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Phosphorus status of soils from contrasting forested ecosystems in southwestern Siberia: effects of microbiological and physicochemical properties

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Abstract. The Siberian forest is a tremendous repository of terrestrial organic carbon (C), which may increase owing to climate change, potential increases in ecosystem productivity and hence C sequestration. Phosphorus (P) availability could limit the C sequestration potential, but tree roots may mine the soil deep to increase access to mineral P. Improved understanding and quantification of the processes controlling P availability in surface and deep soil layers of Siberian forest ecosystems are thus required. The objectives of the present study were to (1) evaluate P status of surface and deep soil horizons from different forest plots in southwestern Siberia and (2) assess the effects of physicochemical soil properties, microbiological activity and decomposition processes on soil P fractions and availability. Results revealed high concentrations of total P (879–1042 mg kg^{-1} in the surface mineral soils) and plant-available phosphate ions. In addition, plant-available phosphate ions accumulated in the subsoil, suggesting that deeper root systems may mine sufficient available P for the trees and the potentially enhanced growth and C sequestration, may not be P-limited. Because the proportions of total organic P were large in the surface soil layers (47–56 % of total P), we concluded that decomposition processes may play a significant role in P availability. However, microbiological activity and decomposition processes varied between the study plots and higher microbiological activity resulted in smaller organic P fractions and consequently larger available inorganic P fractions. In the studied Siberian soils, P availability was also controlled by the physicochemical soil properties, namely Al and Fe oxides and soil pH.

1 Introduction

Terrestrial ecosystems, particularly forests, are expected to sequester a part of the increased atmospheric carbon (C) originating from anthropogenic activities (Norby et al., 2005). However, the extent to which this happens may depend on local site conditions such as soil fertility, moisture and temperature (Loustau et al., 2005; de Graaff et al., 2006; Dijkstra and Cheng, 2008). For rising levels of carbon dioxide (CO_2) in the atmosphere, low nitrogen (N) availability has been shown to limit the C sequestration potential of vegetation (Oren et al., 2001; Reich et al., 2006). Phosphorus (P) was not studied in this scope but is likely to be also a major obstacle to an enhanced C sequestration, because P is often a limiting or co-limiting factor of ecosystem productivity (Elser et al., 2007; Harpole et al., 2011) and low P availability can constrain N_2 fixation (Wang et al., 2007; Vitousek et al., 2010). Moreover, anthropogenic activity could result in a shift from an N limitation to a P limitation, owing to chronic

atmospheric deposition of N compounds, even at long distances from emitting sources (Elser, 2011; Hietz et al., 2011; Holtgrieve et al., 2011). In forest ecosystems, P-fertilization is rarely used (Trichet et al., 2009) and is not likely to become a common practice, because there is increasing concern regarding appropriate management of P resources, since existing P reserves are finite and are rapidly being depleted (Gilbert, 2009). However, increases in atmospheric CO_2 and forest productivity were found to enhance C allocation to roots in deep soil layers (Thomas et al., 1999; Iversen, 2010). Therefore, in response to P scarcity, trees may mine the soil deeper to take up more nutrients. Improving our understanding and quantification of the processes controlling P availability in surface and deep soil layers of forest ecosystems is thus required.

The Russian boreal forest is the largest continuous forest region on Earth (809×10^6 ha) and represents approximately 20 % of the world's forests and 70 % of the world's boreal forests (FAO, 2006; Chytry et al., 2008; http://www.terrestrial-biozones.net/index.html). Consequently, the Russian forest is a tremendous repository of terrestrial organic C (14 % of total C stock in world's forest biomass; 30 % including C stocks in soils; FAO, 2006; Shuman et al., 2011). These C stocks may increase owing to the potential increase in plant biomass and productivity during the next century (MEA, 2005; Luo et al., 2006; IPCC, 2007).

Organic P fractions can represent high proportions of total P in ecosystems with permanent vegetation, such as forests (e.g. Cross and Schlesinger, 1995; Johnson et al., 2003; Achat et al., 2009). Mineralization of non-microbial organic P and remineralization of microbial P (Achat et al., 2010; Richardson and Simpson, 2011; Bünemann et al., 2012) are assumed to play a significant role in P availability in these ecosystems (Walbridge et al., 1991; Attiwill and Adams, 1993). However, decomposition processes generally depend on microbiological activity as well as organic matter quality (Ushio et al., 2010; Voriskova et al., 2011). Organic matter quality has been linked to the lignin and nutrient concentrations in the forest floor and the lignin/N, C/N and C/P ratios (Hättenschwiler and Gasser, 2005; Berg et al., 2010; Blanco et al., 2011). P availability is further controlled by physico-chemical processes (e.g. diffusion of phosphate ions at the solid-to-solution interface; Morel et al., 2000; Achat et al., 2009), which depend on the reactive surface of soils, such as Al and Fe oxides in acidic forest soils (Walbridge et al., 1991; Achat et al., 2011).

The objectives of the present study were to (1) evaluate P status (total P, relative contributions of total organic and total inorganic P, plant-available inorganic P : phosphate ions in soil solution and diffusive phosphate ions) of surface and deep forest soil horizons from contrasting sites in southwestern Siberia and (2) assess the effects of the main physico-chemical soil properties (e.g. Al and Fe oxides, pH), microbial (microbial biomass, soil respiration) and enzymatic ac-

tivities, organic matter quality and decomposition processes on soil P fractions and availability.

2 Material and methods

2.1 Study sites and soils

The low Salair mountains (400–500 m a.s.l.), with blackish (*chernevaya* in Russian) taiga as vegetation, are formed by the northwest extreme branch of the Altai–Sayan mountain system and are situated in the southwest of Siberia. This mountainous chain is bordered by the forest steppes of the West Siberian Plain (Chytry et al., 2008; http://www.terrestrial-biozones.net/index.html).

Due to its location in the centre of Eurasia, the macroclimate of the study area is continental, with long cold winters and short warm summers. Local climate, however, is modified by the mountainous topography. In the low Salair mountains, average annual precipitation reaches 700–1000 mm and air temperatures are on average –20.6 °C in January and +19 °C in July, with a mean annual temperature of –1.1 °C. The soil remains unfrozen during all the winter period due to insulating effect of a permanent snow cover, which reaches 100–250 cm depth during 160–180 days. For the forest steppe zone, average annual precipitation is only 450 mm and average temperatures are –18.5 °C in January and +18.9 °C in July, with an annual temperature of +0.1 °C. A permanent snow cover reaches 80–120 cm depth and remains 160 days on average. In contrast with the low Salair mountains, soils in the forest steppe zone are frozen in winter down to 60–80 cm.

We studied three adjacent plots located in the low Salair mountains (plot 1 with a deciduous broadleaved species dominating the canopy (*Populus tremula*); plot 2 with an evergreen needle-leaved species dominating the canopy (*Abies sibirica*); plot 3 in a forest gap with only forbs and grasses, mainly *Aconitum septentrionale, Heracleum dissectum, Calamagrostis langsdorffii*), in the Kemerovo region, at 54°10′(38–41″) N latitude, 85°10′(24–31″)E longitude, and at an altitude of 450 m a.s.l. The last plot (plot 4 with *P. tremula* dominating the canopy) was located in the forest steppe zone, in the Novosibirsk region, near Chebula village, at 55°33′31″ N latitude, 84°00′24″ E longitude and at an altitude of 204 m a.s.l. All studied stands with *P. tremula* and *A. sibirica* were mature and displayed closed canopies, thus limiting any effects due to differences of forest development and stand age on soil properties and distribution of soil P in the different organic and inorganic fractions (De Schrijver et al., 2012). All stands displayed similar ages (45–60 years) and densities (150–230 tree ha^{-1}). For the Salair mountain site and the forest steppe site, respectively, tree height was 22–26 and 16–18 m, stand basal area 3.5–5.5 and 2.4 m^2 ha^{-1} and mean tree diameter at breast height 18–20 and 14–15 cm.

Soils of plots 1 to 3 are Orthieutric Albeluvisols (WRB, 2006), also known as soddy deeply podzolic soils in the Russian soil classification, whereas Albic Luvisols (grey forest soils) characterize plot 4. Beneath the forest floors (F), soil profiles are differentiated between humus accumulation, eluvial and illuvial soil horizons (A + AE, E, EBt and Bt in plots 1 to 3; A, AE and Bt in plot 4). All soils have been developed from loess deposits (Chlachula, 2011) and have comparable particle size distribution (1–7 % sand, 73–84 % silt, 13–21 % clay).

