Biogeochemistry (2009) 95:199–213
DOI 10.1007/s10533-009-9331-y

Soil phosphorus and microbial response to a long-term wildfire chronosequence in northern Sweden

Anna Lagerström · Camilla Esberg · David A. Wardle · Reiner Giesler

Received: 27 November 2008 / Accepted: 9 May 2009 / Published online: 29 May 2009

Abstract In the prolonged absence of major disturbances, ecosystems may enter a stage of retrogression, which is characterized by decreased ecosystem process rates both above and belowground, and often reduced availability of phosphorus (P). Disturbance through wildfire can increase soil P losses through leaching or erosion, but in the long-term absence of fire, soil P could potentially become increasingly bound in more stable forms that are less available to microbes. We studied forms of P and microbial respiration kinetics in the humus layer of a group of islands that vary considerably in wildfire frequency (40–5,300 years since last fire), and which are known to enter retrogression in the prolonged absence of fire. We found a decrease in labile P with decreasing fire frequency but no change in total P. Soil microorganisms responded more strongly to N than to P addition, and microbial biomass N:P ratios remained unchanged across the gradient. However, the concentration of labile P was the best predictor of microbial respiration responses across the islands, and this provides some evidence that declining access to P could contribute to the decline in soil microbial activity during retrogression. Our results show that even though N is arguably the main limiting nutrient during retrogression in this chronosequence, long term absence of fire also causes a decline in P availability which negatively affects microbial activity. This in turn could potentially impair microbially driven processes such as decomposition and mineralization and further contribute to the reduced availability of soil nutrients during retrogression.

Keywords Boreal forest · Microbial respiration · Phosphorus · Retrogression · Succession · Wild fire

A. Lagerström (✉) · D. A. Wardle
Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden
e-mail: anna.lagerstrom@svek.slu.se

C. Esberg · R. Giesler
Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, P.O. Box 62, 981 07 Abisko, Sweden

Introduction

During long-term succession (in the order of millennia), nutrient limitation of plants and soil microorganisms often shifts from being mainly nitrogen (N) limited, to being co-limited by N and phosphorus (P), and eventually to being mainly P-limited (Walker and Syers 1976; Walker et al. 1983; Vitousek 2002; Wardle et al. 2004a; Coomes et al. 2005; Allison et al. 2007). This increasing limitation by P occurs because P is derived mainly from the bedrock and over time becomes increasingly depleted or bound in more stable forms (Walker and Syers 1976; Walker et al. 1983; Crews et al. 1995; Vitousek and Farrington

1997; Turner et al. 2007). In contrast, inputs of N to the ecosystem through biological N fixation and atmospheric N deposition can occur even in late successional stages (Crews et al. 2000; Lagerström et al. 2007). Ecosystem productivity characteristically peaks at the stage of succession at which N and P are co-limiting, and declines in the final P-limited stage (Walker and Syers 1976; Walker et al. 1983; Vitousek 2002; Wardle et al. 2004a; Richardson et al. 2004; Coomes et al. 2005; Lecomte et al. 2006). The stage at which productivity declines is often referred to as 'ecosystem retrogression' (Walker et al. 2001; Walker and del Moral 2003; Walker and Reddell 2007) and characteristically involves reduced plant litter quality, microbial biomass and rates of decomposition and microbial respiration (Wardle et al. 2004a; Parfitt et al. 2005; Williamson et al. 2005). A decline in soil P quality and abundance has been well documented in retrogressive chronosequences aged in the order of 20,000 years or more in tropical and temperate climates (Walker and Syers 1976; Crews et al. 1995; Vitousek and Farrington 1997; Turner et al. 2007; Allison et al. 2007). However, it has not been demonstrated in the boreal zone where ecosystem retrogression has been observed to occur over a few 1,000 years (Wardle et al. 2003, 2004a) or where retrogression has resulted from the prolonged absence of wildfire.

Wildfire is the main natural cause of disturbance in the boreal forest (Zackrisson 1977; Niklasson and Granström 2000). Several studies have shown that fire can increase losses of P in the boreal landscape in the short term (Burke et al. 2005; Prepas et al. 2003; Bayley et al. 1992; Spencer and Hauer 1991; McColl and Grigal 1975). Most of these losses are in particulate form (Burke et al. 2005; Prepas et al. 2003), because P is non-combustible and tends to accumulate in surface soils after fire (Neff et al. 2005), from where it is easily lost, mainly through surface run-off. When fires are frequent, there will be a net loss of P from the surface soil, which requires replenishment by weathering of parent material. Previous studies in the boreal landscape have shown that with frequent fire there is a rapid depletion (<2,000 years) of easily weatherable minerals in the soil mineral horizon (Hoffland et al. 2002), and the amount of P in the humus soil may therefore be expected to decrease with time. In contrast, the long term absence of fire will result in continual release of mineral P by weathering and transfer of P to the surface via plant uptake (Attiwill and Adams 1993); this P will eventually be returned as plant litter and incorporated as organic P in the humus layer. Ecosystem losses of P can thus be expected to be slow in areas with low fire frequency. Long-term absence of disturbance in the boreal forest involves the gradual build-up of an increasingly thicker humus layer (Wardle et al. 2003), and it is conceivable that as this occurs P may become bound in more stable organic forms, causing a shift in the proportions of different forms of P with increasing time since fire. However, to date this issue remains unexplored.

In this study we use a well characterized retrogressive boreal forest chronosequence in northern Sweden that spans over 5,000 years. The system involves a series of 30 lake islands across which fire frequency varies greatly because large islands get struck by lightning more often than do smaller ones (Wardle et al. 1997, 2003). As such, some of the largest islands have burned within the past 100 years, whereas some smaller islands have not experienced a major fire for over 5,000 years. Coupled with a decreased fire frequency is an increased depth of the humus layer, increased C sequestration, and elevated humus N:P ratios (Wardle et al. 2004a) due to increased N concentrations caused by higher N fixation rates on islands that have not burned for a long time (Lagerström et al. 2007). With decreased fire frequency there is also a decrease in litter quality and an increase in concentrations of polyphenolic compounds (Wardle et al. 1997, 2003, 2004a). The system provides a unique opportunity for studying how differences in long-term fire history can affect ecosystem P dynamics in the time scale of centuries to millennia in the boreal forest. We hypothesize that the very low fire frequency on small islands has lead to an increased proportion of humus P being locked up in stable organic forms, leading to higher total P but low P availability compared to large islands that burn more frequently. To test this hypothesis we compared the abundance of different P forms across all islands as determined through Hedley extraction (Hedley et al. 1982; Saggar et al. 1990; Binkley et al. 2000). We also used soil respiration parameters as indicators of the degree of availability of soil P to the microbial community across the chronosequence, following the method by Nordgren (1988, 1992).

By conducting these measurements we hope to gain further insight into the nature of P dynamics and limitation during ecosystem retrogression caused by the long-term absence of wild fire in the boreal forest.

Materials and methods

Study site and soil sampling

The study was conducted on 30 forested islands in Lake Hornavan and Lake Uddjaure in northern Sweden (65° 55′N to 66° 09′N and 17° 43′E to 17° 55′E). The main disturbance factor on these islands is wildfire by lightning strike; large islands are struck more often by lightning than are smaller ones and have therefore burned more frequently (Wardle et al. 1997, 2003). The islands were divided into three size classes with ten islands in each; large (>1 ha), medium (0.1–1.0 ha) and small (<0.1 ha) with an average time since the last major fire of 585, 2,180 and 3,250 years respectively (Wardle et al. 2003). The bedrock consists of granite boulders and the soils are podsols. The depth of the humus layer increases with decreasing island size and increasing time since fire, from around 0.1 m on large islands to an average of 0.65 m (and up to 0.9) on small islands (Wardle et al. 2003). Mean annual precipitation is 750 mm and the mean temperature is +13°C in July and −14°C in January. The vegetation is dominated by the tree species *Pinus sylvestris*, *Picea abies* and *Betula pubescens* and the dwarf shrubs *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Empetrum hermaphroditum*. Feather mosses dominate the ground layer.

