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Phosphorus availability and microbial respiration across different tundra vegetation types

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Abstract Phosphorus (P) is an important nutrient in tundra ecosystems that co-limits or in some cases limits primary production. The availability of P is largely driven by soil characteristics, e.g., pH, organic carbon, and abundance of P-sorbing elements such as aluminium (Al) or iron (Fe). We tested how vegetation and soil properties relate to P availability across different tundra vegetation types. The different soil P fractions in the organic horizon were measured and plant foliar nitrogen (N) to P ratio and a plant bioassay was used as indicators of plant nutrient status. Microbial bioassays were used to study microbial respiration kinetics and in response to carbon, N, and P amendments. The distribution of P fractions differed significantly across vegetation types; labile fractions of P were less abundant in meadow sites compared to heath sites. Calcium-phosphates seemed to be an important P-fraction in meadows, but were only found in lower concentrations in the heath. There were only small differences in NaOH–extractable P between the vegetation types and this correlated with the distribution of oxalate-extractable Al. Plant N:P ratios and the plant bioassay indicated decreasing P availability from dry heath to mesic heath to mesic meadow. The microbial bioassay suggests that the heterotrophic microbial community is C-limited with N as a secondary limiting nutrient although there were indications that microbial P availability was lower in the meadow sites. Overall, we suggest that the observed variations in soil P across vegetation types are affecting both plant and microbial function although the differences seem to be relatively small.

Keywords Phosphorus availability · Subarctic tundra · Hedley fractionation · Soil respiration · N:P ratio

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Introduction

Nitrogen (N) has generally been considered the most limiting nutrient for plant production in most northern ecosystems (Aerts and Chapin 2000, Vitousek and Howarth 1991); however, a growing number of studies suggest that phosphorus (P) limits or co-limits plant production in arctic and alpine tundra ecosystems (Bowman et al. 1993; Bowman 1994; Shaver

and Chapin 1995; Aerts and Chapin 2000; Seastedt and Vaccaro 2001; Hobbie and Gough 2002; Soudzilovskaia et al. 2005). Limitation by P is commonly related to a number of abiotic factors affecting P availability such as sorption (Sanchez 1976), formation of Ca-phosphates in calcareous soils (Griffin and Jurinak 1973) or depletion of the soil P pool and changes to more recalcitrant P forms over time (Walker and Syers 1976; Vitousek 2002). Knowledge about soil P forms can provide information about mechanistic causes behind a possible P limitation. These factors tend to vary with topography (Giesler et al. 1998; Giblin et al. 1991; Schimel et al. 1985), depth of the organic horizon (Shaver et al. 1998; Lagerström et al. 2009) and over time (Vitousek 2002; Hobbie and Gough 2002), which can lead to variation in the relative availability of P (and N) sometimes within relatively short distances across topographic gradients (Giesler et al. 2002; Giblin et al. 1991). Plant N:P ratios, fertilization, microbial bioassays and measures of N and P availability give indications of the nutrient limitation experienced by plants and microbes at a particular site (Aerts and Chapin 2000; Koerselman and Meuleman 1996; Güsewell 2004). However, the distribution of soil P forms across topographic gradients can provide information about mechanistic causes behind variations in relative P availability. Despite this, few studies are available that describe different soil P forms and how they relate to different vegetation types in high-latitude tundra ecosystems (Turner et al. 2004).

In tundra soils the cold climate will restrict both weathering release of P and P mineralization (Stark 2007); the latter considered being a major pathway for P release (Chapin et al. 1978). Additionally, microorganisms in tundra soils are strong competitors for P (Jonasson et al. 1999) and can affect plant P availability (Jonasson et al. 1996). Control mechanisms for P release differ from those of N in that both biotic (mineralization) and abiotic (desorption, dissolution) processes are involved, whereas N availability is primarily driven by biotic processes. For instance, sorption of both phosphate and organic P compounds can reduce plant and microbial P availability (Giesler et al. 2002, 2004) and can also affect mineralization rates of P (Magid et al. 1996; Stewart and Tiessen 1987). Though sorption processes are generally assumed to play a minor role in organic soils, while biotic processes dominate the P dynamics (Wood et al. 1984), recent studies have shown that high concentrations of aluminium (Al) and iron (Fe) can increase the sorption capacity of organic soils substantially (Giesler et al. 2005; Dell'Olio et al. 2008; Kang et al. 2009), leading to a decrease in P availability and causing plants to become P limited (Giesler et al. 1998, 2002). There is also evidence of variation in tundra or alpine soil Al and Fe being linked to topography, with higher Al and Fe concentrations e.g. at the bottom of a hill slope or in depressions (Litaor 1992; Ping et al. 1998; Strand et al. 2005) or related to soil age (Giblin et al. 1991). Whether inherent differences in the distribution of Al and Fe also can affect P availability in tundra ecosystems still remains unknown; we do, however, believe that accumulation of Al and Fe in organic soils might be a factor that hitherto has been overlooked.

In the Scandinavian tundra landscape topography and hydrology related co-variations in plant and microbial community composition and below-ground soil properties can be found over very short distances (Sundqvist et al. 2010; Björk et al. 2007). As such, the vegetation forms a mosaic of patches of largely contrasting soil fertility resulting in two co-dominating vegetation types; heath and meadow. Meadows are typically found in depressions or slopes where there is leaching from adjacent upland soils. Moreover, meadows in Fennoscandia are characterized by high pH and soil Ca content, high N turnover rates, and low soil C:N ratios compared to heath vegetation where the reverse is true (Sundqvist et al. 2010; Björk et al. 2007; Arnesen et al. 2007; Eskelinen et al. 2009). Similar variations in soil properties related to vegetation type are also found in the tundra landscape of North America (Chu and Grogan 2009) and Siberia (Virtanen et al. 2006). Conditions in tundra meadows may potentially have similar conditions as those found in the toe slope areas of the boreal forest where the accumulation of Al and Fe in the humus soils drastically decreases P availability and is the likely cause to a plant P limitation in these sites (Giesler et al. 1998, 2004).

In order to test if this is also the case also on the Scandinavian tundra we compared a number of indices for P availability across three different tundra vegetation types: dry heath, mesic heath, and mesic meadow (MM). Soil P forms were determined using a

modified Hedley fractionation (Giesler et al. 2004) together with different forms of Al and Fe. These measures can provide information about the biogeochemical processes involved in P cycling in the study area. We combined this with an array of indices for P availability and a possible P limitation such as plant N:P ratios and plant and microbial bioassays. Specifically, we hypothesize that meadow vegetation have a lower P availability than heath vegetation due to their inherent difference in topographic landscape position. Our main aims were to (I) test for differences in soil P availability across the three different vegetation types, (II) to test for linkages between plant and microbial indices for P availability and soil P forms as determined by a modified Hedley fractionation (Giesler et al. 2004) as well as soil Al and Fe concentrations, and finally (III) to test for linkages between basal respiration (BR) and soil P forms. This may provide important clues about abiotic versus biotic processes regulating P availability in a tundra ecosystem and how this relates to topography and vegetation types.