2.2 Description of soil profiles, soil sampling and soil preparation

Soil description and soil sampling were carried out in June and July 2010. Plots with undisturbed and homogeneous vegetation and three zones per plot were used in this study. Each plot was approximately $1000\,m^2$, and the distance between two zones in a given plot was $\approx 20\,m$. In each zone, the forest floor was sampled on a surface of $1\,m^2$ and a soil pit of approximately 100 cm wide and 110 cm deep was dug. On one vertical side of each soil pit, the different soil horizons were identified and their thicknesses were measured (five measures per soil horizon and per pit). Prior to the description of the soil profile, the soil surface in the vertical plane had been cut back with a spade and flattened so as to reach clean observation surfaces. After the description of the soil profiles, two series of soil sampling were carried out. A first soil sampling was carried out in each soil horizon of each soil profile by inserting small metal cores of $96.2\,cm^3$ horizontally into the vertical plane to assess the soil bulk density (three sub-replicates or zones per plot and per soil horizon). A second soil sampling was carried out for further soil analyses by taking samples from the whole soil horizons. Subsamples of forest floors and subsamples of the surface mineral soils (A + AE or A horizon) were kept moist and stored at 2 °C before the incubation experiment and the quantification of soil respiration, microbial biomass C, N and P and acid phosphomonoesterase activity. Other subsamples of forest floors and surface mineral soils and all other mineral soils were dried (60 °C for the forest floors, air-dried for the mineral soils) before the quantification of physicochemical soil properties and P status (total P, total organic P, total inorganic P, diffusive phosphate ions and phosphate ions in soil solution). All analyses on dried mineral soils were carried out on each individual soil replicate (three replicates per plot and per soil horizon). For moist samples (forest floors, A + AE or A horizon) or dried forest floors, samples were mixed to obtain one composite sample for each plot and analyses were carried out on 3–5 aliquots to compare composite samples in a given soil layer.

2.3 Main physicochemical soil properties

Total C and N concentrations in forest floor and mineral soil samples were determined by flash combustion at 900–1000 °C with oxygen using a FlashEA 1112 NC Analyzer. Poorly crystalline Al and Fe oxides were extracted with an ammonium oxalate solution (McKeague and Day, 1966). We measured pH-H_2O with a Mettler Delta 340 pH-meter (20g : 50 mL). Concentrations of K, Ca, Mg, Mn and lignin were also determined in the forest floor samples. Aliquots of forest floor were reduced to ashes at 550 °C for 5 h, and the resulting ashes were dissolved in 5 mL HNO_3 solution and placed on a hotplate to evaporate. After mineralization, solutions were analysed for their K concentration by flame emission spectrometry and for their Ca, Mg and Mn concentrations by atomic absorption spectrometry (Varian SpectraAA300). Klason lignin was determined as the insoluble fraction persisting after acid hydrolysis of the residue remaining after extraction with acetone (Vazquez et al., 1995).

2.4 Microbiological soil properties and net C mineralization

Microbial C and N were determined by comparing fumigated and non-fumigated soil samples in the amount of total C and N extracted with $0.5\,M\,K_2SO_4$ (Brookes et al., 1985; Vance et al., 1987). Total C and N in K_2SO_4 extracts were determined using a combustion TOC/TN Shimadzu analyzer. Acid phosphomonoesterase activity was evaluated following the procedure of Alef et al. (1995).

Water-holding capacity was measured in the laboratory as the water content of the soil after saturation followed by 48 h of free drainage. Then, soil respiration (i.e. net C mineralization) was quantified during long-term incubation experiments (126 days for the surface mineral soils and 188 days for the forest floors). Moist fresh composite samples were retrieved from the storage room (2 °C), brought to 70 % of water holding capacity (0.33–0.38 mL g^{-1} of mineral soil; 1.51–1.97 mL g^{-1} of forest floor; oven-dry soil basis) and incubated at 20 °C. Moist soils equivalent to 50 g of dry soil for the mineral soils and 5 g of dry forest floors (4 replicates for each composite soil sample) were put into tightly closed 750 mL glass pots for the quantification of soil respiration (CO_2 released). Within each 750-mL pot, we introduced a vial containing sodium hydroxide (0.5 M or 1 M NaOH) and a vial with 5 mL water to balance NaOH-related dehydration. The amount of CO_2 released from the soils and absorbed by the NaOH was quantified by a back titration method (Alef, 1995). Respiration measurements were carried out on days 1, 2, 5, 7, 9, and 13, and then done less frequently (every six to 19 days). Soil moisture was controlled and adjusted after 85 days (mean amount of added water = 0.02 mL g^{-1} for mineral soils and 0.24 mL g^{-1} for forest floors) and 126 days (mean of 0.04 mL g^{-1} for forest floors).

The cumulative net C mineralization (in $\mu g\,C\,g^{-1}$ soil) was described using a two-pool model, in which a readily available organic pool was assumed to mineralize according to first-order kinetics, and a recalcitrant organic pool according to zero-order kinetics (Eq. (1); Li et al., 2003).

$$\text{Cumulative net C mineralization} = \qquad (1)$$
$$\text{AO} \times \left(1 - e^{-k_{AO} \times \text{time}}\right) + k_{RO} \times \text{time}$$

where AO (in $\mu g\,C\,g^{-1}$ soil) and k_{AO} represent the pool size and the first-order rate of mineralization of the readily available organic pool, respectively, and k_{RO} (in $\mu g\,C\,g^{-1}\,\text{soil day}^{-1}$) is the rate of mineralization of the recalcitrant organic pool.

2.5 Soil P status

2.5.1 Total, total organic, total inorganic and microbial P

Total P concentration (in $\mu g\,g^{-1}$) of soil samples was determined by wet digestion with concentrated fluoric (HF) and perchloric acids after calcination at $450\,^{\circ}C$ based on a normalized procedure (NF X 31-147; AFNOR, 1999). Compared to other extractants (e.g. sulphuric acid [H_2SO_4]), HF was found to be more appropriate for the extraction of total P after calcinations (Achat et al., 2009). It was also the case for the study mineral soils and forest floors since P extracted with P-H_2SO_4 was lower than total P extracted with HF (total P-HF = $1.00 \times$ P-H_2SO_4 + 163.98; $r^2 = 0.99$; $P < 0.0001$; $n_{obs} = 54$). Total soil organic P concentration was determined using the procedure of Saunders and Williams (1955), which estimates it as the difference between ignited and non-ignited soil samples in H_2SO_4-extracted P (2 g of dry soil for 70 mL of 0.2 N H_2SO_4; 16 h of extraction). Total inorganic P concentration was subsequently calculated as total P-HF minus total organic P. Microbial P concentration was quantified in moist soils using a fumigation–sorption–extraction method (Morel et al., 1996), which accounts for the rapid sorption reactions of phosphate ions that occur during the chloroform fumigation (1 h 30 min) and water extraction procedure (24 h; soil-to-solution ratio of 1 g : 10 mL for the mineral soils and 1 g : 20 mL for the forest floors).

2.5.2 Plant-available phosphate ions

In this study, we quantified the phosphate ions in soil solution (C_P in $\mu g\,mL^{-1}$ or Pw in $\mu g\,g^{-1}$ soil) and the diffusive phosphate ions at the solid-to-solution interface, resulting from molecular agitation (Pr in $\mu g\,g^{-1}$; physicochemical process). The diffusion leads to a transfer of phosphate ions from the solid constituents to the soil solution under a gradient of concentration (Jungk and Claassen, 1997). The Pr values were determined as a function of time using an isotopic labelling and dilution procedure during batch experiments with soil suspensions at steady state (e.g. constant C_P values;

Fardeau, 1996; Frossard and Sinaj, 1997; Morel, 2007). As previously demonstrated (e.g. Morel and Plenchette, 1994; Fardeau, 1996), C_P and Pr values as evaluated with the isotopic dilution method correspond to the gross amounts of plant-available phosphate ions. Phosphate ions in soil solution are readily plant-available phosphate ions, while Pr depends on time. The Pr values can therefore be subdivided into different pools in relation to the functioning of roots and root systems and P-uptake periods (e.g. an annual vegetation uptake; Fardeau, 1993; Chen et al., 2003).

For each of the mineral soil and forest floor samples, 4–5 soil suspensions (1 g : 10 mL distilled water for the mineral soils; 1 g : 20 mL distilled water for the forest floors) were prepared. A biocide (0.1 mL of toluene) was added to avoid microbial activity. Then, soil suspensions were equilibrated for 16 h on a roller (40 cycles min^{-1}) at $20\,^{\circ}C$. The phosphate ions in soil solution of the pre-equilibrated soil suspensions were isotopically labelled by introducing a known amount of carrier-free ^{32}P as phosphate ions (R) into the solution. Soil suspensions were then sampled with a plastic syringe after 4, 40, 100 and 400 min (and 10 min for only a few soil samples) and filtered through 0.2-μm membrane filters (one replicate for each isotopic dilution period). The filtered solution was used to determine the radioactivity remaining in the soil solution (r) and C_P values for a given time of isotopic dilution. The radioactivity r was counted in a counter (Packard TR 1100) using a liquid scintillation cocktail. C_P was determined using a malachite green colorimetric method (van Veldhoven and Mannaerts, 1987), and P_W was calculated using the volume of water (V in mL) and the mass of soil (M in g):

$$P_W = C_P \times \frac{V}{M}. \qquad (2)$$

During the 400-min period of isotopic dilution with pre-equilibrated soil suspensions, C_P was constant (see examples in Appendix A1a). In such a steady state, the gross transfer of phosphate ions from the soil solid constituents to the soil solution is equal to the gross transfer of phosphate ions onto the solid constituents. We further assumed that no isotopic discrimination occurs between the two P isotopes ($^{31}PO_4$ and $^{32}PO_4$) during the transfers between the solution and the solid constituents. The amount of unlabelled phosphate ions newly transferred from the solid constituents to the solution (i.e. Pr) was thus calculated from P_W and r values, using the principle of isotopic dilution and the isotopic composition ratio:

$$\text{Isotopic composition ratio} = \frac{r}{P_W} = \frac{R-r}{Pr}. \qquad (3)$$

Rearranging Eq. (3) gives

$$Pr = \frac{P_W \times (R-r)}{r} = P_W \left(\frac{1}{r/R} - 1\right) \qquad (4)$$

where r/R (dimensionless) is the isotopic dilution ratio.