Sampling took place in mid August 2005. Six randomly placed soil cores were collected from permanent 20 × 20 m plot on each of the 30 islands (one plot per island). These plots have been used for previous work on these islands (Wardle et al. 2003, 2004a); all plots are similar distance from the shore regardless of island size. Cores were retrieved with a soil auger (diameter: 0.10 m) at a distance of at least 2 m between samples. The upper 10 cm of the humus was used; this was the humus depth on the islands with the shallowest humus, and the depth layer in which most of the soil microbial activity is concentrated (Fang and Moncrieff 2005). Vegetation and litter was removed from the cores, after which they were packed in polyethylene bags, and stored in a freezer (−20°C) from the day of sampling until they were analysed. As the soil profile is normally frozen for 6 months of the year and routinely subjected to temperatures in this range, it is assumed that storage of samples in a freezer would not subject the soils to any unnatural effects. However, because of the freezing our samples may be most characteristic of spring soils rather than August soils. Before analysis, the soils were sieved to 3 mm and roots were removed. The six soil cores from each island were then bulked into one composite island sample for analysis.

Microbial respiration

Soil microbial respiration was measured using a respirometer (Respicond IV; A. Nordgren Innovations, Djäkneboda, Sweden), which calculates the amount of respired CO_2 from the change in conductivity caused by accumulated CO_2 in a KOH trap, as described by Nordgren (1988, 1992). For each island humus sample, four subsamples, corresponding to 1 g organic matter (determined by loss on ignition, 550°C, 5 h), were each placed in 250 ml plastic vessels. They were adjusted to 230% gravimetric moisture content (dry weight basis), which was the mean gravimetric moisture content (70°C, 72 h) of all samples at the time of sample collection and is close to the optimum for microbial growth in humus samples (e.g., Ilstedt et al. 2000). The vessels were placed in the respirometer (which was run at 20°C) and respiration then measured hourly (see Fig. 1 for schematic graph of soil microbial respiration kinetics before and after substrate addition). Carbon is known to be limiting to microbial growth in these soils and glucose (Glu) was therefore added in excess to all samples.

In order to estimate the nature of nutrient limitation of the microbial community, additions of N and P were made to the four 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 microbial organisms (e.g., Demetz and Insam 1999; Vesterdal 1998; Ilstedt et al. 2003; Giesler et al. 2004; Ilstedt and Singh 2005; Gnankambary et al. 2007). Glucose + N and Glu + P was added in excess to the first and second vessel respectively to ensure that P was the

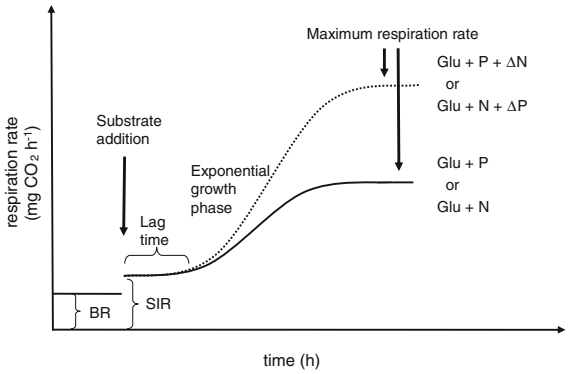

Fig. 1 Schematic graph of soil microbial respiration kinetics before and after substrate addition. Basal respiration (*BR*) is the mean value of 20 hourly measurements. Glucose (Glu) + P or Glu + N were added in excess to the soil samples as described in the text, in a duplicate vessel a limited amount of N (ΔN) or P (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

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). The amount of Glu added was 400 mg. Phosphorus was added as NaH_2PO_4 and the amounts were 2.28 mg P to achieve P in excess and 0.114 mg P as ΔP. Nitrogen was added as $(NH_4)_2SO_4$ and the amounts were 13.8 mg N to achieve excess N and 1.00 mg for ΔN. These amounts have previously been shown to be appropriate for quantifying N and P limitation of the microbial community in boreal forest systems by using this approach (Nordgren 1992; Giesler et al. 2004).

Measurements of CO_2 production from each vessel was made every hour. When respiration was stable, basal respiration (BR) was calculated as the mean value of 20 hourly measurements. Substrate additions were made when respiration rate had been stable for 40 continuous hours. Substrate-induced respiration (SIR) was determined as the respiration rate immediately following the addition of glucose (Anderson and Domsch 1978; Fig. 1). Some time after glucose and N and/or P addition, respiration starts to increase exponentially (Fig. 1) and this rate of exponential growth (μ) was measured as the slope of the log-transformed respiration rate plotted against time during the exponential growth phase (Nordgren 1988; Giesler et al. 2004). The time period between substrate addition and the start of the exponential growth phase, i.e., the lag time (Fig. 1), is calculated as the time from substrate addition to the intercept between the regression line of log transformed respiration rate during exponential phase and log SIR (Nordgren 1988).

Soil and microbial C, N and P determinations

In order to examine different forms of soil P in each soil sample, sequential extraction of P was performed in five steps using the approach of Hedley and Stewart (1982) as modified by Binkley et al. (2000) and Giesler et al. (2004).

In the first step, inorganic P was extracted using anion exchange membranes (55164 2S, BDH Laboratory Supplies, Poole, England) (Saggar et al. 1990). For each soil sample, an anion exchange membrane (4.5×8.5 cm^2) was placed in a 250 ml plastic centrifuge bottle with 2 g d.w. of soil and 180 ml deionised water, and placed on an orbital shaker (150 rev min^{-1}, 18 h). The membrane was then removed and soil that was adhered to it was rinsed back into the bottle, which was then placed in a high speed centrifuge (JA rotor 14, 14,000 rev min^{-1}, 15 min, 10°C). The water was then discarded, leaving the soil pellet in the centrifuge bottle. The membrane was transferred to a 150 ml bottle where it was eluated with 40 ml NaCl on a shaker (1 h). In the second step 180 ml $NaHCO_3$ (0.5 M) was added to the soil pellet remaining in the centrifuge bottle from the previous step. The pellet was resuspended before the bottle was placed on a shaker for 18 h and thereafter centrifuged for 15 min. Forty millilitres of

the supernatant was saved in a freezer for analysis and the rest was discarded, leaving the soil pellet in the bottle. We extracted the soil pellet remaining from step 2 with NaOH (0.2 M), using the same procedure as described for $NaHCO_3$ extraction in step 2. In the fourth step 180 ml HCl (1.0 M) was added using the same procedure as described in Step 2. To determine the residual P fraction, the soil remaining from Step 4 was washed with 180 ml deionised water through shaking for 1 h. The solution was centrifuged, the water discarded and the residual fraction left to air dry.

All extractants were analysed for molybdate reactive P using a flow injection analyzer (FIAstar^{TM} 5000 Analyzer, FOSS Analytical AB, Höganäs, Sweden). We assume that this mainly is inorganic P (P_i). The $NaHCO_3$ and NaOH solutions were filtered (Millex-HV 0.45 μm, Millipore, Molsheim, France) prior to analysis thereafter amended with sulphuric acid (20 μl concentrated H_2SO_4 to 5 ml solution). Since the HCO_3 and NaOH solutions were dark in colour, the measured P concentration was corrected by subtracting the effect of the colour in the analysis. Acidified potassium persulfate ($K_2S_2O_8$) digestion was used to determine total P in the HCO_3 and NaOH solutions and P_i analysed as above. The concentration of organic P was calculated as the difference between total P and P_i. The residual fraction was determined by acid digestion with 5 ml H_2SO_4 (soil-solution ratio 1:10) in a block digestor (360°C) with H_2O_2 as a catalyst. P was analysed as above.