Materials and methods

Location and vegetation types

The study was performed at three different locations in the subarctic tundra of northern Sweden in the vicinity of Abisko Scientific Research Station: Latnjajaure (68°21′N, 18°30′E, 993–1,009 m above sea level, a.s.l.), Suourojaure (68°17′N, 19°05′E, 1,000–1,041 m a.s.l), and Kärkevagge (68°25′N, 18°19′E, 616–720 m a.s.l.). All three sites are located above the tree line. Mean annual temperature and precipitation at Latnjajaure is −2.5°C and 809 mm (Molau and Larsson 2000), −2.0°C and 1,000 mm at Kärkevagge (Eriksson 1982), and −5.0°C and 230–290 mm (summer precipitation) at Suourojaure (Karlsson et al. 2005).

At each location we selected sites within three dominant vegetation types, i.e., dry heath, mesic heath, and MM. The dry heath vegetation is sparse, patchy, and found on well-drained acidic glacial moraine ridges and flats and water is supplied mainly by precipitation. The vascular vegetation is dominated by the evergreen dwarf shrubs *Empetrum hermaphroditum* and *Vaccinium vitis-idaea* and the deciduous dwarf shrubs *Vaccinium uliginosum* and *Betula nana*. The mesic heath community occurs on moister soils and the vascular vegetation is dominated by dwarf shrubs; however, deciduous dwarf shrubs are more abundant in this vegetation type at the expense of *E. hermaphroditum*. The MM community commonly occurs along slopes or depressions in landscapes receiving water from higher elevations, which results in moister habitats. The vascular vegetation is dominated by a rich herbaceous flora, e.g., *Carex vaginatum*, *Carex bigelowi*, *Solidago virgaurea*, *Salix herbacea*, *Salix reticulata*, *Polygonum viviparum*, *Silene acaulis*, *Tofieldia pusilla*, *Parnassia palustris*, *Astragulus alpinus*, and several species in the families *Ranunculaceae*, *Rosaseae*, and *Saxifragaceae*. Some dwarf shrubs are present in the vegetation, in particular *Dryas octopetala*, and smaller patches of *E. hermaphroditum*, *V. uliginosum*, *B. nana*, and *Cassiope tetragona*.

Sampling of soil and plant material

Soil and plant samples were collected in late August 2006. At each location, we selected one site in each vegetation type, for a total of nine sites. At each site, five plots were randomly selected within a 25 m radius with at least two meters separating each plot, for a total of 45 plots. Two soil cores (10 cm diameter) of the organic horizon were collected from each plot. The organic horizon independent of vegetation type were generally less than 10 cm thick and never exceeded 15 cm. The soil samples were stored in a freezer within 30 h of sampling until they were analyzed. Prior to analysis, the two soil cores from each plot were sieved to three mm, roots were removed, and two samples from each plot were bulked into one composite sample.

Within 50 cm from the two soil cores, plant leaves from four plant species were collected and placed in polyethylene bags at the time of soil sampling. Three species, found in both the heath and meadow sites, were collected: *V. uliginosum*, *V. vitis-idaea*, and *C. bigelowi*. The species were chosen because between species variations in N and P contents can be very large, which can make comparisons difficult. We also collected *S. reticulata* (meadow only) and *S. herbacea* (heath only) for comparison. The plant material was stored at +5°C for less than 24 h before it was dried (60°C, 72 h) for N and P analyses.

Microbial respiration measurements

Microbial responses were tested using a microbial bioassay with a controlled experimental setup developed by Nordgren (1992) with a respirometer (Respicond V, Nordgren Innovations, Djäkneboda, Sweden; Nordgren 1988). For each soil sample, five subsamples corresponding to one gram dry weight organic matter [OM; determined by loss on ignition (LOI), 550°C, 5 h] were placed in 250 ml plastic vessels and adjusted to 250% gravimetric moisture content. The subsamples were then placed in the respirometer and incubated at 20°C. Soil respiration was measured hourly using the respirometer and substrate additions were made when respiration rates had been stable for 40 continuous hours.

In order to estimate the nature of nutrient limitation of the microbial community, additions of C (as glucose, henceforth abbreviated Glu), N and P were made to the five incubation vessels prepared for each sample, using the approach described by Nordgren (1992); this approach has previously been used in several studies for estimating the level of availability of soil N and P to microorganisms (e.g., Demetz and Insam 1999; Ilstedt et al. 2003; Giesler et al. 2004; Lagerström et al. 2009). Glucose was added to all vessels in access to ensure that C was not limiting microbial growth. Glucose + N and Glu + P was added in excess to the first and second vessel respectively to ensure that P was the limiting nutrient in the first vessel and N in the second vessel. Maximum respiration rate was assumed to occur when N (for Glu + P) or P (for Glu + N) limits further microbial growth (Fig. 1). In duplicate vessels a limited amount of N (ΔN) or P (ΔP) was also added to the excess Glu + P or Glu + N respectively. The additions of ΔN/ΔP lead to an increase in maximum respiration rate compared to only adding Glu + P/Glu + N, which can give a further indication on the nature of nutrient limitation by showing the response to addition of a third element when Glu and N or P are available in excess (Nordgren 1992). Finally, to the fifth vessel only glucose was added. Substrate additions (C, N, and P) were made in powdered form in the following amount: Glu (400 mg g^{-1} OM), N ($(NH_4)_2SO_4$, 13.8 mg N g^{-1} OM), and P (NaH_2PO_4, 2.3 mg P g^{-1} OM). For the small additions we used 1.0 mg N g^{-1} OM (ΔN) and 0.114 P g^{-1} OM (ΔP).

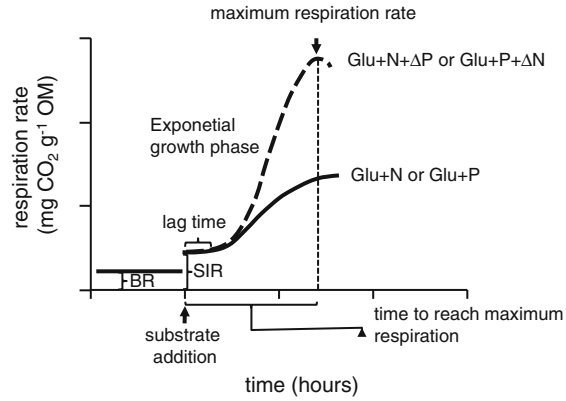

Fig. 1 Schematic graph of soil microbial respiration kinetics before and after substrate addition. BR is the mean value of 30 hourly measurements. Glucose (Glu) + P or Glu + N were added in excess to the soil samples as described in the text. In a duplicate vessel a limited amount of N (ΔN) orP (ΔP) was also added to the excess Glu + P or Glu + N, respectively. Maximum respiration rate is assumed to occur when N (for Glu + P) or P (for Glu + N) limits further microbial growth. The additions of ΔN/ΔP lead to an increase in maximum respiration rate compared to only adding Glu + P/Glu + N, which can give a further indication on the nature of nutrient limitation. The substrate-induced respiration (SIR) is the respiration rate immediately after substrate addition. Lag-time is defined as the time it takes for the microorganisms to start to grow exponentially after substrate addition. The exponential growth phase is expressed as the slope of log respiration rate versus time