The theoretical Eq. (5) adapted by Fardeau (1993, 1996) was used to closely fit the experimental values of r/R as a function of time (see examples in Appendix A1b).

$$r/R = r/R_{1\,\text{min}} \times \left(\text{time}^{-n}\right) \text{ for } r/R \geq r_\infty/R \qquad (5)$$

where r_∞/R (dimensionless) corresponds to the maximum possible dilution of the isotope considering that all inorganic P can take part in the isotopic dilution. The value of r_∞/R can be calculated as the ratio of P_W to total inorganic P (Fardeau, 1993). The $r/R_{1\,\text{min}}$ and n parameters (dimensionless) account for the immediate and the slow physicochemical reactions, respectively (see examples in Appendix A1b). Parameter $r/R_{1\,\text{min}}$ describes the rate of disappearance of the tracer from the solution after 1 min (Frossard and Sinaj, 1997). The parameter n theoretically ranges from 0 to 0.5 (Fardeau, 1993). When n is zero, there is no time dependence of diffusion at the solid-to-solution interface, whereas, when 0.5 is reached, diffusion is at its theoretical maximum. These parameters enable evaluation of phosphate mobility in the soil–water system or phosphate reactivity with the solid constituents: reactivity increases with increasing values of parameter n and/or decreasing values of parameter $r/R_{1\,\text{min}}$ (Frossard et al., 1989).

For a given soil sample, measured values of Pr were described by the kinetic Eq. (6) (Morel et al., 2000) for Pr values inferior to total inorganic P minus P_W, considering that all inorganic P can take part in the isotopic dilution (see examples in Appendix A1c):

$$P_r = \text{Pr}_{1\,\text{min}} \times \text{time}^P \qquad (6)$$

where parameter $\text{Pr}_{1\,\text{min}}$ is the concentration of diffusive phosphates ions after 1 min of isotopic dilution and parameter p accounts for the time dependence. Following previous studies (Fardeau, 1993; Chen et al., 2003), these parameters were used to extrapolate Pr to more relevant time spans (up to one year in the present study, i.e. an annual vegetation uptake).

Values of C_P, isotopic dilution parameters and Pr varied between soils (see examples in Appendix A1). We thus tested whether differences between soil samples in C_P and Pr values resulted from different physicochemical soil properties and therefore different dynamics of the phosphate ions at the solid-to-solution interface (e.g. Pr increases and C_P decreases with increasing amounts of reactive surfaces; Achat et al., 2011) or only from different amounts of inorganic P in soils (Pr increases with increasing time and C_P according to a Freundlich kinetic equation; Morel et al., 2000). Therefore, in addition to the kinetic Eq. (6) used for each individual soil sample (see Appendix A1c), we also tested whether a kinetic Freundlich equation could be used to describe the dynamics of the transfer kinetics at different C_P levels, providing that physicochemical soil properties are similar between soil samples:

$$P_r = v \times C_P{}^w \times \text{time}^P \qquad (7)$$

where v, w and p are adjusted parameters: v is the Pr value after 1 min for C_P values of $1\,\mu\text{g}\,\text{mL}^{-1}$; w accounts for the changes in Pr with increasing C_P values; p accounts for the changes in Pr with time.

2.6 Data processing and statistics

All soil C and nutrient concentrations and soil respiration are reported on an oven-dry (105 °C) basis. In addition to the concentrations of C, N and P in each soil horizon, stocks were calculated in the entire soil profile using the masses of forest floor and the thicknesses of the mineral soil horizons with their bulk density. The C/N, C/P and lignin/N ratios were also calculated.

The two-pool mineralization model, the models describing r/R and Pr as a function of time and the Freundlich kinetic equation were adjusted using a non-linear procedure. Pearson's correlation coefficients were used to highlight the general relationships between soil physicochemical properties, the different P status variables and soil depth. Linear and non-linear procedures were also used to assess the relationships between the isotopic dilution parameters ($r/R_{1\,\text{min}}$ and n), C_P and physicochemical soil properties. One-way ANOVA and the Bonferroni t-test were used to identify within- versus between-plot variability based on within-plot sub-replicates (3 sub-replicates or zones per plot or 3–5 aliquots per composite sample). Prior to this, quantity variables were log-transformed and proportion variables were arc-sine transformed to comply with model prerequisites. Comparisons between plots in each soil horizon, in the surface mineral soils (i.e. A + AE horizon for plots 1 to 3 or A horizon for plot 4) and in the entire soil profile were used to highlight the relationships between soil P status, microbial activity and decomposition processes: differences between plots in P fractions (e.g. organic P) were compared with differences between plots in microbial properties, forest floor stock, humus accumulation in mineral soils and organic matter quality. However, differences between plots cannot be directly used to conclude on any vegetation or climate effect since sites were not replicated (only potential effects were explained in the discussion section). Statistics were preformed with SYSTAT software (2000).

3 Results

3.1 Soil profiles and main physicochemical soil properties

In general, the physicochemical soil properties significantly changed with soil horizons (Tables 1 and 2). Total C and total N continually decreased with increasing soil depth. Concentrations of Al and Fe oxides also decreased with increasing soil depth in the mineral soil profile, but lower values were found in the forest floor. The surface mineral horizons (A + AE or A) displayed the most acidic soil pH (Table 1).

Table 1. Stocks of forest floor, description of the soil profiles and main physicochemical soil properties.

	Plot 1 (*P. tremula*)	Plot 2 (*A. sibirica*)	Plot 3 (forest gap)		Plot 4 (*P. tremula*)
Stocks of forest floor (Mg ha^{-1})					
F	2.4 ± 0.2b	18.6 ± 4.4a	0 ¶	F	10.0 ± 1.6a
Thickness of the soil horizons (cm)					
A + AE	18.5 ± 2.4a	20.0 ± 0.4a	24.7 ± 0.9a	A	31.3 ± 1.4
E	39.1 ± 2.5a	38.0 ± 3.3a	34.0 ± 3.9a	AE	23.0 ± 5.6
EBt	12.9 ± 1.9a	15.7 ± 4.4a	12.3 ± 3.4a		
Bt	$28.5 \pm 2.8+$	$27.0 \pm 2.7+$	$29.1 \pm 1.0+$	Bt	$40.8 \pm 8.7+$
Total C (mg g^{-1})					
F$^{\#}$	451.9 ± 3.6(a)	408.8 ± 4.6(b)	_¶	F$^{\#}$	468.6 ± 4.0(a)
A + AE	34.8 ± 3.4a	31.7 ± 2.6a	31.2 ± 2.9a	A	39.3 ± 2.3a
E	6.9 ± 0.8a	9.1 ± 1.0a	7.1 ± 0.7a	AE	7.9 ± 1.1
EBt	3.6 ± 0.01a	3.9 ± 0.3a	3.3 ± 0.3a		
Bt	2.2 ± 0.3a	3.0 ± 0.1a	2.2 ± 0.3a	Bt	3.2 ± 0.2a
Total N (mg g^{-1})					
F$^{\#}$	25.91 ± 0.05(a)	18.25 ± 0.06(b)	_¶	F$^{\#}$	17.13 ± 0.26(c)
A + AE	3.14 ± 0.28a	2.75 ± 0.21a	2.60 ± 0.02a	A	2.60 ± 0.10a
E	0.83 ± 0.07a	0.95 ± 0.06a	0.77 ± 0.06a	AE	0.75 ± 0.06
EBt	0.62 ± 0.02a	0.60 ± 0.05a	0.49 ± 0.02a		
Bt	0.43 ± 0.04a	0.44 ± 0.002a	0.43 ± 0.02a	Bt	0.47 ± 0.01a
Al + Fe oxides (µmol g^{-1})					
F$^{\#}$	24.1	57.4	_¶	F$^{\#}$	19.5
A + AE	145.4 ± 6.6a	142.3 ± 4.9a	149.7 ± 3.7a	A	105.2 ± 3.2b
E	133.2 ± 8.0a	131.1 ± 4.7a	136.2 ± 1.7a	AE	97.1 ± 3.1
EBt	125.0 ± 6.1a	115.2 ± 0.7a	117.5 ± 1.5a		
Bt	115.2 ± 3.1a	106.2 ± 0.9ab	104.9 ± 2.5ab	Bt	101.3 ± 1.2b
Soil pH					
F$^{\#}$	6.04 ± 0.003(b)	5.79 ± 0.01(c)	_¶	F$^{\#}$	6.58 ± 0.003(a)
A + AE	5.56 ± 0.02a	5.02 ± 0.07b	5.47 ± 0.04a	A	5.73 ± 0.09a
E	5.51 ± 0.05a	5.46 ± 0.06a	5.53 ± 0.03a	AE	6.23 ± 0.09
EBt	5.75 ± 0.06a	5.82 ± 0.13a	5.74 ± 0.04a		
Bt	5.84 ± 0.11b	5.75 ± 0.06b	5.99 ± 0.03ab	Bt	6.26 ± 0.10a

Means $\pm$ standard errors ($n_{\text{obs}} = 3$ zones per plot or 3–4 aliquots of each composite sample$^{\#}$). Different lowercase letters denote significant ($P < 0.05$) differences between plots in a given soil horizon. Different lowercase letters in parentheses denote significant ($P < 0.05$) differences between composite samples.
Depth effect in each plot: $P < 0.001$.
¶ No forest floor in the forest gap.

