	ns	6.03 (0.52)	ns	7.48 (0.56)	ns
Live moss	327.3 (35.6)	ns	417.4 (38.3)	ns	3.67 (0.39)	ns	4.63 (0.50)	ns
Moss and vascular plant litter	274.8 (26.2)	<0.1	*183.8 (14.1)*	*<0.05*	2.93 (0.31)	ns	2.06 (0.19)	<0.1
Microbial biomass					*17.62 (1.17)*	*<0.001*	16.15 (1.90)	ns
Dissolved inorganic nitrogen					*3.29 (0.30)*	*<0.001*	3.53 (0.25)	<0.1
Dissolved organic nitrogen					*5.11 (0.70)*	*<0.05*	4.94 (0.53)	ns
Total soil					372.73		463.08	

Mean values (±S.E.) across four sampling dates, spanning the whole of the high-Arctic plant growing season, are given, along with *P*-values (in italics when $P < 0.05$) testing for the occurrence of seasonal variability in each of the measures.

[a]Above the live moss layer only.

[b]Including aboveground tissue from within the moss layer.

Table 3
Relative contribution of different plant and soil components to the total nitrogen pool size (% ±S.E.) for two contrasting plant communities and four sampling dates, spanning the whole of the high-Arctic plant growing season

	Dry ridge				Moist meadow				*P*-values		
	10 June	24 June	17 July	18 August	10 June	24 June	17 July	18 August	Date	Site	Date × Site
Live aboveground vascular	0.08 (0.02)	0.20 (0.06)	0.14 (0.03)	0.13 (0.02)	0.04 (0.01)	0.17 (0.03)	0.15 (0.02)	0.10 (0.02)	*0.0014*	0.3824	0.8210
Live belowground vascular	1.76 (0.35)	1.66 (0.23)	1.15 (0.22)	1.74 (0.28)	1.48 (0.28)	1.68 (0.24)	1.52 (0.21)	1.56 (0.19)	0.5659	0.7504	0.5299
Live moss	1.01 (0.25)	0.68 (0.16)	1.20 (0.20)	0.93 (0.18)	1.26 (0.31)	0.84 (0.19)	0.75 (0.11)	1.02 (0.14)	0.2384	0.8818	0.2140
Moss and vascular plant litter	0.92 (0.22)	0.74 (0.10)	0.48 (0.12)	1.03 (0.14)	0.36 (0.07)	0.28 (0.06)	0.48 (0.06)	0.59 (0.09)	0.0696	*<.0001*	0.1004
Microbial biomass	2.74 (0.58)	4.82 (0.39)	6.10 (0.48)	4.71 (0.48)	4.05 (1.29)	3.71 (0.53)	3.59 (0.61)	2.13 (0.42)	*0.0303*	*0.0042*	*0.0117*
NH_4^+	0.07 (0.04)	0.20 (0.03)	0.28 (0.03)	0.28 (0.03)	0.13 (0.07)	0.21 (0.03)	0.24 (0.02)	0.24 (0.02)	*0.0003*	0.7599	0.4026
NO_3^-	0.23 (0.05)	0.81 (0.12)	0.91 (0.13)	0.62 (0.09)	0.40 (0.07)	0.55 (0.08)	0.65 (0.06)	0.53 (0.05)	*<.0001*	0.1768	*0.0331*
Dissolved organic nitrogen	0.96 (0.27)	1.29 (0.16)	2.30 (0.54)	0.65 (0.07)	1.17 (0.23)	1.15 (0.23)	1.11 (0.27)	0.70 (0.11)	*0.0089*	0.1196	0.0748
Total soil	96.23(0.37)	96.73(0.33)	97.04(0.47)	96.16(0.35)	96.86(0.43)	97.03(0.37)	97.11(0.27)	96.73(0.23)	0.2972	0.0531	0.8103

P-values in italics indicate significant main effects from GLMMs. All plant pools together with the total soil N pool together represent 100%. The other soil fractions are part of total soil N pool.