Basal respiration was defined as the average of the last 30 hourly measurements before substrate addition. The substrate addition was followed by an immediate increase in respiration rate or substrate induced respiration (SIR) (Anderson and Domsch 1978), which persists until the microorganisms start to grow exponentially. SIR was calculated from glucose only additions. The exponential growth rate (μ) is calculated as the slope of the log-transformed respiration rate plotted against time. Lag time is defined as time between substrate addition and exponential growth. The lag time was calculated as the time between substrate addition and the time when the regression line for the slope intercepts log SIR (Nordgren 1988). Since Glu and N or P are added in excess of microbial demand, the maximum respiration rate is assumed to occur when the available P or N pool in the native soil is exhausted (Nordgren 1992). The time to reach maximum respiration rate is defined as the time between substrate addition and the peak respiration rate (Fig. 1). A previous study from

boreal forests has show a strong relationship between microbial growth rate (after Glu + N additions) and soil P as well as Al and Fe contents (Giesler et al. 2004). We thus used the microbial growth rate as an index of microbial P availability under P limiting conditions (Demetz and Insam 1999; Giesler et al. 2004; Esberg et al. 2010). Therefore, this is not a quantitative, but rather a relative measure of the microbial P availability. Lag time and time to reach maximum respiration has also been shown to relate to the P availability of soils (Giesler et al. 2004) similar to growth rate.

Soils

Phosphorus fractions in the soil were measured using modifications of the Hedley (Hedley et al. 1982) sequential extraction procedure (Binkley et al. 2000). Although, instead of an iron-oxide impregnated filter strip (Binkley et al. 2000) we used an anion exchange membrane (Saggar et al. 1990). Sequential extractions have been widely used to characterize soil P availability in a continuum of increasingly strong extractants, under the assumption that the different fractions also reflect differences in P availability (see Cross and Schlesinger 1995). We used the following sequential extraction steps: membrane extractable P; 0.5 M $NaHCO_3$ extractable P; 0.2 M NaOH extractable P; and 1.0 M HCl extractable P. The remaining residual P was determined by acid digestion using concentrated H_2SO_4. The procedure is described in detail in Lagerström et al. (2009).

The first two extraction steps, which involved an anion exchange membrane and extraction with $NaHCO_3$ solution, were designed to extract labile inorganic and organic P fractions. The third step, with NaOH extraction, presumably extracted Al and Fe surface-bound P, as well as partially stabilized organic P in soil OM. In the fourth step (1.0 M HCl), inorganic P in calcium phosphates, as well as inorganic P occluded within Al and Fe oxides, was assumed to be extracted (Cross and Schlesinger 1995). The remaining residue fraction extracted mainly recalcitrant P.

Aluminium and Fe concentrations in the soil samples were determined using two extractants: 0.1 M sodium pyrophosphate ($Na_4P_2O_7$) and 0.2 M acid oxalate ($C_2H_8N_2O_4$) adjusted to pH 3 (Buurman et al. 1996). Phosphorus was also determined in the oxalate extraction. Pyrophosphate solution mainly extracts organically bound Fe and Al, whereas the oxalate extracts both organically bound and amorphous Fe and Al. For each soil sample, about 2 g dry weight (dw) soil was weighed and combined with each extracting solution at a ratio of 1:20, shaken on an orbital shaker for 18 h (pyrophosphate) or 4 h in darkness (oxalate), and then extracted. The extracts were filtered (00H, Munktell Filter AB, Grycksbo, Sweden) and stored at +5°C until analyzed. An estimated P sorption maximum (S_{max}) was calculated from the relationship between oxalate-extractable Al and Fe following the relationship found for S_{max} and Al + Fe in organic soils ($S_{max} = 14.93 \times \ln \quad (Al_{oxalate} + Fe_{oxalate}) - 29.61$; Kang et al. 2009).

Total C and N in soil samples was determined after drying (70°C, 3 days) and milling with a ball mill. Total P was defined as the sum of the different P fractions in the extractions steps described above. OM content was determined following heating at 550°C for 5 h. Soil pH was measured in water after shaking the samples overnight at a soil-solution ratio of 1:8.

Plant bioassay

A plant bioassay to test plant response to N, P, and NP treatments was conducted using humus layer soils from mesic heath and meadow collected at the Kärkevagge location. Acid-washed (0.01 M HCl) silica sand (Silversand 90; Ahlsell Mineral, Sweden) was mixed with humus to achieve a LOI of approximately four percent. About 280 g of the substrate was used for each 0.3 l pot in each treatment. Four different treatments: control, N, P, and NP and one plant, the herb *S. virgaurea* L found in both the heath and meadow sites, was used in the plant bioassay. Each treatment was replicated 10 times ($N = 10$ replications × 4 treatments × 2 soils) and only one plant was growing in each plot. Seeds collected from the vicinity of Abisko were used for the plant bioassay and 10 seeds were initially planted in each pot. After germination only one plant was left in each pot. Each pot was treated with de-ionized water every second day and N and/or P each week during the experiment and the same water content was

maintained during the experiment. The total amount of added solution was always the same for all treatments. Phosphate was added as NaH_2PO_4 (122 mg N l^{-1}) and N as NH_4NO_3 (408 mg N l^{-1}). The control treatment received an equal amount of solution (de-ionized water) as the N and P treatments. All additions were made with a dispenser (100 ml dispenser; Socorex, Switzerland) and the volume of each addition was noted to calculate the total amount of fertilizer added. A climate chamber (Sanyo MLR 351) was used for the study and day length was set to 12 h (80% of full illumination). Temperature was 20°C during the day and 10°C during the night. Pots were moved systematically during the experiment. The plants were harvested after 55 days and shoot and root biomasses were determined after drying (70°C, 3 days).

Analysis

Phosphorus analyses were performed using a flow injection analyzer (5012 Analyzer, Tecator, Höganäs, Sweden). All soil extracts and the 0.5 M NaCl solution were analyzed for inorganic P (P_i). The $NaHCO_3$ and NaOH extracts were also analyzed for total P. Prior to analysis, the $NaHCO_3$ and NaOH extracts were filtered (Millex-HV 0.45 μm, Millipore, Molsheim, France), diluted to a volume of 5 ml ($NaHCO_3$ was diluted 1:5 and NaOH 1:10), 20 μl sulphuric acid was added, and thereafter centrifuged before analysis. Because the $NaHCO_3$ and NaOH extracts were colored, we adjusted the measured P concentration by subtracting the effect of the color in the analysis. The color was determined separately using the same matrix as in the phosphate determination but without the P reagents. Total P in $NaHCO_3$ and NaOH extracts was determined using acidified potassium persulfate digestion. Organic P (P_o) in the two extracts was calculated as the difference between total P and P_i. All supernatants analyzed above were stored in a freezer until analyzed with the exception of the digest which was stored at +5°C. The dried plant material was measured for N and P using a modified semi-micro Kjeldahl method (Blakemore et al. 1987). Total C and N in the soil samples was measured using a Perkin Elmer Elemental CHNS analyzer and pyrophosphate and oxalate extractable Al, Fe, and P were analyzed by ICP-OES (Varian Vista Ax Pro).