Stocks of forest floor were significantly lower in plot 1 than in the two other forested plots, while there was no forest floor in plot 3 (Table 1). In addition, results suggest that the thicknesses of the humus accumulation soil horizon (A + AE or A) generally tended to be lower in plots 1 to 3 (particularly in plot 1) than in plot 4. For a given soil layer, concentrations of total C and total N were not significantly different between plots (except for the forest floor; Table 1). However, owing to thinner humus accumulation horizons, stocks of total C in the entire soil profile tended to be slightly, but insignificantly, lower in plots 1 to 3 (particularly in plot 1) than in plot 4 (Table 3a). Concentrations of Al and Fe oxides were

significantly lower in plot 4, while no differences were found between the three other plots. Soil pH was more acidic in plots 1 to 3 (particularly in plot 2) than in plot 4 (Table 1).

3.2 Microbiological activity, net C mineralization and quality of organic matter

Microbiological activity inferred by microbial biomass and soil respiration, as well as by acid phosphatase activity, significantly changed with soil depth and was higher in the forest floors (Table 4a; Fig. 1a–d). There were also differences between plots. The forest floor from plot 4 displayed the highest microbial biomass and cumulative and daily soil

Table 2. Correlations between P status variables, physicochemical soil properties and soil depth (Pearson's correlation coefficients; n_{obs} =45 mineral soils[†])

	Soil depth	Total organic P	Total organic P (% total P)	Total inorganic P	Phosphate ions in solution (C_P)	Diffusive phosphate ions (Pr 400 min)	Parameter $r/R_{1\ min}^{£}$	Parameter n[¶]
Soil depth	–	−0.87***	−0.87***	0.68***	−0.70***	0.23	−0.93***	0.62**
Total C	−0.86***	0.89***	0.84***	−0.55**	0.89***	0.20	0.96***	−0.81***
Total N	−0.88***	0.93***	0.87***	−0.58***	0.88***	0.22	0.97***	−0.75***
pH	0.58**	−0.64***	−0.70***	0.67***	−0.27	0.15	−0.60**	−0.04
Al + Fe oxides	−0.61**	0.71***	0.69***	−0.49	0.31	−0.10	0.63***	0.02
C/N	−0.86***	0.77***	0.77***	−0.53*	0.69***	−0.17	0.84***	−0.77***
C/P	−0.87***	0.86***	0.83***	−0.57**	0.86***	0.14	0.94***	−0.82***

[†] Forest floor samples were removed from the analysis to limit covariate effects (i.e. soil depth effect).
*, significant at $P < 0.05$; **, significant at $P < 0.01$; ***, significant at $P < 0.001$.
[£] Parameter $r/R_{1\ min}$ also significantly correlated with the phosphate ions in soil solution (0.83***).
[¶] Parameter n also significantly correlated with the phosphate ions in soil solution (−0.86***).

Table 3. Stocks of C, N, and P and P fractions as a % of total P in the entire forest floor + mineral soil profile (100 cm).

	Plot 1 (P. tremula)	Plot 2 (A. sibirica)	Plot 3 (forest gap)	Plot 4 (P. tremula)
3.a C and N stocks (Mg ha^{-1})				
Total C	108 ± 6a	117 ± 13a	113 ± 6a	138 ± 3a
Total N	12.4 ± 0.6a	11.7 ± 0.8a	11.3 ± 0.4a	10.8 ± 0.1a
3.b P stocks (kg ha^{-1})				
Total P	9810 ± 424a	8560 ± 354ab	9147 ± 100a	7414 ± 109b
Total organic P	2814 ± 199a	3201 ± 273a	3251 ± 45a	1827 ± 33b
Total inorganic P	6997 ± 226a	5359 ± 106b	5896 ± 65b	5587 ± 138b
Pr$_{400\ min}$	279 ± 16a	213 ± 15a	242 ± 18a	219 ± 11a
Pr in one week[¶]	1078 ± 74a	902 ± 57ab	923 ± 78ab	736 ± 54b
Pr in one month[¶]	1959 ± 145a	1706 ± 104ab	1702 ± 162ab	1259 ± 96b
Pr in one year[¶]	5120 ± 380a	4392 ± 102ab	4296 ± 414ab	3186 ± 264b
3.c P fractions (% of total P stocks)				
Total organic P	29 ± 1b	37 ± 2a	36 ± 0a	25 ± 1b

Means ± standard errors (n_{obs} = 3 zones per plot). Different lowercase letters denote significant ($P < 0.05$) differences between plots.
Stocks were calculated using the masses of forest floor (0–19 Mg ha^{-1}) and the thickness of the mineral soil layers (0.12–0.41 m; see Table 1) with their bulk density (0.70–1.56 g cm^{-3}).
[¶] Extrapolated values of diffusive phosphate ions using Eq. (6).

respirations and high contribution of the readily available organic fraction (% AO) to the total amount of mineralized C. Inversely, the forest floor from plot 2 generally displayed the lowest microbiological activity (Table 4a and Fig. 1a, b). However, differences in daily soil respiration between plots 1 and 2 were only visible during the first 20 days of incubation (Fig. 1b). In the surface mineral soil horizons, plot 1 generally displayed the highest microbial biomass, enzymatic activity, soil respiration and contributions of the readily available organic fraction (% AO). Plots 3 and 4 showed the lowest values (Table 4a and Fig. 1c, d). However, differences in soil respiration occurred mainly during the first 55–70 days of incubation (Fig. 1d).

Variability was found between soil horizons and plots in the microbiological activity, and the different microbiological soil properties were in general well correlated. There were close relationships between microbial C, N and P (Spearman's correlation coefficients = 0.88–0.99; n_{obs} = 7). Microbial biomass was also correlated with soil respiration (Spearman's correlation coefficients = 0.96) and phosphatase activity (Spearman's correlation coefficients = 0.85–0.86). Furthermore, microbial biomass was well correlated with total C or N (Spearman's correlation coefficients = 0.81–0.96).

In addition to differences in microbiological activity, there were also differences between plots in organic matter quality, inferred by the concentrations of nutrients and lignin in the

forest floor and the lignin/N, C/N and C/P ratios (see Table 4b and details in the discussion section).

3.3   Soil P status

3.3.1   General description and depth effect

Total P ranged from 645 to 1042 μg g^{-1} in the mineral soils and was up to 2380 μg g^{-1} in the forest floors (Table 5). The different P fractions significantly changed with soil horizons. Total P, total organic P and microbial P continually decreased with increasing soil depth, while total inorganic P was higher in the subsoil (Bt horizon) than in the surface soil horizons of the mineral soil profile. Up to 56 % of total P was in organic form, and this proportion decreased with increasing soil depth (Tables 2 and 5). Microbial P represented 10.4–15.8 % of total P in the forest floors, and less than 3.2 % in the surface mineral soils.

Concerning the plant-available inorganic P, phosphate ions in soil solution (C_P) and diffusive phosphate ions (Pr in 400 min) were respectively 0.24–0.65 μg mL^{-1} and 23–32 μg g^{-1} in the surface mineral soils (Table 6). Using the parameters of kinetic Eq. (6) ($Pr_{1\ min}$ and p), extrapolated Pr values reached 379–466 μg g^{-1} after one year, which were equivalent to total inorganic P (405–472 μg g^{-1}). Values of C_P, parameters of the Eqs. (5) and (6) describing the isotopic dilution ratio and Pr as a function of time, and Pr in 400 min varied between soil horizons (Tables 2 and 6). In particular, parameter $r/R_{1\ min}$ decreased, parameter n increased, and therefore the reactivity of phosphate ions with the solid constituents increased with increasing soil depth.

3.3.2   Comparison between the study plots

Total, total organic and total inorganic P concentrations (in μg g^{-1}) were generally higher in the forest floor from plot 1 than in the forest floors from the two other forested plots (Table 5). Considering the mineral soil horizons (Table 5) or the entire soil profile (Table 3b), total P was significantly lower in plot 4, while there were no significant differences between the three adjacent plots 1 to 3. Total organic P in a given mineral soil layer (in μg g^{-1} or as a % of total P; Table 5) or in the entire soil profile (in kg ha^{-1} or as a % of total P; Table 3b, c) was in general significantly lower in plots 1 and 4 than in plots 2 and 3. Plot 1 also displayed the highest concentrations and stocks of total inorganic P.

For the forest floor and the surface mineral soil horizon (A + AE or A), available phosphate ions (C_P and Pr) were significantly higher in plot 1 than in plot 2, values for the two other plots being intermediate (Table 6). However, there was no significant difference between plots in available phosphate ions in the deep soil horizons (except C_P in the EBt horizon; Table 6). Consequently, differences in available phosphate ions in the entire soil profile were small (significant differences only between plots 1 and 4; Table 3b).