The membrane and $NaHCO_3$ extractable P fractions are assumed to be labile and readily available to plants and microbes (Cross and Schlesinger 1995). The NaOH extractable P is assumed to be adsorbed more strongly to Al and Fe complexes and the organic P (P_o) is assumed to be more resistant compared to the labile fractions, but still available over an intermediate time scale (Cross and Schlesinger 1995). The HCl fraction contains occluded P_i and the residual fractions contain both occluded P_i and more stable organic P_o. These P forms are considered unavailable to plants and microbes except possibly over a very long time scale (Cross and Schlesinger 1995).

Total C and N in each soil sample were determined after drying a subsample (70°C, 3 days) and milling with a ball mill, using a Perkin Elmer Elemental CHNS analyzer. Total P is calculated as the sum of P_i and P_o in the five extraction steps above. Total microbial biomass C, N and P was determined through fumigation extraction. For C and N the extraction followed Vance et al. (1987) as modified by Daly and Wainiqolo (1993) and Sparling (1994). Fumigated and non-fumigated soil samples were extracted with 0.5 M K_2SO_4 in order to estimate microbial biomass C and N. Extractable C and N was then determined with a TOC analyser. For microbial biomass N there was an additional step of converting all of the N into inorganic forms suitable for analysis. This was done through oxidizing extractable organic N with $K_2S_2O_8$ by heating in an autoclave (Ross 1992). For estimating microbial biomass P, the soil was fumigated with $CHCl_3$, using 0.5 M $NaHCO_3$ for P_i extraction (Brookes et al. 1982; Hedley et al. 1982). To estimate the microbial biomass C, N and P, the increase in C, N or P in the fumigated sample was divided by a factor to correct for the assumed efficiency of microbial biomass extraction. Extraction efficiency for C, N and P was assumed to be 41, 45 (Jenkinson 1988) and 40% (Brookes et al. 1982) respectively.

Data analyses

Individual islands were used as the basis of replication for all analyses. The effect of island size class on respiration parameters, soil phosphorus forms, and soil and microbial C, N and P concentrations was tested using one-way ANOVA. The effect of additions of ΔN or ΔP, and island size class on microbial respiration parameters was analysed using two-way ANOVA. Two-way ANOVA was also used to analyse the difference between Glu + N and Glu + P additions on maximum respiration, growth rate, lag phase and time to maximum respiration, with these respiration parameters as independent variables and Glu + N or Glu + P addition and island size classes as factors. The relationships between microbial response variables and soil chemical data were analysed using multiple stepwise regression, in which variables were entered when probability of *F* was less or equal to 0.05. As more variables are entered stepwise into the regression the probability of *F* for a previously entered variable can change, and when this happened variables were removed if their influence on the dependent variable had a probability of *F* higher than or equal to 0.10. The relationships between humus C:N and N:P

ratios with islands size and times since fire was analysed with linear regression. All data was analysed using SPSS 12.0.1 for windows (SPSS, Chicago, IL, USA). When necessary, data was log-transformed to fulfil the assumptions of normality and homogeneity of variance required for parametric analyses.

Results

Microbial respiratory responses to N and P additions

Across all islands, the lag time for the microbial community (i.e., the time from substrate addition to when the microbes begin to access the added nutrients and start the exponential growth phase) was significantly longer for the Glu + N addition treatment (on average 22 h) than for the Glu + P addition treatment (average of 9 h) ($F_{1,\ 28} = 217$, $P < 0.001$) (Fig. 2). The duration of the lag time was not significantly different between island size classes (Table 1). Addition of a limited amount of P, i.e., ΔP, significantly reduced the lag time, but this effect was not dependent on island size class (Table 1).

The maximum respiration rate was four times higher after addition of Glu + N than after addition of Glu + P when averaged across all island size classes (Fig. 2). There was a significant difference in maximum respiration rate between island size classes (Table 1). After addition of Glu + N, maximum respiration was significantly lower on small than on medium islands, while addition of Glu + P gave significantly lower maximum respiration on small islands than on both medium and large islands (Figs. 3, 4a). Addition of ΔN and ΔP both caused significantly higher maximum respiration across all island size classes (Table 1; Fig. 4a). Time to maximum respiration was significantly less for soils amended with Glu + P (on average 44 h) than for samples with Glu + N addition (on average 64 h) ($F_{1,\ 28} = 784$, $P < 0.001$) (Fig. 2). The time to reach maximum respiration following Glu + N addition was significantly longer for small islands than for medium or large islands (Table 1, Fig. 4b). Additions of ΔN and ΔP both significantly reduced the time required to reach maximum respiration, and there was an almost significant interactive effect between island size and ΔN addition (Table 1). The average growth rate in the exponential growth phase was significantly lower in soils amended with Glu + P (0.013 h^{-1}) than with Glu + N (0.031 h^{-1}) ($F_{1,\ 28} = 156$, $P < 0.001$) (Figs. 2, 3), and the difference between Glu + P and Glu + N amendments was significantly smaller on small than on large islands ($F_{1,\ 28} = 4.7$, $P = 0.013$). Growth rate was significantly lower on small islands than on medium islands after addition of Glu + N, but growth rate after Glu + P addition was unaffected by island size class (Table 1) (Fig. 4c). Additions of both ΔP and ΔN significantly increased growth rate (Table 1), on average by 11 and 100% respectively but these increases were not significantly different between island size classes (Table 1, Fig. 4c). The growth rate for samples amended with Glu + N was negatively related to humus depth on the islands ($R^2 = 0.255$, $P = 0.004$,

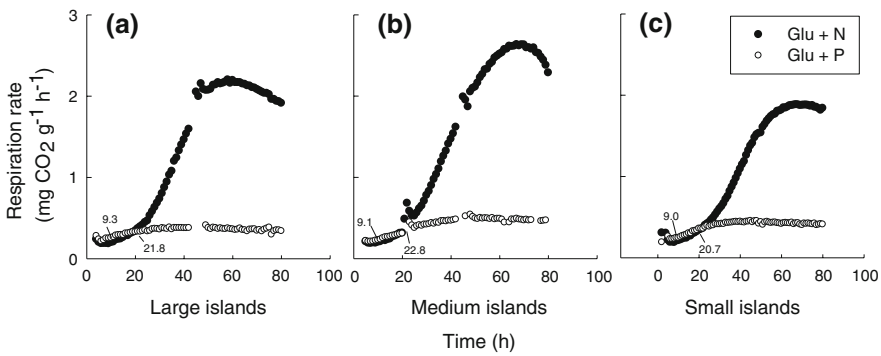

Fig. 2 Soil microbial respiration kinetics after addition of glucose (Glu) + P and Glu + N for (**a**) large islands, (**b**) medium islands, and (**c**) small islands. Each value represents the average respiration for the 10 islands in each size class. The end of the lag phase is indicated for each island size and treatment (i.e., Glu + P: 9.3, 9.1, 9.0 h and Glu + N: 21.8, 22.8, 20.7 h for large, medium and small islands respectively)

Table 1 ANOVA results (F values with P values in brackets) testing for the response of microbial respiration variables to island size class, the addition of a small amount of limiting nutrient (ΔN to C + P and ΔP to C + N), and the interaction between these two factors

		Island size category	Addition of ΔP or ΔN	Interaction term
Lag time (h)	Glu + P	0.16 (0.853)	20.0 (<0.001)*	0.42 (0.659)
	Glu + N	0.85 (0.432)	5.32 (0.025)*	0.70 (0.500)
Growth rate (log (CO_2 mg^{-1} h^{-1}))	Glu + P	2.95 (0.061)	46.55 (<0.001)*	2.02 (0.143)
	Glu + N	14.1 (<0.001)*	5.82 (0.019)*	0.77 (0.468)
Time to max respiration (h)	Glu + P	3.00 (0.058)	23.7 (<0.001)*	0.152 (0.859)
	Glu + N	16.1 (<0.001)*	9.70 (0.003)*	2.75 (0.073)
Max respiration (CO_2 mg g^{-1} h^{-1})	Glu + P	10.9 (<0.001)*	1,358 (<0.001)*	1.45 (0.245)
	Glu + N	33.7 (<0.001)*	123.3 (<0.001)*	1.17 (0.318)

* $P < 0.05$

$n = 30$), while growth rate after the other three addition treatments (Glu + N + ΔP, Glu + P and Glu + P + ΔN) did not show a significant relationship with humus depth. Basal respiration was significantly higher on medium islands than on small and large islands (Fig 4d) and SIR did not differ between island size classes (data not presented).