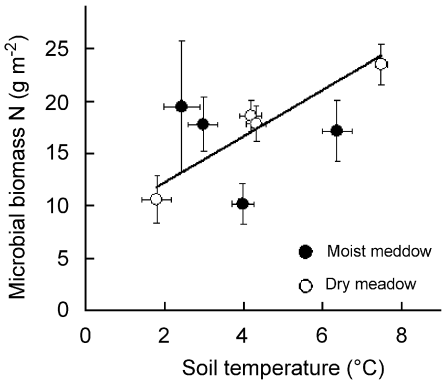

Fig. 3. Relationship between soil microbial biomass N and soil temperature for two contrasting high-Arctic plant communities based on data collected at four sampling dates for which means + S.E. are shown. Summary GLMM statistics: Soil temperature $F_{1,62} = 2.03$, $P > 0.15$, Site $F_{1,17} = 0.55$, $P > 0.4$, Soil temperature × Site $F_{1,64} = 6.24$, $P < 0.02$.

components NH_4^+-N and NO_3^--N) increased gradually over the season but tended to drop again in August. Across both plant communities, DIN was strongly and negatively related to soil moisture (Fig. 4a) and this relationship was consistent across sampling dates (Moisture × Date $F_{1,58} = 2.71$, $P > 0.1$). The seasonal pattern of DON was comparable to that of microbial biomass N, showing a gradual decline over the season in the moist meadow, whereas DON in the dry meadow built up to a peak in late July after which concentrations dropped. Indeed, microbial biomass N was strongly ($P < 0.0001$) and positively related to DON across both sites (Fig. 4b). This relationship was strongest in June ($\log \text{DON} \times \text{Date}$ $F_{3,54} = 6.16$, $P < 0.01$); by mid August, the positive relationship between microbial biomass N and DON was no longer apparent.

4. Discussion

We set out to determine the extent of temporal variability in labile N pools (plant and soil) in two contrasting plant communities in a high-Arctic ecosystem. While we detected differences in the size of N pools between contrasting plant communities, most variation in plant and microbial N pool sizes was attributed to temporal variability. In particular, we found that both absolute and relative quantities of N within the microbial biomass and live vascular aboveground plant material, along with DIN and DON, varied significantly across the short-Arctic growing season. This temporal variability was related to fluctuations in key environmental variables such as soil moisture and soil temperature. For example, aboveground plant biomass clearly tracked soil temperature across both sites, which is consistent with the view that temperature, more than moisture, is the primary determinant of vascular plant biomass in Arctic ecosystems (Gold and Bliss, 1995; Van der Wal and Brooker, 2004). We also found that the availability of inorganic N (DIN) in soil was negatively and significantly related to moisture, which was

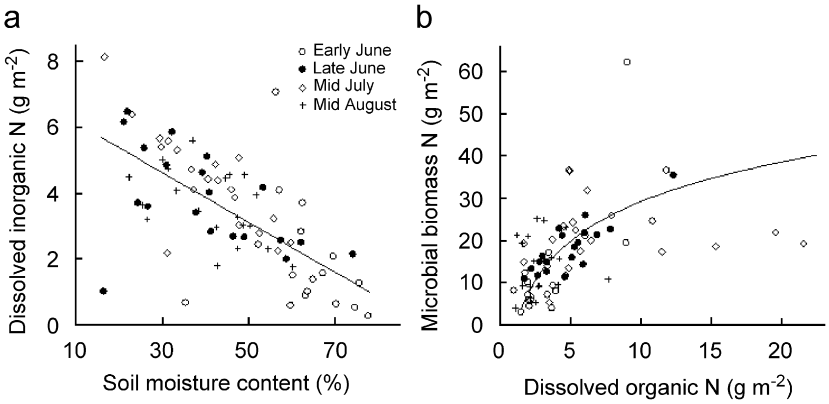

Fig. 4. Relationship between (a) dissolved inorganic nitrogen and soil moisture content and (b) microbial biomass N and dissolved organic nitrogen based on data collected at four moments in time. Summary GLMM statistics (a): Moisture $F_{1,63} = 68.60$, $P < 0.0001$; (b): log DON $F_{1,55} = 39.45$, $P < 0.0001$.

initially very high after snowmelt and dried considerably afterwards, confirming the importance of soil moisture for plant nutrient availability in Arctic ecosystems (Zimov et al., 1995; Hodkinson et al., 1999).

We found that the relationships between soil temperature and microbial N differed markedly between the two plant communities: microbial N was strongly and positively related to soil temperature in the dry meadow, whereas this relationship did not hold true in the wet meadow where other factors, such as wetter soil conditions, might constrain biological activity. This finding suggests that microbial N dynamics of dry meadows may be more susceptible to changes in growing season temperature, for example under climate change, than in wet meadows, where moisture may be of overriding importance. One other notable pattern that was detected at both sites was a marked decline in microbial C:N over the growing season: across wet and dry meadow sites, we found that the microbial C:N ratio declined from approximately 16 at the first sampling after snowmelt, to <12 and <5, respectively, during plant senescence at the final sampling, suggesting that microbes become progressively less N limited as the growing season proceeds. This pattern has also been shown to occur in high alpine ecosystems, and has been attributed to high rates of microbial N immobilisation in the autumn, after plant senescence (Jaeger et al., 1999; Bardgett et al., 2002). This N is retained within the microbial biomass over winter, until it is released and utilised by plants in the spring after snowmelt (Bardgett et al., 2005).