3.3.3   Relationships with physicochemical soil properties

Total organic and inorganic P fractions were significantly correlated with each soil property, except total inorganic P with Al and Fe oxides (see Pearson's correlation coefficients in Table 2). However, with some exception (e.g. organic P concentration vs. total C or N), correlations were mainly or exclusively the result of a covariate effect since P fractions as well as soil properties changed with soil depth (Table 2; low or no relationships in a given soil horizon). Similarly, correlations between C_P, the isotopic dilution parameters and soil properties were generally the result of a depth effect. Therefore, only the most relevant relationships are shown through regressions. In particular, variability in the isotopic dilution parameters was mainly related to the variability in the C_P values (Table 2; Fig. 2a, b). However, the relationships between the isotopic dilution parameters and C_P varied between soil horizons (see residual variability, in Fig. 2a, b), owing to differences in physicochemical soil properties, namely Al and Fe oxides, soil pH and total C (Fig. 2c, d). In a given soil horizon, dynamics of phosphate ions were similar between the three adjacent plots 1 to 3 and Pr was closely described as a function of time and C_P based on a single Freundlich kinetic equation (Fig. 2e, f).

4   Discussion

4.1   General P status of surface and deep Siberian forest soils

Total P in the surface mineral soils (879–1042 μg g^{-1}) was in the upper ranges of values reported in other ecosystems with permanent vegetation from different locations in the world (e.g. mean of 30 forest soils = 557 μg g^{-1}; mean of 71 grassland soils = 919 μg g^{-1}; in Achat et al., 2009). Similarly, based on the Hedley sequential fractionation, total P (defined as the sum of the different extracted P fractions) was found to range from an average of 523 μg g^{-1} for 131 forest soils to 949 μg g^{-1} for 110 grassland soils in Germany (Alt et al., 2011). Still based on the Hedley sequential fractionation and literature reviews, total P concentrations were reported to range from an average of 200 μg g^{-1} to 684 μg g^{-1} in natural ecosystems depending on soil type (Cross and Schlesinger, 1995; Johnson et al., 2003), but higher total P values were found in some forest soils (up to 1109–1426 μg g^{-1}; Johnson et al., 2003; Negassa and Leinweber, 2009). Our studied Siberian soils may be thus qualified as relatively rich in P.

The concentrations of plant-available phosphate ions resulting from the physicochemical processes (diffusive phosphate ions in one week = 83–126 μg g^{-1} in the surface mineral soil layer) were comparable to mean values reported in the literature for grasslands (mean of 20 soils = 126 μg g^{-1}) and agricultural croplands (mean of 31 soils = 75 μg g^{-1})

Table 4. Microbiological soil properties and organic matter quality.

	Plot 1 (*P. tremula*)	Plot 2 (*A. sibirica*)	Plot 3 (forest gap)		Plot 4 (*P. tremula*)
4.a Microbiological soil properties					
Microbial C (mg g^{-1})					
F[#]	5.2 ± 0.8(b)	5.6 ± 1.0(ab)	_¶	F[#]	9.3 ± 0.4(a)
A + AE[#]	0.29 ± 0.001(a)	0.24 ± 0.002(b)	0.15 ± 0.001(d)	A[#]	0.17 ± 0.003(c)
Microbial N (mg g^{-1})					
F[#]	1.06 ± 0.01(a)	0.32 ± 0.02(b)	_¶	F[#]	1.02 ± 0.04(a)
A + AE[#]	0.051 ± 0.002(a)	0.043 ± 0.001(b)	0.027 ± 0.0004(c)	A[#]	0.027 ± 0.001(c)
Microbial C/microbial N					
F[#]	5.0 ± 0.8(b)	18.2 ± 4.4(a)	_¶	F[#]	9.2 ± 0.1(a)
A + AE[#]	5.8 ± 0.2(a)	5.7 ± 0.1(a)	5.6 ± 0.1(a)	A[#]	6.3 ± 0.1(a)
Microbial C/microbial P					
F[#]	18.8 ± 2.4(b)	34.8 ± 7.0(a)	_¶	F[#]	35.0 ± 2.4(a)
A + AE[#]	8.8 ± 0.1(bc)	9.2 ± 0.2(b)	10.4 ± 0.3(a)	A[#]	8.2 ± 0.2(c)
Acid phosphatase activity (phosphomonoesterase; µg *p*-nitrophenol g^{-1} h^{-1})					
F[#]	1996 ± 206(a)	2111 ± 91(a)	_¶	F[#]	1462 ± 71(b)
A + AE[#]	541 ± 33(a)	590 ± 30(a)	277 ± 4(b)	A[#]	310 ± 21(b)
4.b Organic matter quality					
Concentrations of total K, Ca, Mg, Mn and lignin (mg g^{-1})					
K–F[#]	3.92 ± 0.25(a)	1.93 ± 0.01(c)	_¶	F[#]	2.55 ± 0.06(b)
Ca–F[#]	24.80 ± 1.60(a)	15.78 ± 0.04(b)	_¶	F[#]	26.20 ± 0.73(a)
Mg–F[#]	1.75 ± 0.11(c)	3.03 ± 0.04(a)	_¶	F[#]	2.39 ± 0.07(b)
Mn–F[#]	0.37 ± 0.01(c)	0.63 ± 0.01(a)	_¶	F[#]	0.45 ± 0.01(b)
Lignin–F[#]	506 ± 8(b)	581 ± 4(a)	_¶	F[#]	491 ± 4(b)
Lignin/total N					
F[#]	19.5 ± 0.3(c)	31.8 ± 0.2(a)	_¶	F[#]	28.7 ± 0.2(b)
Total C/total N					
F[#]	17.4 ± 0.1(c)	22.4 ± 0.2(b)	_¶	F[#]	27.4 ± 0.2(a)
A + AE	11.1 ± 0.1b	11.5 ± 0.1b	12.0 ± 1.0b	A	15.1 ± 0.3a
E	8.4 ± 0.5a	9.5 ± 0.4a	9.2 ± 0.3a	AE	10.4 ± 0.6
EBt	5.8 ± 0.2a	6.7 ± 1.2a	6.8 ± 0.4a		
Bt	5.1 ± 0.2b	6.8 ± 0.1a	5.2 ± 0.5b	Bt	6.8 ± 0.5ab
Total C/total P					
F[#]	189.9 ± 1.5(c)	259.4 ± 2.9(b)	_¶	F[#]	272.4 ± 2.4(a)
A + AE	33.7 ± 4.3a	35.1 ± 1.4a	31.6 ± 3.6a	A	44.7 ± 2.2a
E	9.7 ± 0.3b	12.0 ± 0.4a	9.2 ± 0.5b	AE	11.1 ± 1.2
EBt	5.6 ± 0.2a	5.6 ± 0.2a	4.7 ± 0.4a		
Bt	3.2 ± 0.3ab	4.2 ± 0.2ab	3.0 ± 0.4b	Bt	4.6 ± 0.4a

Means ± standard errors (n_{obs} = 3 zones per plot or 3–5 aliquots of each composite sample[#]). Different lowercase letters denote significant ($P < 0.05$) differences between plots in a given soil horizon. Different lowercase letters in parentheses denote significant ($P < 0.05$) differences between composite samples. Depth effect in each plot: $P < 0.0001$.
¶ No forest floor in the forest gap.

and high compared with one P-deficient forest ecosystem in southwestern France (mean of 18 soils = 17 µg g^{-1} in Achat et al., 2009; no data for other forest contexts available for comparison). Labile inorganic P fractions obtained with the Hedley fractionation procedure (e.g. resin + bicarbonate in-