Soil and microbial C, N and P

For the sequential P extraction, residual P was the largest single fraction present, and averaged over all islands it accounted for 47% of total P; this fraction did not differ significantly across island size classes (Fig. 5). The second largest P fraction was NaOH extractable $P_{o,}$ which represented 24% of total P across all islands. The concentration of this pool was significantly higher on medium islands than on large islands (Fig. 5). Membrane extractable P occurred in significantly higher concentration on medium than on small islands and tended to also be lower compared to large islands though not significantly so ($P = 0.13$) (Fig. 5). The labile inorganic P (membrane and $NaHCO_3$ extractable P) was significantly lower on small islands (23% of total P) than on the medium or large islands (28% for both size classes). The $NaHCO_3$-extractable P_o fraction was significantly higher on medium than on small islands (Fig. 5), while the NaOH and HCl extractable P did not differ significantly between island size classes (Fig. 5).

Total soil N concentration in the top 0.1 m of the humus layer was significantly higher on small than on large islands, but neither total C nor total P differed significantly between island size classes (Table 2). The ratio of C to N was significantly higher on large than on small and medium islands (Table 2), and was positively related to island size and negatively related to time since fire (Fig. 6). The ratio of soil N to P was significantly higher on small than on medium or large islands (Table 2), and was negatively related to island size and positively related to time since fire (Fig. 6).

Microbial tissue C and N concentrations, and C:N and C:P ratios, did not differ significantly between island size classes (Table 2). However, microbial P concentration was significantly higher on medium islands than on small and large islands. Consequently the ratio of microbial N:P was significantly higher on small and large islands than on medium islands (Table 2).

Relations between microbial and chemical measurements

According to the stepwise regression analysis, labile P was the most important independent variable predicting both microbial biomass nutrient concentrations and those microbial parameters linked to respiration kinetics (Table 3). All significant relationships involving labile P were positive, except for time to maximum respiration (Table 3). Humus C:P was another important independent variable which was positively related to microbial biomass nutrient concentrations, and negatively related to respiration kinetic parameters (Table 3). Sodium hydroxide extractable P, which is obtained in the step of the P extraction that follows the steps which yield labile P_i, did not show significant relationships with any independent variable in the stepwise regression analysis. Basal respiration was

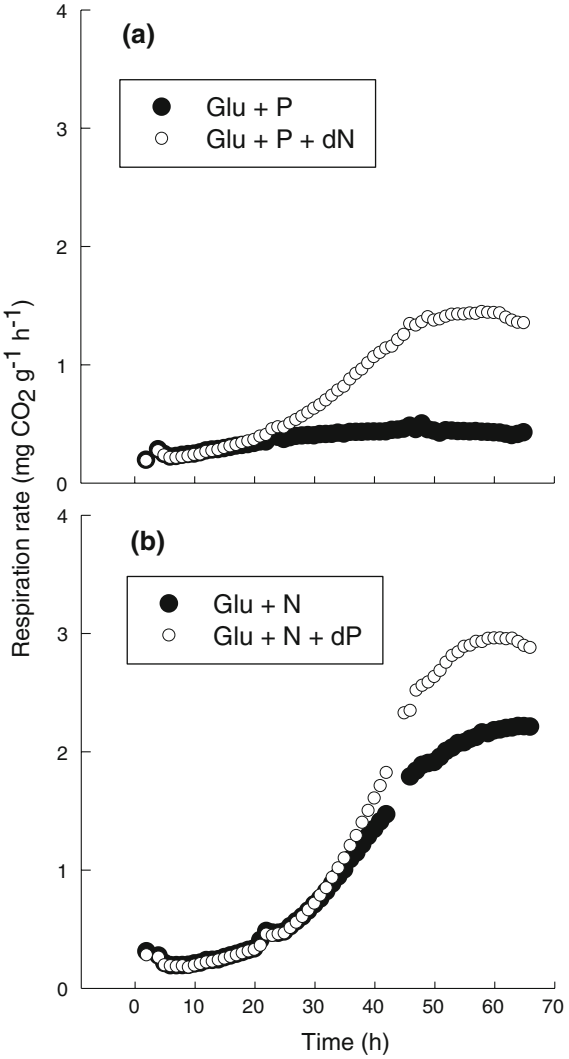

Fig. 3 Microbial respiration kinetics of 1 g organic matter with added (**a**) glucose (Glu) + P and Glu + P + ΔN, and (**b**) Glu + N and Glu + N + ΔP. All presented values are averages of all 30 studied islands

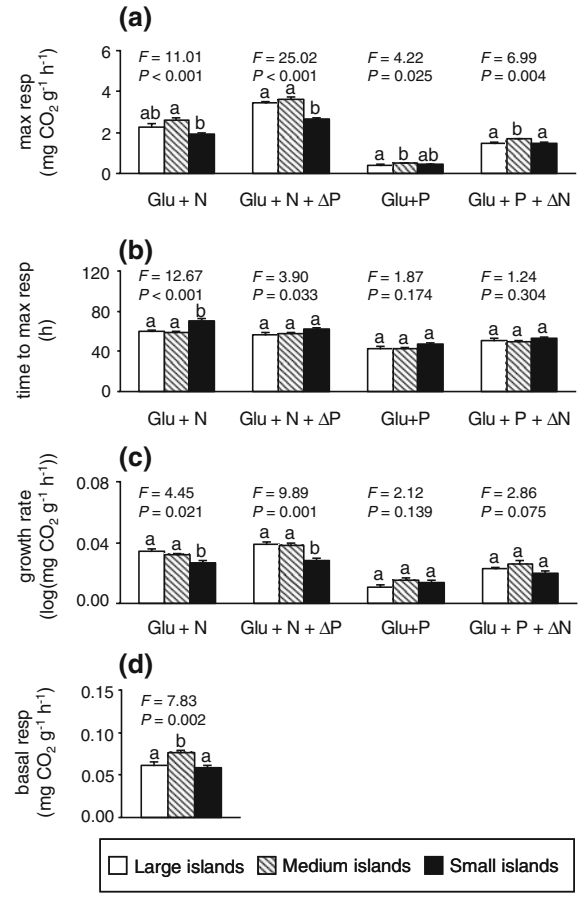

Fig. 4 Microbial parameters obtained from respiration kinetics for large, medium and small islands (10 islands per size class). Within each group of three *histogram bars*, *bars* topped with the *same letter* are not significantly different from each other at $P = 0.05$ (Tukey's test). **a** Maximum respiration rate (max resp.). **b** Time lag to maximum respiration rate after glucose and nutrient additions. **c** Exponential growth rate, i.e., the slope of the log-transformed respiration rate plotted against time during the exponential growth phase. **d** Basal respiration rate for 1 g of organic matter (basal resp.)

negatively related to the microbial biomass N:P ratio ($R^2 = 0.556$, $P = 0.003$).