Statistics

For statistical comparison between the three vegetation types, two-way analysis of variance (ANOVA) were used with vegetation type and location as fixed factors and five replications for each plot (vegetation × location). Multiple comparisons in variance analyses were performed with Tukey's test. Relationships between microbial variables determined from the microbial bioassay (dependent variables) and various soil variables (independent variables) were tested using stepwise linear regression. The variables were entered when the probability of F was less than or equal to 0.05 and removed when it was higher than or equal to 0.10. Treatment effects in the plant bioassay were statistically analyzed using one-way ANOVA with substrate as the independent variable. Dunnet's test was used to test for difference in biomass of *S. virgaurea* plants between the control and the N, P, and NP additions. Statistical analyses were performed using SPSS (SPSS 12.0.1 software, Chicago, IL, USA). For the microbial bioassay, paired-sample t test between different nutrient amendments was used. Uncertainties are reported as 95% confidence intervals. Significant differences refer to the $P < 0.05$ level unless otherwise stated.

Results

Soils

Soil pH was lower in the dry heath compared to the MM, while the reverse trend occurred for soil C:N and C:P ratios (Table 1). Soil pH and C:N ratios were negatively linearly related ($r^2 = 0.55$, $P > 0.001$). There was a trend for somewhat lower total soil P concentrations in the dry heath (984 mg kg^{-1}) compared to the mesic heath and the MM (1,168 and 1,189 mg kg^{-1}, respectively) ($P = 0.061$, two-way ANOVA). However, the distribution of the different P fractions differed significantly between the three vegetation types (Table 2). The most pronounced difference was found for HCl extractable P with nearly a tenfold higher concentration in the meadow compared to the heath sites (Fig. 2). Concentrations of HCl extractable P_i were in many cases not detectable in the heath sites. In the meadow sites, HCl extractable P_i was strongly negatively related to

Table 1 Soil characteristics of three tundra vegetation types

Variable	Unit	Vegetation type		
		Dry heath	Mesic heath	Mesic meadow
Loss on ignition	%	49.2 (6.9)a	58.6 (9.9)a	32.2 (10.3)b
pH		4.42 (0.14)a	4.86 (0.27)b	6.20 (0.22)c
C	%	26.6 (3.7)a	29.6 (4.8)a	17.1 (5.4)b
N	%	1.1 (0.2)a	1.4 (0.2)a	1.1 (0.3)a
P	%	0.10 (0.01)a	0.12 (0.01)a	0.12 (0.02)a
C:N		24.5 (2.1)a	21.6 (1.3)b	15.6 (0.6)c
C:P		273 (38)a	253 (44)a	142 (40)b
N:P		11.1 (1.2)a	11.6 (1.6)a	8.9 (2.4)b
Al_{pyr}	mmol kg^{-1}	46.8 (9.7)a	51.2 (15.0)a	34.8 (9.3)a
Al_{ox}	mmol kg^{-1}	56.8 (7.0)a	61.8 (15.1)a	49.6 (7.4)a
Fe_{pyr}	mmol kg^{-1}	35.3 (7.3)a	36.3 (10.4)a	29.8 (9.3)a
Fe_{ox}	mmol kg^{-1}	51.8 (7.0)a	56.4 (12.1)b	83.7 (13.2)b
S_{max}	mg P kg^{-1}	1154 (67)a	1157 (124)a	1249 (59)a

Average soil concentrations (95% confidence interval in brackets; $n = 15$). Within each row, numbers that are significantly different at $P = 0.05$ are marked with different letters and numbers with the same letter are not significantly different (Tukey's multiple comparison).

Al_{pyr} and Fe_{pyr} pyrophosphate-extractable aluminium and iron, Al_{ox} and Fe_{ox} oxalate-extractable aluminium and iron, S_{max} calculated sorption maximum

LOI ($n = 15$, $r^2 = 0.87$, $P < 0.001$). NaOH extractable P_i and P_o were generally higher in the mesic heath (Fig. 2) and were positively correlated to oxalate extractable Al ($r = 0.56$ and 0.67, respectively, $P < 0.001$). The $NaHCO_3$ extractable P_o and membrane P_i were lower in the meadow sites compared to the heath sites (Fig. 2). The proportion of the more labile fractions of P (sum of membrane P_i and $NaHCO_3$ extractable P) was also less in the meadow sites; 10 percent of total P and about 20 percent in the heath sites. Organically bound fractions of P (sum of $NaHCO_3$ and NaOH extractable P_o and residual P) were dominant in all vegetation types accounting for about 80 percent of total P in the heath sites and 70 percent in the meadow sites. Notably, the percentage P_o was never less than 69 percent in the heath sites, whereas the values ranged from 47 to 88 percent in the meadow sites. The lower values were found in the Suourojaure site, where the OM content was lower than in the two other meadow sites. We found no significant difference in pyrophosphate extractable Al and Fe and oxalate extractable Al between the different vegetation types (Table 1). However, oxalate extractable Fe was significantly higher in the meadow sites (Table 2). The calculated P sorption max (S_{max}) did not differ between the vegetation types (Table 1). More detailed information on variations between across locations and vegetation types is given in Appendix.

Leaf nutrient content

Plants from meadow sites generally had higher leaf N:P ratios compared to plants from heath sites (Fig. 3). The highest plant N:P ratio was found for the dwarf shrub *V. uligonosum*, which increased from an average of 10.2 in the dry heath to 16.4 in the MM (Fig. 3a). The dwarf shrub *V. vitis-idaea* showed a similar trend, but with less difference in N:P ratios (Fig. 3b). The increased N:P ratio could be explained by both increased leaf N concentrations and decreased leaf P concentrations (data not shown) (Table 3).

The combined N + P additions in the plant bioassay increased biomass production in the meadow soil, whereas no response was found when N and P were added separately (Fig. 4). The response in the heath soil differed from the meadow soil; both N and N + P additions increased biomass production compared to the control (Fig. 4).