organic P = 21–37 µg g^{-1} in grassland and forest soils; Johnson et al., 2003; Alt et al., 2011) are also considered to be plant-available. However, these data are not directly comparable with the results obtained with the isotopic dilution method, as shown by Chen et al. (2003). Our comparisons
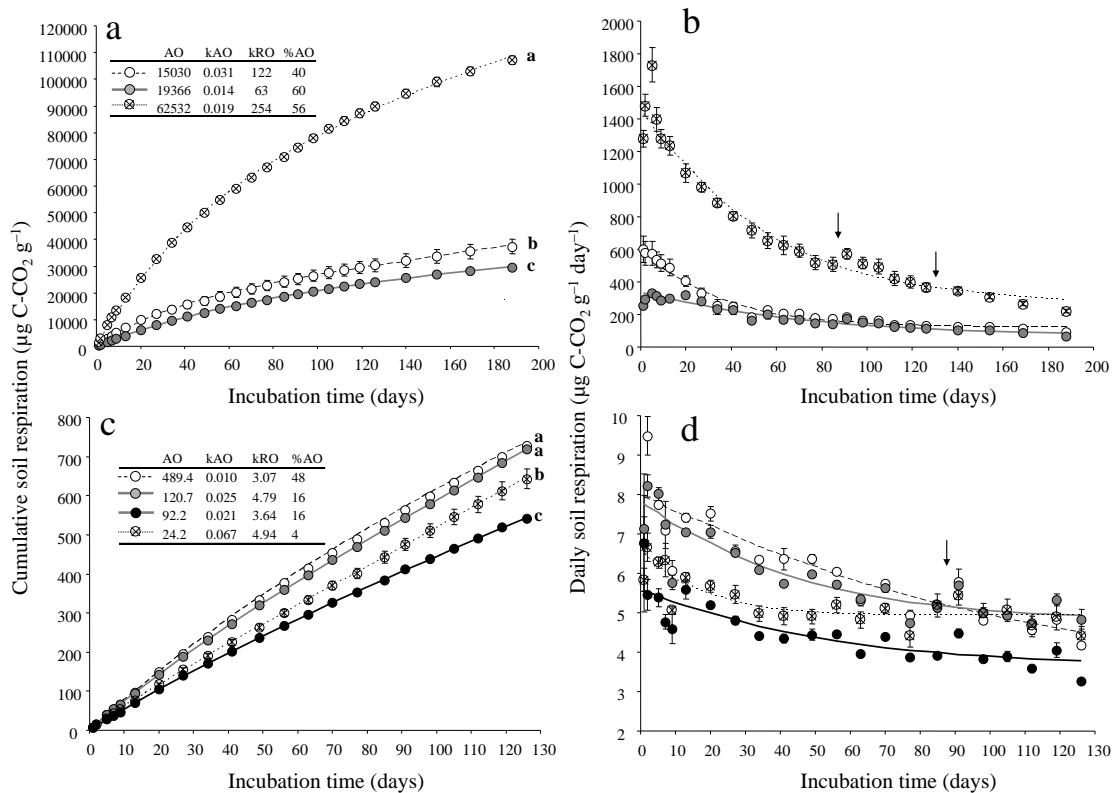
Fig. 1. Cumulative and daily soil respiration of incubated forest floors (**a**, **b**) and surface mineral soils (horizon A or A + AE) (**c**, **d**). Means $\pm$ standard error (n_{obs} = 4 aliquots and jars for each composite sample). Open symbols, plot 1; grey symbols, plot 2; black symbols, plot 3; hatched symbols, plot 4. Solid lines, adjustments (two-pool model; Eq. (1); $r^2 = 0.926 - 1.000$; $P < 0.0001$). Inset tables in (**a**) and (**c**), parameters of the two-pool model (AO = pool size of the readily available organic pool; k_{AO} = first-order rate of mineralization of the readily available organic pool; k_{RO} = rate of mineralization of the recalcitrant organic pool) and readily available organic pool mineralized in 126 or 188 days in % of total mineralized organic C (% AO). Different lowercase letters in (**a**) and (**c**) denote significant differences between composite samples in cumulative soil respiration after 126–188 days. Arrows: adjustment of soil moisture after 85 and 126 days, flush effect due to the adjustment of soil moisture after 85 days.

between total P and available phosphate ions in our study soils and those reported in the literature suggest that the study Siberian forest soils are probably not P-deficient. Moreover, similarly to other forest ecosystems under the same latitude (Hedin et al., 2009), the study forest floors displayed low $N : P$ ratio ($N : P$ ratio = 10–12). This also suggests that P is unlikely to be the first limiting nutrient. According to Huston and Wolverton (2009), very high concentration values of P can be explained by low temperature and/or relatively low precipitation at high latitude, and therefore low rates of nutrient loss through mineral leaching and, for plot 4, slow organic matter decomposition. In addition, loess material depositions (Chlachula, 2011) probably resulted in rejuvenated soils with high levels of P (Elser et al., 2007; Lambers et al., 2008; Huston and Wolverton, 2009). While our results suggest that the studied Siberian forest soils are unlikely to be P-deficient, Giesler et al. (2002) found that P availability could limit plant growth in other boreal forests (e.g. in northern Sweden). However, in their study, P limitation of plant

growth was the result of large accumulations of Al and Fe in the humus layer in groundwater discharge area and consequently high P-fixation capacity. Concentrations of Al and Fe oxides extracted with ammonium oxalate in the studied forest floors (20–57 µmol g^{-1}) were similar to or lower than those found for other forest floors with low or very low P-fixation capacity (92 µmol g^{-1} for one forest site in the southern Appalachians in North Carolina, USA, Walbridge et al., 1991; 11–46 µmol g^{-1} for 21 forest sites in southwestern France, Achat et al., 2011). Consequently, P-fixation capacity is also expected to be small in the forest floors of the studied forest sites.

Total inorganic P and diffusive phosphate ions varied with soil depth and accumulated in the subsoil (Tables 2, 5, 6 and Fig. 3). However, tree fine roots are generally concentrated in the surface soil layers in boreal ecosystems (more than 80 % of tree fine roots in the first 60 cm; Jackson et al., 1996), and the contribution of the subsoil to plant P nutrition may not be significant. Nevertheless, owing to the increase in

Table 5. Total, total organic, total inorganic and microbial P.

	Plot 1 (*P. tremula*)	Plot 2 (*A. sibirica*)	Plot 3 (forest gap)		Plot 4 (*P. tremula*)
Concentrations in $\mu g\,g^{-1}$					
Total P					
F[#]	2379.6 ± 71.9(a)	1576.2 ± 46.3(b)	¶	F[#]	1720.3 ± 13.5(b)
A + AE	1042.1 ± 37.9a	899.4 ± 41.5ab	991.1 ± 25.6ab	A	879.1 ± 12.9b
E	714.6 ± 69.6a	753.9 ± 56.8a	771.4 ± 34.4a	AE	708.8 ± 21.4
EBt	644.7 ± 27.8a	697.1 ± 32.5a	717.5 ± 26.7a		
Bt	686.9 ± 13.9a	703.0 ± 17.5a	753.9 ± 14.6a	Bt	700.0 ± 13.9a
Total organic P					
F[#]	1008.6 ± 18.9(a)	812.7 ± 46.2(b)	¶	F[#]	825.5 ± 0.3(b)
A + AE	570.2 ± 3.0a	494.8 ± 35.0ab	554.5 ± 28.5a	A	415.7 ± 25.2b
E	220.7 ± 28.7a	284.6 ± 23.3a	320.6 ± 23.1a	AE	155.9 ± 20.6
EBt	137.4 ± 7.4b	239.7 ± 35.5a	156.1 ± 14.2ab		
Bt	102.2 ± 2.4b	198.1 ± 6.7a	108.8 ± 2.5b	Bt	81.4 ± 6.4c
Total inorganic P					
F[#]	1371.0 ± 18.9(a)	763.5 ± 46.2(b)	¶	F[#]	894.8 ± 0.3(b)
A + AE	471.9 ± 39.7a	404.6 ± 18.3a	436.6 ± 9.8a	A	463.3 ± 12.4a
E	493.9 ± 41.1a	469.3 ± 36.6a	450.7 ± 13.2a	AE	552.9 ± 5.9
EBt	507.3 ± 21.7a	457.4 ± 30.2a	561.4 ± 15.9a		
Bt	584.8 ± 11.8a	504.9 ± 12.2b	645.1 ± 15.2a	Bt	618.7 ± 20.1a
Microbial P					
F[#]	276.9 ± 8.3(a)	163.5 ± 4.2(b)	¶	F[#]	271.9 ± 31.1(a)
A + AE[#]	33.0 ± 0.3(a)	26.6 ± 0.4(b)	14.4 ± 0.4(d)	A[#]	20.8 ± 0.5(c)
Total organic P as a % of total P					
F[#]	42 ± 1(b)	52 ± 3(a)	¶	F[#]	48 ± 0.02(ab)
A + AE	55 ± 2a	55 ± 2a	56 ± 2a	A	47 ± 2a
E	31 ± 1b	38 ± 1a	41 ± 1a	AE	22 ± 2
EBt	21 ± 1b	34 ± 4a	22 ± 1b		
Bt	15 ± 0.2b	28 ± 0.5a	14 ± 0.5b	Bt	12 ± 1b

Means $\pm$ standard errors ($n_{\mathrm{obs}} = 3$ zones per plot or 3–4 aliquots of each composite sample[#]). Different lowercase letters denote significant ($P < 0.05$) differences between plots in a given soil horizon. Different lowercase letters in parentheses denote significant ($P < 0.05$) differences between composite samples.
Depth effect in each plot: $P < 0.001$.
¶ No forest floor in the forest gap.

atmospheric CO_2, deeper root systems are expected (Thomas et al., 1999; Iversen, 2010) and this would lead to substantial amounts of available phosphate ions for the trees in the study Siberian sites. This suggests that the potential for enhanced growth and C sequestration would a priori not be P-limited. In addition, in acidic soils and in cool conditions, low microbial activity and slow organic matter decomposition lead to the accumulation of organic P compounds that are considered relatively labile in temperate environments (e.g. orthophosphate diesters; Turner et al., 2004; Vincent et al., 2012). This suggests that cold and acidic soils contain a large pool of potentially plant-available soil organic P and that P is unlikely to limit ecosystem productivity during changes induced by climate warming (Turner et al., 2004).

As discussed above, the potential enhanced C sequestration due to an increase in forest productivity may not be P-

limited. Conversely, high levels of available nutrients (such as P) may also enable an increase in microbiological activity and mineralization of soil organic matter during the climate warming and consequently a decrease in C sequestration in soils (Hartley et al., 2010). Therefore, both mechanisms underlying the role of P in C sequestration have to be considered. Further studies should also focus on the potential N limitation of C sequestration by vegetation and mineralization of soil organic matter (Turner et al., 2004; Reich et al., 2006; Hartley et al., 2010).