Discussion

Effects of fire history on P forms and availability

We hypothesized that concentrations of total P and the most stable organic P forms would be highest on small islands which have undergone retrogression as a consequence of the extended absence of wild fire and which show impairment of ecosystem processes such as production, decomposition and nutrient fluxes (Wardle et al. 1997, 2003). However, there was an unexpected lack of variation in the most stable P forms (specifically NaOH extractable and residual P) between island size classes. These results therefore show that the major forms of P in the 0–0.1 m humus layer as defined by the Hedley fractionation remain remarkably invariant across ecosystems that differ greatly in fire history. As the first study on the effect of very long-term fire history on P in boreal forest humus, our results demonstrate that geochemical

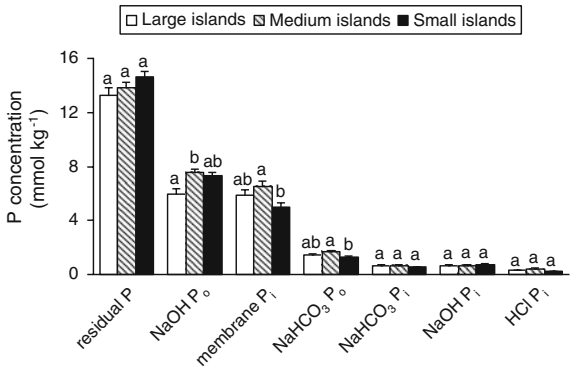

Fig. 5 Concentrations of different P fractions per kg (d.w.) of humus on large, medium and small islands (10 islands per size class) as determined by Hedley P fractionation. Within each group of three *histogram bars*, *bars* topped with the *same letter* are not significantly different from each other at $P = 0.05$ (Tukey's test). *F*-values, with *P*-values in *brackets*, for the one-way ANOVA: residual P: 2.00 (0.154); NaOH extractable P_o: 4.63 (0.019); membrane extractable P_i: 3.67 (0.039); $NaHCO_3$ extractable P_o: 4.89 (0.015); NaHCO3 extractable P_i: 1.54 (0.234); NaOH extractable P_i: 0.24 (0.785); HCl extractable P_i: 0.73 (0.492)

processes likely play only a minor roll in promoting ecosystem retrogression in the boreal forest. This is in contrast with previous studies that have found residual P to increase substantially with soil age in temperate and subtropical chronosequences during retrogression (Walker and Syers 1976; Crews et al. 1995; Turner et al. 2007), and may be because retrogression occurs over a somewhat shorter time-scale in the boreal forest zone (Wardle et al. 2004a).

Despite the lack of variation of the most stable P forms across island size classes, we found a lower concentration of labile P on small islands compared to medium islands, consistent with earlier studies showing a decrease in biologically available P during retrogression (Walker and Syers 1976; Crews et al. 1995; Turner et al. 2007). This response of labile P concentrations to island size is most likely associated with biologically driven processes. Release of P in these humus soils is governed by enzymatic degradation of organic P and soil enzymatic activity will therefore affect the concentrations of labile P. The efficiency of the enzymatic activity in turn depends on the degradability of the organic P present, and the lower litter quality previously observed on small islands (Wardle et al. 1997, 2003, 2004a) may therefore have a negative effect on litter P release. Another possible explanation for lower labile P concentrations on small islands could be a higher plant or microbial demand for P. The dominance of biological sinks or sources of P and absence of

Table 2 Soil and microbial biomass C, N and P data in response to island size class

	Island Size Classes			
	Large	Medium	Small	*F* and *P* level
Humus C (%)	51.7 ± 0.35	51.3 ± 0.33	51.4 ± 0.4	0.24 (0.791)
Humus N (%)	1.28 a ± 0.06*	1.46 ab ± 0.04*	1.59 b ± 0.07*	8.72 (0.001)*
Humus P (%)	0.087 ± 0.005	0.097 ± 0.003	0.091 ± 0.003	1.56 (2.223)
Humus C:N (%)	41.0 a ± 1.7*	35.3 b ± 0.8*	32.8 b ± 1.2*	10.79 (<0.001)*
Humus C:P (%)	600 ± 30.5	532 ± 15.9	556 ± 19.6	2.23 (0.127)
Humus N:P (%)	14.7 a ± 0.5*	15.1 a ± 0.5*	17.5 b ± 0.8*	5.65 (0.009)*
Microbial C (mg kg^{-1})	4,025 ± 310	3,711 ± 276	3,581 ± 120	0.84 (0.445)
Microbial N (mg kg^{-1})	561 ± 45.1	537 ± 53.3	461 ± 26.3	1.31 (0.287)
Microbial P (mg kg^{-1})	329 a ± 29.7*	545 b ± 52.2*	298 a ± 24.4*	11.67 (<0.001)*
Microbial C:N ratio	7.4 ± 0.3	7.4 ± 0.8	7.7 ± 0.2	0.04 (0.961)
Microbial C:P ratio	12.9 a ± 1.1*	7.2 b ± 0.9*	12.2 a ± 0.9*	10.97 (0.001)*
Microbial N:P ratio	1.7 a ± 0.1*	1.0 b ± 0.1*	1.6 a ± 0.1*	9.93 (0.001)*

The values are means ± SE ($n = 10$ islands for each size class). *F* and *P* levels are derived from one-way ANOVA testing for effects of island size

Within each row, numbers followed by the same letter are not significantly different at $P = 0.05$ (Tukey's test). Ratios are based on mass

* $P < 0.05$

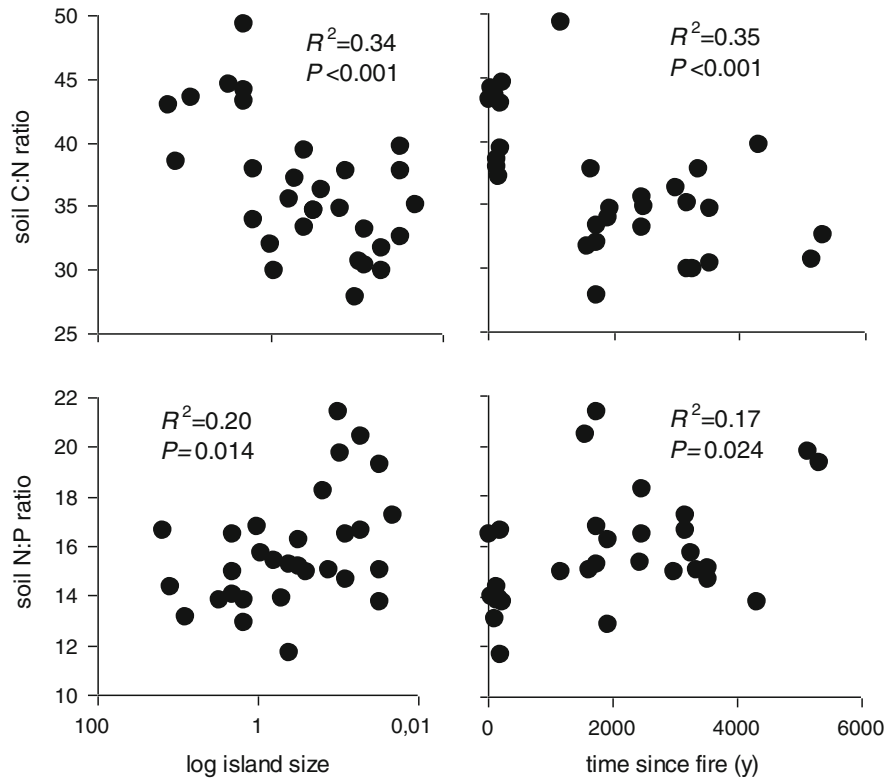

Fig. 6 Relationships between humus C:N, C:P and N:P mass ratios, and island size (an indicator of long term fire history, where fire frequency increases with island size) and time since last fire as determined from C^{14} dating of charcoal (Wardle et al. 2003)