Table 2 ANOVA results (F values with P values in brackets) testing for responses of different soil characteristics and soil P fractions to vegetation type, the effect of site within the vegetation type, and the interaction between these two factors

Variable	Vegetation		
	Type	Location	Type × location
Loss on ignition	16.4 (<0.001)	11.1 (<0.001)	6.3 (<0.001)
pH	96.6 (<0.001)	0.3 (0.723)	5.4 (0.002)
C	14.5 (<0.001)	9.5 (<0.001)	6.8 (<0.001)
N	3.0 (0.062)	4.5 (0.018)	8.1 (<0.001)
P	3.1 (0.059)	0.1 (0.889)	2.3 (0.082)
C:N	70.7 (<0.001)	10.9 (<0.001)	5.8 (0.001)
C:P	30.0 (<0.001)	23.9 (<0.001)	6.1 (0.001)
N:P	4.8 (0.014)	13.3 (<0.001)	8.3 (0.001)
Al_{pyr}	2.9 (0.071)	3.1 (0.056)	4.0 (0.009)
Fe_{pyr}	0.7 (0.489)	4.8 (0.015)	3.3 (0.022)
Al_{ox}	1.2 (0.306)	3.7 (0.032)	1.6 (0.204)
Fe_{ox}	18.1 (<0.001)	16.5 (<0.001)	3.7 (0.013)
S_{max}	2.2 (0.125)	7.3 (0.002)	3.3 (0.021)
Membrane P	3.8 (0.031)	0.8 (0.431)	8.0 (<0.001)
P_i $NaHCO_3$	2.1 (0.138)	1.4 (0.251)	1.0 (0.406)
P_o $NaHCO_3$	12.0 (<0.001)	4.7 (0.016)	4.7 (0.004)
P_i NaOH	19.6 (<0.001)	6.2 (0.005)	4.9 (0.003)
P_o NaOH	5.1 (0.011)	0.9 (0.383)	5.0 (0.003)
P_i HCl	77.4 (<0.001)	7.3 (0.002)	8.3 (<0.001)
Residual P	1.3 (0.290)	1.9 (0.164)	3.7 (0.013)
Total P	3.0 (0.061)	0.1 (0.890)	2.3 (0.081)

Abbreviations (see Table 1)

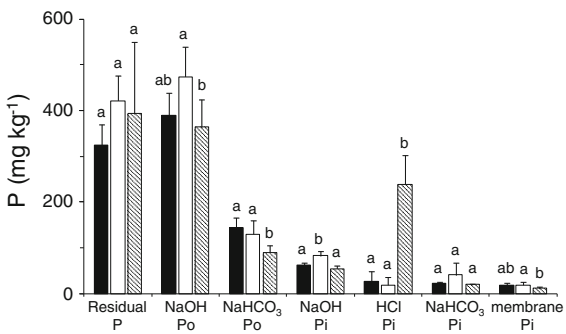

Fig. 2 Average values for different P fractions in dry heath (*filled bars*), mesic heath (*unfilled bars*), and MM (*hatched bars*). *Error bar* denotes 95% confidence interval. Values are significantly different ($P \leq 0.05$) if indicating *letter* differs

Microbial responses

There were clear differences in the respiration responses to nutrient additions (Table 4; Fig. 5). Generally, amendment with N or N and P always gave a larger maximum respiration rate compared to glucose only, independent of vegetation type (Table 4). Glucose and Glu + P amendments did not differ, whereas a small addition of N in combination with Glu + P (Glu + P + ΔN) always increased the maximum respiration rate (Table 4).

The microbial growth rate after Glu + N additions was significantly higher for the dry heath compared to the two other vegetation types (Table 4). The time to reach max respiration was, however, higher for the meadow compared to the two heath sites (Table 4). The microbial growth rate after Glu additions was negatively related to soil C:N ratios (Fig. 6c), but the relationship did not remain if Glu and N was added together, i.e., under P limiting conditions (Fig. 6d). The microbial growth rate after Glu and N addition was, however, weakly positively related to $NaHCO_3$ extractable P_o and negatively to soil N:P ratio (stepwise linear regression including all soil P fractions, soil C:N, C:P, N:P and soil pH, $r^2 = 0.38$, $P = 0.001$).

Both BR and SIR expressed as mg CO_2 h^{-1} g^{-1} dw were positively correlated to the soil C content, $r = 0.79$ and 0.65, respectively. BR expressed per g

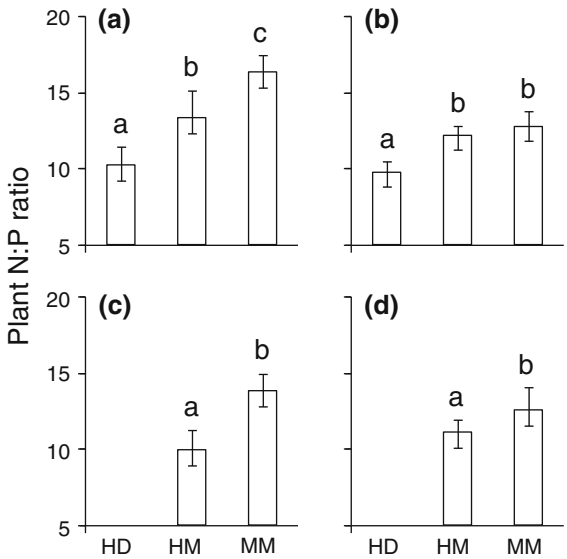

Fig. 3 Plant N:P ratios for **a** *Vaccinium uliginosum*; **b** *Vaccinium vitis-idaea*; **c** *Salix reticulate/herbacea*; and **d** *Carex bigelowi*. The plants are from dry heath (HD), mesic heath (HM), and MM. *S. reticulate* is only found in HD and *S. herbacea* only in MM. *Error bar* denotes 95% confidence interval

dw was significantly lower in the meadow sites compared to the heath sites; 0.018 mg CO_2 h^{-1} g^{-1} dw for the meadow versus 0.038 and 0.044 mg CO_2 h^{-1} g^{-1} dw for the dry and mesic heath sites ($P < 0.001$; two-way ANOVA). The difference between vegetation types did diminish if BR was expressed as mg CO_2 h^{-1} g^{-1} OM; the respiration rate was about 0.076 mg CO_2 h^{-1} g^{-1} OM (Table 2). SIR showed similar trends as BR; the overall average was 0.20 mg CO_2 h^{-1} g^{-1} OM. BR and SIR normalized for OM content was unrelated to soil C:N ratios (Fig. 6a). We used stepwise linear regression to test if BR (expressed as mg CO_2 g^{-1} OM) was related to various soil P forms, soil C:N and N:P ratios and soil pH. We found that BR strongly related to soil N:P ratios and more labile P fractions ($BR = 0.087 - 0.003 \times$ soil N:P $+ 0.008 \times NaHCO_3\text{-}P_o + 0.031 \times NaHCO_3P_i - 0.002 \times NaOH\text{-}P_o$; Fig. 5b) and a similar relationship was also true for SIR (not shown).