4.2 Availability of phosphate ions in relation to the physicochemical soil properties

In good agreement with previous studies (e.g. Fardeau, 1993; Morel et al., 2000; Achat et al., 2009), the parameters of isotopic dilution were C_P-dependent: The parameter $r/R_{1\;\mathrm{min}}$
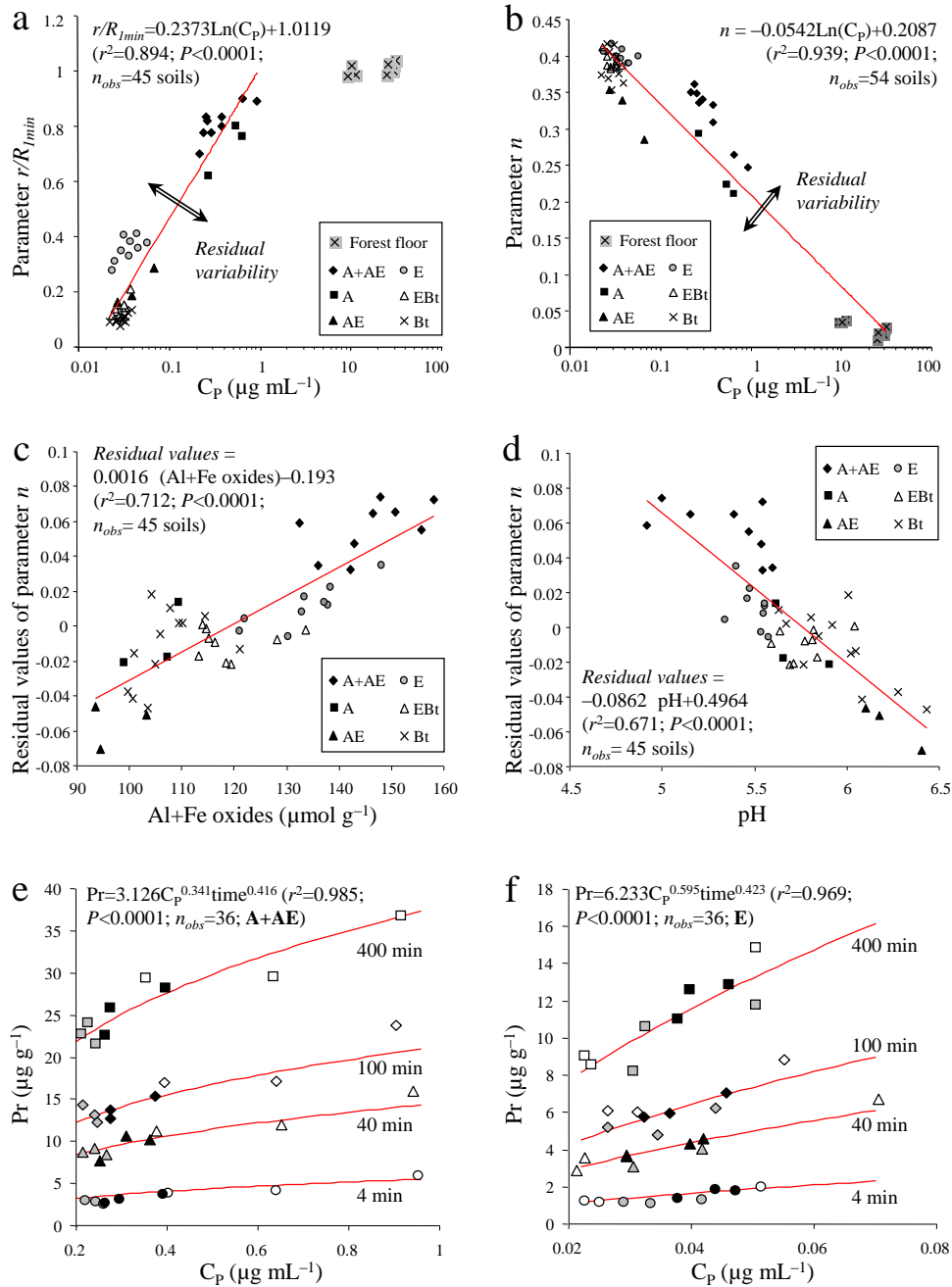
Fig. 2. Effects of soil properties on isotopic dilution parameters and diffusive phosphate ions. Isotopic dilution parameters ($r/R_{1\ \text{min}}$ in **a**; n in **b**) as a function of the concentration of phosphate ions in soil solution (C_P), considering all plots (3 zones per plot) and soil horizons. Relationships between the residual variability of parameter n (measures – estimated values with C_P; see arrow in **b**) and Al + Fe oxides extracted with ammonium oxalate (**c**) and soil pH (**d**). Diffusive phosphate ions (Pr) as a function of time and C_P in a given mineral soil horizon of the three adjacent plots (A + AE horizon in **e**; E horizon in **f**; open symbols, plot 1; grey symbols, plot 2; black symbols, plot 3). *Solid lines*, non-linear or linear adjustments (adjustments of the Freundlich kinetics Eq. (7) in **e** and **f**). Stepwise procedure: residual values on parameter $n = 0.108 + 0.000937 \times (\text{Al} + \text{Fe oxides}) - 0.039 \times \text{pH} + 0.000416 \times \text{total C}$ ($r^2 = 0.816$; $P < 0.0001$; $n_{\text{obs}} = 45$ mineral soils).
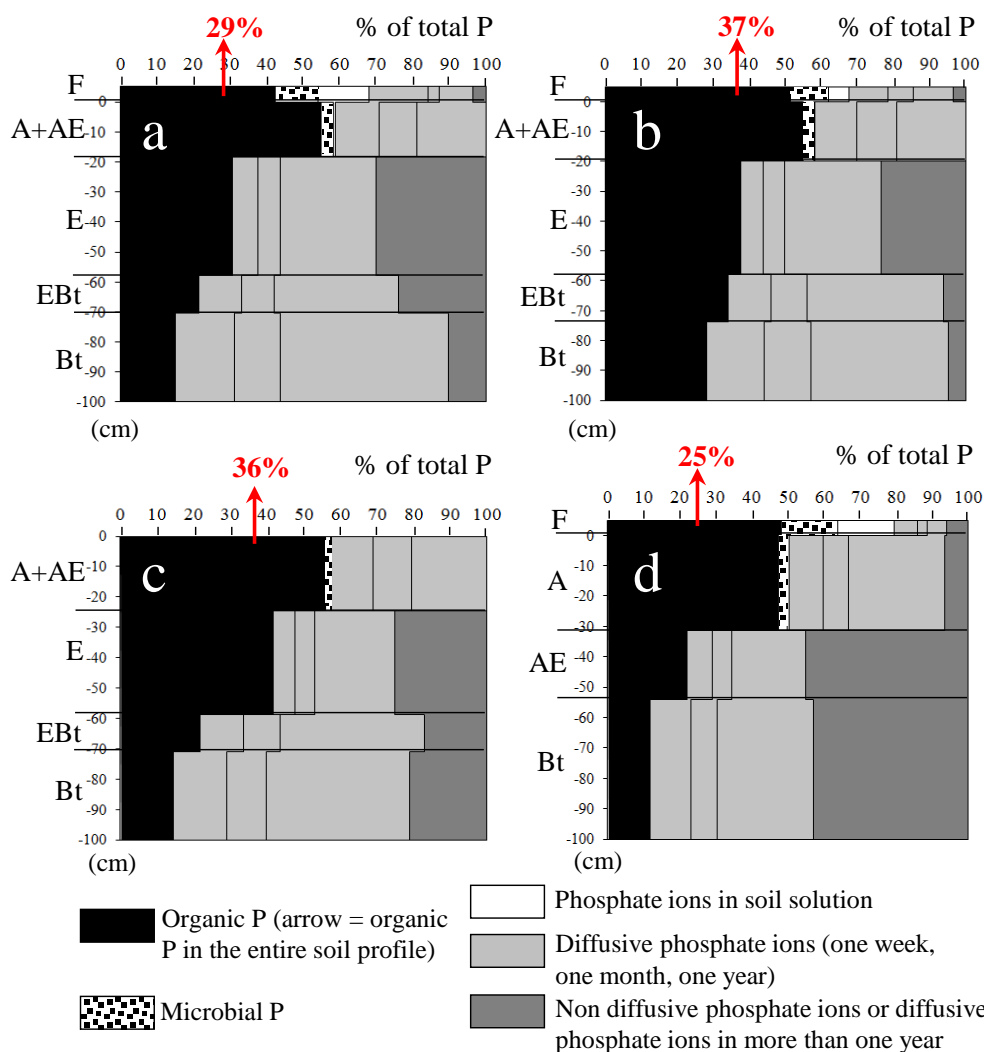
Fig. 3. Conceptual diagram of the different P fractions as a percentage of total phosphorus and as a function of soil depth in the four study plots. Plot 1 in (**a**), plot 2 in (**b**), plot 3 in (**c**), plot 4 in (**d**).

increased; the parameter *n* decreased; and therefore reactivity of phosphate ions with the soil solid constituents decreased with increasing concentration of phosphate ions in soil solution (Table 2; Fig. 2). Contrary to other studies (e.g. Achat et al., 2011), there were no strong relationships between the parameters of isotopic dilution and Al and Fe oxides (see correlation coefficients in Table 2). However, our results showed that the residual variability of parameter *n* (i.e. the difference between the measured values minus estimated values using relationships with the concentration of phosphate ions in soil solution) was positively correlated with Al and Fe oxides and negatively correlated with the soil pH. Such relationships can be explained by an increase in the reactive surfaces with increasing Al and Fe oxide concentrations in acidic soils (Walbridge et al., 1991; Achat et al., 2011) together with changes in surface charges of the Al and Fe ox-

ides with soil pH (Strauss et al., 1997; Hinsinger, 2001). The parameters of isotopic dilution, as well as the concentration of phosphate ions in soil solution, were also correlated with total C or N (Table 2), but it was mainly the result of a depth effect.