Table 3 Results from stepwise linear regression testing for relationships between microbial or respiration kinetic properties as the dependent variables and soil abiotic properties as the independent variables

	Dependent variable	Independent variable(s)[a]	Adj. R^2	P
Microbial biomass	N	Highly labile P[b] (+)	0.252	0.003
	P	Highly labile P (+)	0.319	0.001
	N: ratio	Soil C:P ratio (+)	0.235	0.005
	C:P ratio	Soil C:P ratio (+)	0.331	0.001
Respiration kinetics	Basal respiration	Highly labile P (+)	0.738	<0.001
	SIR Glu + P[c]	Highly labile P (+)	0.336	<0.001
	SIR Glu + N[c]	Highly labile P (+)	0.412	<0.001
	Maxresp Glu + P[d]	C:P ratio (−)	0.514	<0.001
	Maxresp Glu + N[d]	Highly labile P (+)	0.483	<0.001
	Tmax Glu + N[e]	Highly labile P (−)	0.195	0.008
	Tmax Glu + P[e]	Highly labile P (−)	0.104	0.046

Only independent variables that explained a statistically significant amount of variation for each dependent variable at $P = 0.05$ are presented in the table

[a] Signs (+ and −) indicates a positive or negative relationship between the dependent and the independent variable

[b] Highly labile P = membrane extractable + $NaHCO_3$ extractable P

[c] SIR Glu + P and SIR Glu + N = Substrate induced respiration after addition of glucose (Glu) and either P or N

[d] Maxresp Glu + N and Maxresp Glu + P = Maximum respiration rate after addition of glucose (Glu) and either P or N

[e] Tmax Glu + N and Tmax Glu + P = time from glucose (Glu) and nutrient (either N or P) addition to maximum respiration

geochemical sinks in the humus layer is in accordance with the findings of Wood et al. (1984). Variation in surface sorption across island size classes in contrast is unlikely to be important in explaining these results. In particular, NaOH extractable P_i binds strongly to Al and Fe compounds and high levels of this P form are usually indicative of high surface sorption (Giesler et al. 2004), while for all our samples there was a low amount of NaOH extractable P_i.

The absence of difference between island size classes in the dominating P forms (i.e., residual and NaOH extractable organic P) suggests that there is a rather rapid replacement of P lost through fires. The main source for build-up of organic P in the humus layer is plant litter and this lack of difference suggests that plants, presumably trees, can take up P from the mineral soil to compensate for the lost P. Further, even though the wet-chemical extraction procedures that we used did not reveal significant differences between island size classes, qualitative differences in the organic P fractions may still exist. The lower microbial growth rates on the smaller islands (Fig. 4) may be related to organic P being less available. Demetz and Insam (1999) found that microbial growth rate was related to P availability and we expect that similar effects could be caused by variations in organic P quality. However, 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 the small but still lower labile P concentrations on small islands.

Microbial nutrient limitation

Microbial respiration after nutrient additions did not reveal any evidence of a higher microbial P demand on small islands. The response to addition of P in the presence of excess N and C was not stronger on small islands, as would have been expected if microbes on small islands were relatively more limited by P compared to on larger islands. This was further supported by the microbial biomass N:P ratio. Recent evidence suggests that the N to P ratio of the soil microbial biomass can be used for detecting relative microbial nutrient limitation (Cleveland and Liptzin 2007). All islands had microbial biomass N:P ratios within the range typical of limitation by N rather than by P (Cleveland and Liptzin 2007). In addition, the lack of significant difference in the microbial biomass N:P ratio between island size classes suggests that relative limitation of N and P was the same across island size classes. That N is the main limiting nutrient in the studied system is also supported by the much stronger respiration responses to N additions compared to P additions across all island size classes.

The absence of difference in microbial N:P ratio across island size classes contrasts with what we found for humus N:P ratios, which were higher on small islands. The ratio of N to P in soil has also been widely used to predict nutrient limitation in terrestrial systems (Koerselman and Meuleman 1996; Güsewell 2004; Reich and Oleksyn 2004; Richardson et al. 2004; Wardle et al. 2004a; Coomes et al. 2005; Parfitt et al. 2005), and is known to increase during retrogression in subtropical and temperate chronosequences (Richardson et al. 2004; Wardle et al. 2004a; Coomes et al. 2005). The increase in humus N:P ratio on smaller islands is mainly a result of increasing humus N concentration caused by elevated rates of biological N fixation during retrogression (Lagerström et al. 2007) and reduced rates of N release during decomposition (Wardle et al. 1997). There is an obvious lack of a relationship between the microbial N:P ratios and the humus N:P ratios. Opposite trends in humus N:P ratios and microbially available P has previously been demonstrated in the boreal forest and are best explained in terms of the relative amounts of the different P forms present rather than the humus N:P ratio (Giesler et al. 2004). Despite the obvious lack of difference in major P forms across island size classes, the size of the labile P pool frequently served as the best predictor of a range of microbial respiration parameters, notably basal respiration. This indicates that P availability may still exert some influence on microbial activity in our study system despite it being primarily N limited, and is consistent with the concept of multiple resource limitation of microbially driven processes within ecosystems (Kaspari et al. 2008).

Ecosystem loss of P during absence of fire

The lack of differences in total P concentrations across the island size classes is interesting as there must be large differences in the total P stored in the humus through large islands having much shallower humus than smaller ones (Wardle et al. 2003). If we assume that that the interval between fires on the large islands is around 200 years (Wardle et al. 2003), then the

larger islands have burned about 25 times in the past 5,000 years, compared to none or only a few fires over this period for the small islands. An estimate of total humus P pool for large islands would be 90 kg P ha^{-1} (assuming a bulk density of 100 kg m^{-3}, a total P content of 0.087% and an average humus thickness of 0.1 m). Given the deeper humus on the small islands, and assuming that P concentrations do not differ greatly with depth, the total humus P pool for the small islands would be in the order of 600 kg P ha^{-1} (assuming a bulk density of 100 kg m^{-3}, a total P content of 0.091% and an average humus thickness of 0.65 m). This suggests that the amount of ecosystem loss of P due to wildfire on the large islands over the past 5,000 years could be as high as 500 kg ha^{-1}. Large losses of P from the ecosystem would result in P depletion, and eventually in a reduction of P concentration in the humus layer over the long term. However, soils in the boreal zone, including in our study system, are relatively young from a global perspective (less than 10,000 years since the retreat of the last glacial ice). Therefore there may have been insufficient time for P losses caused by regular burning to result in reduced P concentration or greatly altered composition of P forms in the humus.

Replenishment of P from parent material to compensate for losses due to fire on the large islands must contribute to delaying P depletion in the humus layer over this timeframe. This is interesting since it implies that plants (presumably trees) will over time shift their utilization of P in the mineral soil to less available P forms or to deeper soil layers in order to replenish P in the humus layer. This is enforced by a rapid depletion of primary mineral P in the mineral surface soil (see Hoffland et al. 2002), and podzol formation increasing the geochemical sinks for P (Starr 1991; Hoffland et al. 2002). These processes are relatively rapid and occur within a time frame of <2,000 years (B horizon formation within 500 years). During the last few centuries fire regimes in the Swedish boreal zone have changed with wild fires being less frequent (Niklasson and Granström 2000). Today, nutrient losses (including P) in the boreal zone are instead governed mainly by forest harvesting. These nutrient losses have been suggested to potentially cause a P limitation in Swedish boreal forests, though assuming that root uptake is limited to the upper 0.5 m including the humus layer (Akselsson et al. 2008). Our study shows that such assumptions may be too simplified and that there is a large capacity to replenish even relatively large losses over time. The absence of difference in total P concentration between the different island classes also suggests continuous replenishment of P via plant uptake on the small islands. On those islands, trees with deeper roots may still be able to obtain P from the underlying mineral soil and parent material, and input P to the upper parts of the humus layer via litter-fall.