Discussion

Vegetation type and soil P fractions

We hypothesized that P fractions that are assumed to be more available should be lower in the meadow compared to the heath and this was supported by the

Table 3 Microbial respiration parameters responses to vegetation type, the effect of site within vegetation type, and the interaction between these factors

Variable	Vegetation		
	Type	Location	Type × location
BR[a]	0.5 (0.594)	13.3 (<0.001)	4.6 (0.004)
SIR[a]	1.8 (0.167)	15.2 (<0.001)	2.7 (0.043)
Maximum respiration rate			
Glu	3.5 (0.041)	8.9 (0.001)	7.23 (>0.001)
Glu + N	6.3 (0.004)	11.1 (>0.001)	4.5 (0.005)
Glu + N + ΔP	7.4 (0.002)	5.4 (0.009)	5.4 (0.002)
Glu + P	6.1 (0.005)	9.3 (0.001)	6.9 (>0.001)
Glu + P + ΔN	1.1 (0.330)	4.7 (0.016)	2.0 (0.116)
Microbial P indices			
Growth rate	26.6 (>0.001)	13.9 (>0.001)	7.0 (>0.001)
T_{max}	12.4 (<0.001)	9.6 (<0.001)	11.4 (<0.001)

F- and *P*-values (within brackets) are derived from ANOVA. Tested variables are BR, SIR and maximum respiration rate (five different treatments). Treatments include addition of glucose (Glu) alone or in combination with nitrogen (N) or phosphorus (P) in excess. Addition is denoted as ΔN or ΔP is a small addition of the respective nutrient. Microbial P indices (growth rate and time to reach maximum respiration rate after substrate addition; T_{max}) are based on Glu + N additions only

[a] Expressed per g OM

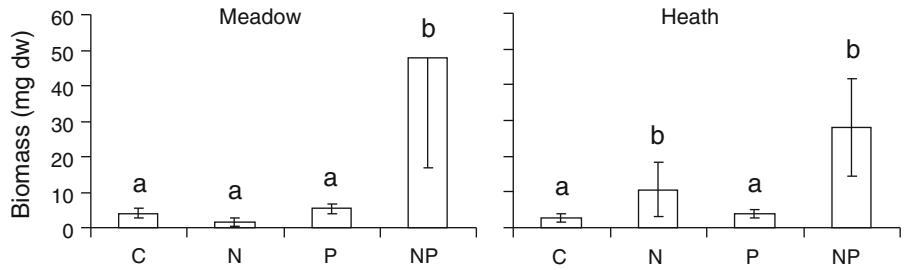

Fig. 4 Effects of N, P, and N + P additions in a plant bioassay with *Solidago virgaurea* (mean and 95% confidence interval) using humus layer soils from a mesic heath (HM) and a MM. Control treatment is denoted by C. Values are significantly different from the control ($P \leq 0.05$) if indicating *letter* differs

Table 4 Average values of parameters extracted from microbial respiration kinetics in three tundra vegetation types (95% confidence interval in brackets)

Variable	Unit	Vegetation type		
		Dry heath	Mesic heath	Mesic meadow
BR	mg CO_2 h^{-1} g^{-1} OM	0.079 (0.010)a	0.076 (0.008)a	0.073 (0.016)a
SIR	mg CO_2 h^{-1} g^{-1} OM	0.208 (0.025)a	0.175 (0.033)a	0.212 (0.052)a
Maximum respiration rate				
Glu	mg CO_2 h^{-1} g^{-1} OM	0.45 (0.08)a,a	0.57 (0.12)ab,a	0.62 (0.17)b,a
Glu + N	mg CO_2 h^{-1} g^{-1} OM	1.96 (0.21)a,b	1.84 (0.29)a,b	1.42 (0.37)b,b
Glu + N + ΔP	mg CO_2 h^{-1} g^{-1} OM	2.55 (0.20)a,c	2.41 (0.38)a,c	1.85 (0.42)b,bc
Glu + P	mg CO_2 h^{-1} g^{-1} OM	0.44 (0.06)a,a	0.57 (0.10)b,a	0.62 (0.14)b,a
Glu + P + ΔN	mg CO_2 h^{-1} g^{-1} OM	1.41 (0.18)a,d	1.57 (0.17)a,bd	1.41 (0.22)a,bd
Microbial P indices				
Growth rate	h^{-1}	0.020 (0.003)a	0.011 (0.001)b	0.014 (0.004)b
T_{max}	h	106 (13)a	109 (14)a	144 (25)b

Presented parameters are BR, SIR and maximum respiration rate (five different treatments). Treatments include addition of glucose (Glu), Glu + nitrogen (N), Glu + phosphorus (P). Phoshorus and N were also added in small amounts in combination with Glu + N and Glu + P, respectively (abbreviated ΔN and ΔP, respectively). Microbial P indices (growth rate and time to reach maximum respiration rate after substrate addition; T_{max}) are based on Glu + N additions only. Across vegetation types, numbers marked with the same letter are not significantly different at $P = 0.05$. For maximum respiration rate, the second letter denotes treatment differences within each vegetation type

lower concentrations of the more labile fractions of P, such as membrane P_i and $NaHCO_3$ P_o in the meadow. The differences are, however, relatively small and most likely not related to differences in sorption properties of the organic horizon. The distributions of P forms indicative of P sorption, i.e. NaOH extractable P (Cross and Schlesinger 1995; Giesler et al. 2002), was somewhat higher in mesic heath than in meadow, in contrast with the hypotheses of a higher P sorption in the meadow. The calculated P sorption maximum (S_{max}) did not indicate any difference between the three vegetation types either. In addition, the sum of oxalate extractable Al and Fe was much lower than what has been previously reported from other P sorbing organic soils in boreal forests (Giesler et al. 2002, 2005) and were in the lower range of organic soils reported by Kang et al. (2009). Therefore, our data suggest that variation in Al and Fe concentrations or P sorption capacity of the soil is not likely to be of major importance in separating meadow from heath in this subarctic tundra ecosystem.

The much higher HCl extractable P concentrations in the MM suggest a presence of Ca-phosphates. The HCl extraction may also dissolve Al or Fe-phosphates (Cross and Schlesinger 1995); however, this is less

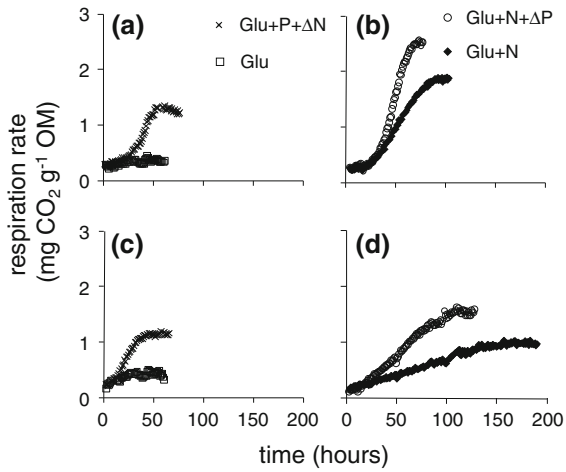

Fig. 5 Respiration curves from a dry heath (**a**, **b**) and MM (**c**, **d**) after addition of glucose (Glu), nitrogen (N) and phosphorus (P). The abbreviations denote Glu addition, Glu + N addition, Glu + N and a small addition of P (ΔP), and Glu + P and a small addition of N (ΔN). Nitrogen was added as $(NH_4)_2SO_4$ and P as NaH_2PO_4