The level of temporal variation in plant, microbial and soluble (DIN and DON) N pools, while significant, was unexpectedly low relative to that shown to occur over the growing season in other seasonally cold ecosystems, such as alpine regions. For instance, studies of high mountain moss-dominated heath in the UK revealed steep gradients across the growing season in N pools, including DIN, DON, microbial N, and N in vascular plant biomass (Bardgett et al., 2002) and in microbial activity (Bardgett and Leemans, 1996). Similarly, Jaeger et al. (1999) reported large shifts across the growing season in N pool sizes of plant and soil microbial biomass of an alpine meadow at Niwott Ridge, Colorado. The reduced amplitude of temporal variation in N pool sizes in our high-Arctic system relative to that observed in the alpine ecosystems might be explained by greater temperature constraints during the growing season in the former. This view is supported by the fact that soil temperatures at our high-Arctic sites reached a maximum of 8.3 °C at 5 cm depth, whereas soil temperature at Niwott Ridge, Colorado, reached a summer peak of 14 °C at the same depth (Jaeger et al., 1999); soil temperatures of up to 17 °C have been reported for high mountain moss heaths in the UK (Bardgett and Leemans, 1996).

The availability of DON has been suggested to be an important rate-limiting step in the process of N mineralisation in strongly N-limited ecosystems (Chapin et al., 2002; Bardgett et al., 2002; Schimel and Bennett, 2004). Although we did not measure N mineralisation, our finding of a positive and highly significant relationship between the availability of DON and microbial biomass N across both sites is in line with this notion (Fig. 4b); this relationship was most apparent early in the growing season, after snowmelt, when the microbial community was most N limited. Although not tested, it is likely that DON also provides a direct source of N for plants in these high-Arctic ecosystems, short circuiting the microbial mineralisation step. There is a growing body of evidence showing the importance of organic N in the form of amino acids for plant nutrition in Arctic and other strongly N-limited ecosystems (Chapin et al., 1993; Kielland, 1994; Schimel and Chapin, 1996; McKane et al., 2002; Henry and Jefferies, 2003; Nordin et al., 2004). We do not have data on the availability of amino acids in these plant communities, but studies have revealed that the portion of DON that is amino acid can constitute some 10–20% of the N pool in other Arctic ecosystems (Jones and Kielland, 2002), suggesting that they represent a key component of the N cycle.

Total soil N was greater in the moist than the dry meadow, reflecting the greater amounts of organic matter

in these systems. However, the relative contribution of different N pools to the total detected, both aboveground and belowground, was remarkably similar. In both sites, the microbial biomass contained approximately 4.6% and 3.4% of the total ecosystem N pool across the growing season, in the dry and moist meadow, respectively, which is lower than has been reported for alpine (seasonal mean of 6.5%; Bardgett et al., 2002) and sub-Arctic (10%; Jonasson et al., 1999) ecosystems. Vascular plant belowground parts represented the single largest plant N pool in both dry and moist meadow, constituting an average of 1.6% of the total N pool in both systems; this value did not vary across the growing season or between plant communities. We did detect significant temporal variation in aboveground N pool size in both plant communities, in that the proportion of total N in aboveground tissue was maximal in late June at the peak of the growing season. However, only a very small portion of the total N was contained in live tissue at this time (0.2% in both the dry and moist meadow). In general, these data further enforce the view that plant and microbial N pools make up a low portion of the total N pool of Arctic ecosystems and that they are subject to surprisingly low temporal variation.

Overall, we report a number of key findings. First, we show that plant and microbial N pools in the high Arctic are subject to significant, but surprisingly low, growing season temporal variability that is controlled primarily by changes in temperature and soil moisture over the short growing season. This temporal variability is much less than that experienced in other seasonally cold ecosystems such as alpine tundra where strong seasonal partitioning of N occurs between plant and soil microbial pools (Jaeger et al., 1999; Bardgett et al., 2002, 2005). Second, we show that while only a small portion of the total N pool, the microbial biomass represents the single largest of the dynamic N pools in both moist and dry meadows, pointing to the importance of soil microbial community dynamics for N cycling in high-Arctic ecosystems. Overall, our data illustrate a surprisingly low growing season variability in labile N pools in high-Arctic ecosystems, which we propose is controlled primarily by temperature and moisture.

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