Conclusions

This is, to our knowledge, the first study that has explored the long-term effect of different wildfire regimes on soil P concentration and availability in the boreal forest. Our results suggests that within the studied time frame (5,000 years), retrogression in these boreal forest sites is primarily driven by biological processes rather than P-limitation induced by geochemical processes. Ecosystem losses of P due to wildfire, such as occurs on the large islands, can be replenished in the humus layer in the boreal forests without any dramatic changes in P forms or total P concentrations, at least in the first few 1,000 years following soil formation. This is in accordance with the general assumption that phosphorus is unimportant in boreal ecosystems because of the strong domination of N limitation in the boreal zone (Rees et al. 2001; Chapin et al. 2002). However, though we do not find strong evidence of microbial P limitation, either for regularly burnt large islands or for small islands that have undergone retrogression, this study has nevertheless observed some trends towards decreased P availability during retrogression. While the effect of P availability on microbial activity during retrogression is likely to be weaker than that of declining N availability, our study has showed that it can nevertheless contribute to the impairment of microbial activity during retrogression, and therefore presumably microbially driven processes such as decomposition and mineralization. This may in turn feed back to the plant community (Wardle et al. 2004b) and contribute to the reduction in plant productivity characteristic of ecosystems that have undergone retrogression (Walker et al. 2001, 2004a; Walker and Reddell 2007).

Acknowledgments This study was part of the PhD thesis research of both C. Esberg and A. Lagerström. The authors thank Thomas Westin for laboratory assistance. We are grateful to Michael Gundale and Ulrik Ilstedt for providing helpful comments on earlier versions of the article. This work was supported by a grant from FORMAS to D. A. Wardle.

References

Akselsson C, Westling O, Alveteg M, Thelin G, Fransson AM, Hellsten S (2008) The influence of N load and harvest intensity on the risk of P limitation in Swedish forest soils. Sci Total Environ 404:284–289. doi:10.1016/j.scitotenv.2007.11.017

Allison VJ, Condron LM, Peltzer DA, Richardson SJ, Turner BL (2007) Changes in enzyme activities and soil microbial community composition along carbon and nutrient gradients along the Franz Josef chronosequence, New Zealand. Soil Biol Biochem 39:1770–1781. doi:10.1016/j.soilbio.2007.02.006

Anderson JPE, Domsch KHA (1978) A physiological method for the quantitative measurement of microbial biomass in soils. Soil Biol Biochem 10:215–221. doi:10.1016/0038-0717(78)90099-8

Attiwill PM, Adams MA (1993) Nutrient cycling in forests. New Phytol 124:561–582. doi:10.1111/j.1469-8137.1993.tb03847.x

Bayley SE, Schindler DW, Beaty KG, Parker BR, Stainton MP (1992) Effects of multiple fires on nutrient yields from streams draining boreal forest and fen watersheds—nitrogen and phosphorus. Can J Fish Aquat Sci 49:584–596. doi:10.1139/f92-068

Binkley D, Giardina C, Bashkin MA (2000) Soil phosphorus pools and supply under the influence of Eucaluptus saligna and nitrogen-fixing *Albizia facaltaria*. For Ecol Manage 128:241–247. doi:10.1016/S0378-1127(99)00138-3

Brookes PC, Powlson DS, Jenkinson DS (1982) Measurement of microbial biomass phosphorus in soil. Soil Biol Biochem 14:319–329. doi:10.1016/0038-0717(82)90001-3

Burke JM, Prepas EE, Pinder S (2005) Runoff and phosphorus export patterns in large forested watersheds on the western Canadian Boreal Plain before and for 4 years after wildfire. J Environ Eng Sci 4:319–325. doi:10.1139/s04-072

Chapin FS, Matson PA, Mooney HA (2002) Principles of terrestrial ecosystem ecology. Springer, New York

Cleveland CC, Liptzin D (2007) C:N:P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? Biogeochem 85:235–252. doi:10.1007/s10533-007-9132-0

Coomes DA, Allen RB, Bentley WA, Burrows LE, Canham CD, Fagan L, Forsyth DM, Gaxiola-Alcantar A, Parfitt RL, Ruscoe WA, Wardle DA, Wilson DJ, Wrights EF (2005) The hare, the tortoise and the crocodile: the ecology of angiosperm dominance, conifer persistence and fern filtering. J Ecol 93:918–935. doi:10.1111/j.1365-2745.2005.01012.x

Crews TE, Kityama K, Fownes JH, Riley RH, Herbert DA, Mueller-Dombois D, Vitousek PM (1995) Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. Ecology 76:1407–1424. doi:10.2307/1938144

Crews TE, Farrington H, Vitousek PM (2000) Changes in asymbiotic, heterotrophic nitrogen fixation on leaf litter of *Meterosideros polymorpha* with long-term ecosystem development in Hawaii. Ecosyst 3:386–395. doi:10.1007/s100210000034

Cross AF, Schlesinger WH (1995) A literature-review and evaluation of the Hedley fractionation-applications to the biogeochemical cycle of soil-phosphorus in natural ecosystems. Geoderma 64:197–214. doi:10.1016/0016-7061(94)00023-4

Daly BK, Wainiqolo JL (1993) Methods of analysis for agricultural samples: soil, plant, animal feed and water. Fiji Agricultural Chemistry Laboratory Tech Report 03/93:115

Demetz M, Insam H (1999) Phosphorus availability in a forest soil determined with a respiratory assay compared to chemical methods. Geoderma 89:259–271. doi:10.1016/S0016-7061(98)00090-1

Ekblad A, Nordgren A (2002) Is growth of soil microorganisms in boreal forests limited by carbon or nitrogen availability? Plant Soil 242:115–122. doi:10.1023/A:1019698108838

Fang CM, Moncrieff JB (2005) The variation of soil microbial respiration with depth in relation to soil carbon composition. Plant Soil 268:243–253. doi:10.1007/s11104-004-0278-4

Freese D, Vanderzee SEATM, Vanriemsdijk WH (1992) Comparison of different models for phosphate sorption as a function of the iron and aluminium-oxides of soils. J Soil Sci 43:729–738. doi:10.1111/j.1365-2389.1992.tb00172.x

Giesler R, Satoh F, Ilstedt U, Nordgren A (2004) Microbially available phosphorus in boreal forests: effects of aluminium and iron in the humus layer. Ecosyst 7:208–217

Gnankambary Z, Ilstedt U, Nyberg G, Hien V, Malmer A (2007) Nitrogen and phosphorus limitation of soil microbial respiration in two tropical agroforestry parklands in the south-Sudanese zone of Burkina Faso: the effects of tree canopy and fertilization. Soil Biol Biochem 40:350–359. doi:10.1016/j.soilbio.2007.08.015

Güsewell S (2004) N:P ratios in terrestrial plants: variation and functional significance. New Phytol 164:243–266. doi:10.1111/j.1469-8137.2004.01192.x

Hedley MJ, Stewart JWB (1982) Method to measure microbial phosphate in soils. Soil Biol Biochem 14:377–385. doi:10.1016/0038-0717(82)90009-8

Hedley MJ, Stewart JWB, Chauhan BS (1982) Changes in inorganic and organic phosphorus fractions induced by cultivation practices and by laboratory incubation. Soil Sci Soc Am J 46:970–976

Hoffland E, Giesler R, Jongmans T, van Breemen N (2002) Increasing feldspar tunnelling by fungi across a north Sweden podzol chronosequence. Ecosyst 5:11.22

Ilstedt U, Singh S (2005) Nitrogen and phosphorus limitations of microbial respiration in a tropical phosphorus-fixing acrisol (ultisol) compared with organic compost. Soil Biol Biochem 37:1407–1410. doi:10.1016/j.soilbio.2005.01.002