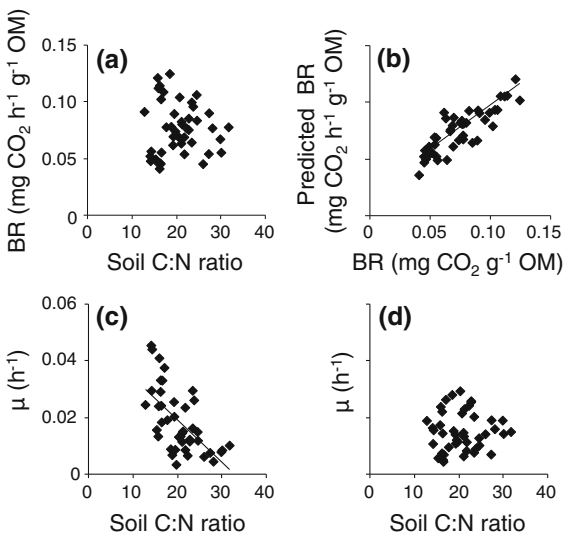

Fig. 6 Relationship between **a** soil C:N ratio and BR; **b** BR and predicted BR (BR = 0.087 − 0.003 × soil N:P + 0.008 × $NaHCO_3$-P_o + 0.031 × $NaHCO_3P_i$ − 0.002 × NaOH-P_o; r^2 = 0.72, $P < 0.001$); **c** soil C:N ratio and growth rate (μ) after addition of glucose (Glu); and **d** soil C:N ratio and growth (μ) rate after addition of Glu + N

likely to explain the observed differences since our results do not show any major differences in extractable Al or Fe between the vegetation types. Since none of the sites are situated directly on calcareous bedrock (although it is found within the area), water-fed inputs of Ca could potentially favour formation of Ca-phosphates in the meadow as well as explain the higher pH and high soil Ca-saturation (Tunesi et al. 1999; Darmody et al. 2004). A mixing of apatite-containing mineral grains into the organic horizon could also cause a more direct effect, consistent with the negative relationship between HCl extractable P_i and LOI in the meadow. However, the fact that the HCl extractable P_i was higher at meadow soils with similar LOI as in heath soils, despite similar organic horizon thickness, supports the first assumption. This is also in agreement with findings from vegetation gradients in the boreal forest (Giesler et al. 1998).

Overall, the distribution of P fractions and especially the dominance of the organic and residual P fractions across all three vegetation types (accounting for about 80% of the total P) are similar to what is found in other high-latitude tundra ecosystems (Chapin et al. 1978; Giblin et al. 1991) and are probably indicative of low decomposition rates. In comparison to organic horizons in boreal forest soils not influenced by high Al + Fe concentrations (Lagerström et al. 2009), labile P forms were much lower in our tundra soils and is most likely also indicative of lower mineralization rates. The distribution of P fractions is also comparable to those found in other cold environments like alpine tundra (Litaor et al. 2005). We do, however, also find differences in comparison to other tundra ecosystems. Variations in Al and Fe-bound P along an Alaskan tundra toposequence (Giblin et al. 1991) were attributed to differences in soil age; the younger alluvial soils along a river side containing the lowest proportion of Al and Fe bound P. This was also the explanation to the higher amounts of HCl extractable P in the younger soils. Soil age was also suggested to explain differences between 0.025 M HCl extractable PO_4-P in an older and younger moist tussock tundra that were deglaciated at different time periods; the higher concentrations found in the younger site (Hobbie and Gough 2002). In our case soil age is the same and it is only topographic position that separates the vegetation types; shifts in vegetation types can be found within very short distances with dry heath on a small ridge and meadow type vegetation just a few meters away in a depression. In comparison to the vegetation types described by Giblin et al. (1991) our heath sites seems to be most comparable with regards to soil P, soil pH and C:N ratio to their hilltop heath whereas

our meadow site resembles their riverside willow although both vegetations and soil age probably differ substantially between the two latter.

Relationship between vegetation type and biotic indices of P availability

Our comparison is restricted to a few species that occurred in both the heath and meadow and the results are thus indicative and not necessarily representative of the whole plant community. However, there was a clear trend of increasing N:P ratios from heath to meadow, with meadow plants often having N:P ratios in the range of co-limitation of N and P, and in some cases well into the range for P limitation suggested for upland and grassland ecosystems (Tessier and Raynal 2003; Güsewell 2004). The deciduous dwarf shrub *V. uligonosum* had an average N:P ratio of 16.4 in meadows and similar values has been found for the same species in P-poor sites in sub-alpine plant communities in northern Italy (Gerdol 2005). The trends we see in N:P ratios are in line with the lower content of labile P in the meadow and a higher N availability. The latter has been shown in a previous study from the same area in which net N mineralization rates were much higher in the meadow compared to the heath, and the net N mineralization was negatively related to the soil C: N ratio (Björk et al. 2007). As such, both soil N and P would contribute to higher plant N:P ratios and a stronger relative limitation by P in MM plant communities. The plant bioassay with *S. virgaurea* also suggested a co-limitation of N and P that was most pronounced for plants grown in the MM soil while plants grown in the heath soil were N-limited. This is in accordance with a number of fertilizer experiments from alpine or high-latitude tundra sites, which also suggest that plant communities in these ecosystems can be co-limited by N and P (Bowman et al. 1993, Bowman 1994, Shaver and Chapin 1995; Aerts and Chapin 2000, Seastedt and Vaccaro 2001; Soudzilovskaia et al. 2005; Litaor et al. 2008). Seasonal variability in N and P availability (see for instance Weintraub and Schimel 2005), especially if it differs in time between N and P, may also have implications for the plant nutrient acquisition. This is not likely to change the overall difference in N availability between heath and meadow but may have implications for the P acquisition.

The results from the microbial bioassay indicated that the microbial P availability was lower in the meadow than the heath, however, the difference was more subtle than previous comparisons of microbial responses in N and P limited boreal forest (Giesler et al. 2004). For instance, additions of Glu + N gave a lower growth rate for the MM compared to the dry heath, but the response was not different from the mesic heath. The time to reach maximum respiration was, however, longer for the meadow compared to both the mesic and dry heath sites, which corresponds with our expectation of less available P in the MM and previous results comparing humus soils from N and P limited forests (Giesler et al. 2004). The positive relationship between the slope after Glu + N additions and the soil N:P ratio and $NaHCO_3$ extractable P_o is not surprising since Glu + N is added in excess of microbial demand and P limitation was induced.

It should be stressed that the above results are only indicative although they point to the same conclusion; i.e. that the meadow sites differ from heath sites with regards to P availability. The mechanisms behind this are, however, not clear. Since sorption does not separate the vegetation types, other factors must also be important in determining P availability. Organic fractions of P are dominant, as in other tundra ecosystems, and qualitative differences between the meadow and heath sites could possibly affect mineralization rates and thus the release rate of P. Turner et al. (2004) who used ^{31}P-NMR on organic soils in mountain birch-tundra heath ecotones in the Fenno-scandian subarctic found an abundance of organic P compounds that are considered easily degradable in temperate environments. They suggested that the accumulation of these compounds is probably related to the low degradation rates in cold, acidic soils. Release rates of P from organic P is probably a key factor in determining P availability in tundra ecosystems (Chapin et al. 1978) and more detailed studies on both enzymatic activity of P degrading enzymes and organic P quality using for instance ^{31}P-NMR are needed in order to untangle the causes of difference in P availability across different tundra vegetation types.