Ilstedt U, Nordgren A, Malmer A (2000) Optimum soil water for soil respiration before and after amendment with

glucose in humid tropical acrisols and a boreal mor layer. Soil Biol Biochem 32:1591–1599. doi:10.1016/S0038-0717(00)00073-0

Ilstedt U, Giesler R, Nordgren A, Malmer A (2003) Changes in soil chemical and microbial properties after a wildfire in a tropical rainforest in Sabah, Malaysia. Soil Biol Biochem 35:1071–1078. doi:10.1016/S0038-0717(03)00152-4

Jenkinson DS (1988) Determination of microbial biomass carbon and nitrogen in soil. In: Wilson JR (ed) Advances in nitrogen cycling in agricultural ecosystems. CAB International, Wallingford, pp 368–386

Kaspari M, Garcia MN, Harms KE, Santana M, Wright SJ, Yavitt JB (2008) Multiple nutrients limit litterfall and decomposition in a tropical forest. Ecol Lett 11:35–43

Koerselman W, Meuleman AFM (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. J Appl Ecol 33:1441–1450. doi:10.2307/2404783

Lagerström A, Nilsson M-C, Zackrisson O, Wardle DA (2007) Ecosystem input of nitrogen through biological fixation in feather mosses during ecosystem retrogression. Funct Ecol 21:1027–1033. doi:10.1111/j.1365-2435.2007.01331.x

Lecomte N, Simard M, Fenton N, Bergeron Y (2006) Fire severity and long-term ecosystem biomass dynamics in coniferous boreal forests of eastern Canada. Ecosyst 9:1215–1230. doi:10.1007/s10021-004-0168-x

McColl JG, Grigal DF (1975) Forest fire—effects on phosphorus movement to lakes. Science 188:1109–1111. doi:10.1126/science.188.4193.1109

Neff JC, Harden JW, Gleixner G (2005) Fire effects on soil organic matter content, composition, and nutrients in boreal interior Alaska. Can J For Res 35:2178–2187. doi:10.1139/x05-154

Niklasson M, Granström A (2000) Numbers and sized of fires: long-term spatially explicit fire history in a Swedish boreal landscape. Ecology 81:1484–1499

Nordgren A (1988) Apparatus for the continuous, long-term monitoring of soil respiration rate in large numbers of samples. Soil Biol Biochem 20:955–957. doi:10.1016/0038-0717(88)90110-1

Nordgren A (1992) A method for determining microbially available N and P in an organic soil. Biol Fertil Soils 13:195–199. doi:10.1007/BF00340575

Parfitt RL, Ross DJ, Coomes DA, Richardson SJ, Smale MC, Dahlgren RA (2005) N and P in New Zealand chronosequences and Relationships with foliar N and P. Biogeochem 75:305–328. doi:10.1007/s10533-004-7790-8

Prepas EE, Burke JM, Chanasyk DS, Smith DW, Putz G, Gabos S, Chen W, Millions D, Serediak M (2003) Impact of wildfire on discharge and phosphorus export from the Sakwatamau watershed in the Swan Hills, Alberta, during the first two years. J Environ Eng Sci 2:63–72. doi:10.1139/s03-036

Rees M, Condit R, Crawley M, Pacala S, Tilman D (2001) Long-term studies of vegetation dynamics. Science 293:650–655. doi:10.1126/science.1062586

Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. Proc Natl Acad Sci USA 101:11001–11006. doi:10.1073/pnas.0403588101

Richardson SJ, Pelzer DA, Allen RB, McGlone MS, Parfitt RL (2004) Rapid development of phosphorus limitation in temperate rainforest along the Franz Josef soil chronosequence. Oecologia 139:267–276. doi:10.1007/s00442-004-1501-y

Ross DJ (1992) Influence of sieve mesh size on estimates of microbial carbon and nitrogen by fumigation-extraction procedures in soils under pasture. Soil Biol Biochem 24:343–350. doi:10.1016/0038-0717(92)90194-3

Saggar S, Hedley MJ, White RE (1990) A simplified resin membrane technique for extracting phosphorus from soils. Fert Res 24:173–180. doi:10.1007/BF01073586

Sparling GP (1994) Manual of methods to estimate soil microbial biomass and activity. Internal report for The Grains Research and Development Corporation, Western Australia

Spencer CN, Hauer FR (1991) Phosphorus and nitrogen dynamics in streams during a wildfire. J N Am Benthol Soc 10:24–30. doi:10.2307/1467761

Starr MR (1991) Soil formation and fertility along a 5,000 years chronosequence. In: Pulkkinen E (ed) Environmental geochemistry in northern Europe. Geological Survey of Finland, Special Paper 9, pp 99–104

Turner BL, Condron LM, Richardson SJ, Peltzer DA, Allison VJ (2007) Soil organic phosphorus transformations during pedogenesis. Ecosyst 10:1166–1181. doi:10.1007/s10021-007-9086-z

Vance ED, Brookes PC, Jenkinson DS (1987) An extraction method for measuring soil microbial biomass C. Soil Biol Biochem 19:703–707. doi:10.1016/0038-0717(87)90052-6

Vesterdal L (1998) Potential microbial nitrogen and phosphorus availability in forest floors. Soil Biol Biochem 30:2031–2041. doi:10.1016/S0038-0717(98)00078-9

Vitousek PM (2002) Nutrient cycling and limitation. Hawaii as a model system. Princeton University Press, Princeton

Vitousek PM, Farrington H (1997) Nutrient limitation and soil development: experimental test of a biogeochemical theory. Biogeochem 37:63–75. doi:10.1023/A:1005757218475

Walker LR, del Moral R (2003) Primary succession and ecosystem rehabilitation. Cambridge University Press, Cambridge

Walker J, Reddell P (2007) Retrogressive succession and the restoration of old landscapes. In: Walker LR, Walker J, Hobbs RJ (eds) Linking restoration and ecosystem retrogression. Springer, New York, pp 69–89

Walker TW, Syers JK (1976) The fate of phosphorus during pedogenesis. Geoderma 15:1–19. doi:10.1016/0016-7061(76)90066-5

Walker J, Thompson CH, Jehne W (1983) Soil weathering stage, vegetation succession and canopy dieback. Pac Sci 37:471–481

Walker J, Thompson CH, Reddel P, Rapport DJ (2001) The importance of landscape age in influencing landscape health. Ecosyst Health 7:7–14. doi:10.1046/j.1526-0992.2001.007001007.x

Wardle DA, Zackrisson O (2005) Effects of species and functional group loss on island ecosystem properties. Nature 435:806–810. doi:10.1038/nature03611

Wardle DA, Zackrisson O, Hörnberg G, Gallet C (1997) The influence of island area on ecosystem properties. Science 277:1296–1299. doi:10.1126/science.277.5330.1296

Wardle DA, Hörnberg G, Zackrisson O, Kalela-Brundin M, Coomes DA (2003) Long-term effects of wildfire on

ecosystem properties across an island area gradient. Science 300:972–975. doi:10.1126/science.1082709

Wardle DA, Walker LR, Bardgett DR (2004a) Ecosystem properties and forest decline in contrasting long-term chronosequences. Science 305:509–513. doi:10.1126/science.1098778

Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH, Wall DH (2004b) Ecological linkages between aboveground and belowground biota. Science 304:1629–1633. doi:10.1126/science.1094875

Williamson WM, Wardle DA, Yeates GW (2005) Changes in soil microbial nematode communities during ecosystem decline across a long-term chronosequence. Soil Biol Biochem 37:1289–1301. doi:10.1016/j.soilbio.2004.11.025

Wood T, Bormann FH, Voigt GK (1984) Phosphorus cycling in a northern hardwood forest–biological and chemical control. Science 223:391–393. doi:10.1126/science.223.4634.391

Zackrisson O (1977) Influence of forest fires on the North Swedish boreal forest. Oikos 29:22–32. doi:10.2307/3543289