Linkages between soil properties and basal respiration

The absence of differences in BR between vegetation types may seem surprising since meadow vegetation

contains more forbs and graminoids, which produce a more N-rich litter with low C:N ratio and phenolic content that is more degradable compared to shrub litter (Hobbie 1996, Wardle et al. 2004) and with a better substrate quality than low pH heath (Eskelinen et al. 2009). However, these results are consistent with other studies on organic soils from tundra or boreal forests, which indicate that there is no clear relationship between the C:N ratio, vegetation type, and soil respiration (Gough et al. 2000; Hobbie et al. 2002; Vance and Chapin 2001; Grogan and Jonasson 2005; Björk et al. 2007). In our case, the physical structure of the organic material indicates that bulk organic material is more decomposed in the meadow compared to the heath. Degradation of litter may be more rapid at the surface of the humus soil in the meadow, whereas the residue that forms the bulk organic material is more similar to the heath in terms of substrate quality. This could also explain the divergence between differences in litter quality and the absence of differences in respiration of bulk soil organic material in different vegetation types (Grogan and Jonsson 2005; Björk et al. 2007).

We found that labile P was an important predictor for BR when normalized for the OM content, which is similar to recent findings from a boreal forest (Lagerström et al. 2009). This is surprising since the nutrient amendments clearly show that Glu and Glu + P additions were the same, whereas Glu + N gave a significant response in respiration rates and P only gave an increase if Glu + N was also added, which suggests a microbial C limitation with N as a second limiting nutrient. Demoling et al. (2007) showed that only additions of C, N and P together increased bacterial growth rates considerably in a tundra soil from Abisko, indicating that all three nutrients were close to limiting bacterial growth. A comparison of the increase in maximum respiration rate after the nutrient amendments also shows a similar trend; glucose only increased the respiration rate a three-fold compared to SIR whereas Glu + N increased maximum respiration rates a tenfold for the heath and even further when P also was added. The increase after Glu + N was less for the meadow sites and is in agreement with the assumption that lower soil C:N ratios are associated more C-limited heterotrophic microorganisms (Kaye and Hart 1997; Schimel and Weintraub 2003).

Experimental conditions after nutrient amendments inducing high growth rates do, however, differ from those under BR in that the demand for N or P is low during BR since C is mainly used for maintenance. The result still indicates that P may relate to microbial activity. Bicarbonate extractable P was positively related to BR and has been shown to relate positively to phosphatase activity in soils (DeForest and Scott 2010; Rojo et al. 1990). Also microbial community composition has been shown to relate to bicarbonate extractable organic P (DeForest and Scott 2010). The relationship between BR and P that we observe and that was found across a boreal forest chronosequence (Lagerström et al. 2009) may reflect differences in phosphatase activity that also could be linked to differences in microbial community composition. Comparisons of meadow and heath communities using phospholipid fatty acid from the Abisko area (Sundqvist et al. 2010) shows that the microbial community composition differed between meadow and heath: meadow sites having a higher total bacterial biomass, a lower fungal:bacterial ratio and several of the bacterial PFLA's associated to the meadow. It is known that fungi and bacteria differ in their decomposition rates: bacteria-based food webs increasing litter decomposition whereas fungal-based food webs have slower litter decomposition and greater nutrient retention (Holland and Coleman 1987; Beare et al. 1992) and these differences may also be reflected in the relationship between BR and soil P. This hypothesis needs, however, to be tested before more conclusive interpretations can be made.

Conclusion

This study has provided further evidence of the importance of P as a co-limiting nutrient in the subarctic tundra, despite the traditional view of predominating N limitation in northern ecosystems. In addition, we have showed significant differences in P forms and availability across a mosaic of vegetation types on soils of similar age, and these differences were in turn reflected in both above- and belowground ecosystem processes. Our results indicated that abiotic control of P availability through sorption, which can be strong in boreal forest, did not separate the tundra vegetation types despite differences in topography and hydrology. Instead, biotic controls linked to the cold climate, are probably more important. The relationship between BR and soil P that we found resembles that of

a previous study from boreal forest (Lagerström et al. 2009) and from other environments showing that P or N + P additions can have stimulatory effects on respiration (Amador and Jones 1993; Ouyang et al. 2008; Bradford et al. 2008; Hartley et al. 2010) despite the general assumption that heterotrophic microorganisms are C limited. We hypothesise that this could be related to variations in microbial community composition and functioning. This may, hitherto, been unforeseen since studies combining details on soil P forms and microbial measurements are not common.

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Appendix

See Table 5.

Table 5 Average values and 95% confidence interval for soil pH, C:N ratio and P fractions across different locations and vegetation types

Variable	Location	Vegetation type		
		HD	HM	MM
Soil pH	S	4.62 ± 0.2	4.66 ± 0.2	6.35 ± 0.2
	L	4.27 ± 0.2	5.26 ± 0.2	5.78 ± 0.2
	K	4.38 ± 0.2	4.65 ± 0.7	6.49 ± 0.4
C:N	S	22.1 ± 3	21.0 ± 2	16.1 ± 1
	L	22.2 ± 1	20.2 ± 2	15.6 ± 1
	K	29.2 ± 2	23.5 ± 2	15.2 ± 1
Membrane P	S	10.4 ± 7	15.6 ± 6	13.9 ± 9
	L	31.9 ± 2	12.8 ± 11	6.7 ± 3
	K	9.5 ± 6	28.1 ± 12	11.7 ± 3
P_i $NaHCO_3$	S	19.8 ± 8	19.5 ± 5	20.6 ± 7
	L	28.4 ± 4	21.5 ± 7	17.6 ± 6
	K	19.9 ± 3	29.6 ± 10	18.8 ± 3
P_o $NaHCO_3$	S	153.3 ± 61	178.5 ± 37	70.2 ± 7
	L	164.3 ± 12	108.8 ± 4	128.3 ± 16
	K	112.2 ± 10	123.9 ± 40	69.6 ± 3
P_i NaOH	S	67.6 ± 6	96.1 ± 12	62.0 ± 14
	L	52.0 ± 1	87.9 ± 19	40.7 ± 7
	K	66.0 ± 11	62.0 ± 13	58.2 ± 8
P_o NaOH	S	340.2 ± 84	479.4 ± 125	365.0 ± 117
	L	484.8 ± 36	552.5 ± 92	275.1 ± 58
	K	340.2 ± 60	387.3 ± 86	449.2 ± 85
P_i HCl	S	28.7 ± 24	25.6 ± 30	181.1 ± 98
	L	12.9 ± 19	28.3 ± 38	375.3 ± 36
	K	39.5 ± 62	2.7 ± 3	160.5 ± 54
Residual P	S	301.5 ± 73	353.5 ± 64	481.0 ± 244
	L	383.1 ± 65	428.2 ± 79	144.0 ± 48
	K	286.2 ± 85	481.7 ± 117	554.4 ± 318
Total P	S	921.6 ± 146	1168.2 ± 181	1193.9 ± 295
	L	1156.7 ± 129	1265.4 ± 180	987.7 ± 102
	K	873.4 ± 108	1119.3 ± 223	1322.5 ± 402

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