Because, in a given soil horizon, soil properties were generally similar between the three adjacent plots 1 to 3 (Table 1), dynamics of phosphate ions were similar between plots and diffusive phosphate ions could be closely described as a function of time and concentration of phosphate ions in soil solution according to a single Freundlich kinetic equation (Fig. 2e, f). This showed that differences in plant-available phosphate ions (diffusive phosphate ions and phosphate ions in soil solution) between the three adjacent plots 1 to 3 resulted more from different amounts of inorganic P in soils (and therefore different decomposition processes; see below

Table 6. Concentration of phosphate ions in soil solution (C_P), isotopic dilution parameters[§] ($r/R_{1\,min}$ and n) and diffusive phosphate ions (parameters[†] $Pr_{1\,min}$ and p; measured $Pr_{400\,min}$; extrapolated Pr values up to one year).

	Plot 1 (P. tremula)	Plot 2 (A. sibirica)	Plot 3 (forest gap)		Plot 4 (P. tremula)
C_P ($\mu g\,mL^{-1}$)					
F[#]	30.4 ± 0.6(a)	10.3 ± 0.6(b)	¶	F[#]	25.6 ± 0.5(a)
A + AE	0.65 ± 0.16a	0.24 ± 0.01b	0.31 ± 0.04ab	A	0.49 ± 0.11ab
E	0.035 ± 0.011a	0.035 ± 0.005a	0.040 ± 0.003a	AE	0.044 ± 0.012
EBt	0.029 ± 0.002ab	0.034 ± 0.002a	0.026 ± 0.001b		
Bt	0.031 ± 0.002a	0.032 ± 0.004a	0.032 ± 0.001a	Bt	0.026 ± 0.002a
$r/R_{1\,min}$					
F[#]	1.02 ± 0.01(a)	1.00 ± 0.01(a)	¶	F[#]	1.01 ± 0.01(a)
A + AE	0.87 ± 0.02a	0.77 ± 0.04a	0.80 ± 0.01a	A	0.73 ± 0.05a
E	0.32 ± 0.03a	0.39 ± 0.02a	0.36 ± 0.02a	AE	0.21 ± 0.04
EBt	0.13 ± 0.006a	0.17 ± 0.02a	0.12 ± 0.01a		
Bt	0.10 ± 0.004a	0.11 ± 0.01a	0.11 ± 0.01a	Bt	0.09 ± 0.004a
n					
F[#]	0.024 ± 0.003(ab)	0.036 ± 0.001(b)	¶	F[#]	0.017 ± 0.003(a)
A + AE	0.28 ± 0.03ab	0.35 ± 0.004b	0.33 ± 0.01ab	A	0.24 ± 0.03a
E	0.40 ± 0.002a	0.40 ± 0.008a	0.40 ± 0.01a	AE	0.33 ± 0.02
EBt	0.39 ± 0.004a	0.39 ± 0.001a	0.39 ± 0.01a		
Bt	0.40 ± 0.008a	0.39 ± 0.02a	0.40 ± 0.01a	Bt	0.37 ± 0.01a
$Pr_{1\,min}$ ($\mu g\,g^{-1}$)					
F[#]	11.6 ± 5.2(a)	7.9 ± 1.9(a)	¶	F[#]	12.5 ± 2.9(a)
A + AE	2.71 ± 0.46a	1.53 ± 0.06b	1.74 ± 0.18ab	A	2.49 ± 0.31ab
E	0.82 ± 0.17a	0.63 ± 0.02a	0.89 ± 0.07a	AE	1.57 ± 0.23
EBt	2.15 ± 0.16a	1.76 ± 0.10a	1.89 ± 0.17a		
Bt	3.04 ± 0.21a	2.55 ± 0.08a	3.04 ± 0.36a	Bt	3.13 ± 0.45a
p					
F[#]	0.40 ± 0.12(a)	0.34 ± 0.04(a)	¶	F[#]	0.24 ± 0.04(a)
A + AE	0.42 ± 0.02ab	0.46 ± 0.004a	0.45 ± 0.01a	A	0.38 ± 0.02b
E	0.44 ± 0.004a	0.46 ± 0.01a	0.43 ± 0.01a	AE	0.37 ± 0.03
EBt	0.39 ± 0.01a	0.42 ± 0.01a	0.41 ± 0.002a		
Bt	0.39 ± 0.01a	0.41 ± 0.01a	0.39 ± 0.02a	Bt	0.35 ± 0.01a
$Pr_{400\,min}$ ($\mu g\,g^{-1}$)					
F[#]	83.2 ± 6.9(a)	53.9 ± 5.7(b)	¶	F[#]	51.8 ± 1.3(b)
A + AE	31.9 ± 2.5a	22.8 ± 0.7b	25.6 ± 1.6ab	A	23.8 ± 0.4b
E	10.8 ± 2.0a	10.2 ± 1.1a	12.2 ± 0.6a	AE	13.9 ± 0.6
EBt	21.1 ± 0.1a	20.2 ± 1.8a	22.2 ± 1.5a		
Bt	31.4 ± 2.0a	28.2 ± 2.3a	30.9 ± 2.7a	Bt	24.9 ± 1.9a
Pr in one year ($\mu g\,g^{-1}$)[‡]					
F[#]	668.5 ± 35.7(a)	476.7 ± 28.6(a)	¶	F[#]	247.5 ± 46.7(b)
A + AE	465.5 ± 41.2a	402.3 ± 18.2a	433.5 ± 9.5a	A	379.0 ± 33.9a
E	282.5 ± 44.1a	297.4 ± 54.8a	258.2 ± 27.2a	AE	230.4 ± 66.4
EBt	349.6 ± 31.9a	411.8 ± 50.9a	437.6 ± 27.4a		
Bt	516.2 ± 60.2a	471.4 ± 32.6a	482.6 ± 70.2a	Bt	314.9 ± 31.9a

Means ± standard errors ($n_{obs} = 3$ zones per plot or 3 aliquots for each composite sample[#]). Different lowercase letters denote significant ($P < 0.05$) differences between plots in a given soil horizon. Different lowercase letters in parentheses denote significant ($P < 0.05$) differences between composite samples. Significant depth effect in each plot ($P < 0.04$), except for parameter p in plot 1 ($P = 0.84$).

[§] Eq. (5); $r^2 = 0.794 - 0.999$ for the forest floors and $0.980-1.000$ for the mineral soils ($P < 0.0001$).

[†] Eq. (6); $r^2 = 0.832 - 0.994$ for the forest floors and $0.951-1.000$ for the mineral soils ($P < 0.0001$).

[‡] Using parameters $Pr_{1\,min}$ and p (Eq. 6), extrapolated Pr values were $83-126\,\mu g\,g^{-1}$ after one week, $145-233\,\mu g\,g^{-1}$ after one month and $379-466\,\mu g\,g^{-1}$ after one year in the surface mineral soil layer (A + AE or A horizon).

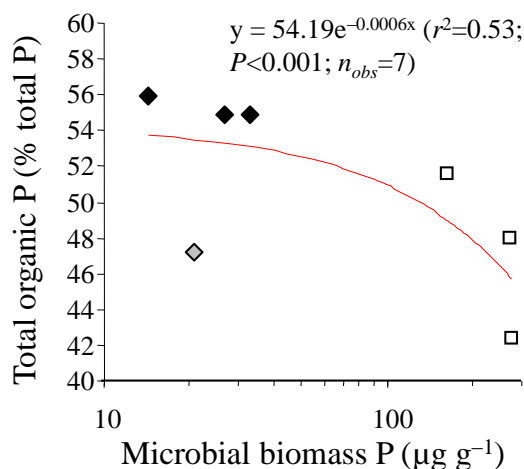¶ No forest floor in the forest gap.

Fig. 4. Total organic P as a function of microbiological activity inferred by microbial biomass P and Al + Fe oxides. Squares, forest floor samples; diamond, surface mineral soils; open symbols, 20–57 µmol Al + Fe oxides g^{-1}; grey symbols, 105 µmol Al + Fe oxides g^{-1}; black symbols, 142–150 µmol Al + Fe oxides g^{-1}.

Sect. 4.3.2.) than from different physicochemical soil properties and therefore different amounts of reactive surface and phosphate dynamic at the solid-to-solution interface (Morel et al., 2000; Achat et al., 2011). Conversely, differences between soil horizons or between plots 1 to 3 and plot 4 in the parameters of isotopic dilution, diffusive phosphate ions and phosphate ions in soil solution (Table 6) could be explained by different concentrations of inorganic P (Table 5), together with differences in soil properties (i.e. Al and Fe oxides and soil pH) and consequently reactivity of phosphate ions with the solid constituents (Table 1 and Fig. 2a–d).

4.3 Organic P fractions and role of microbiological processes

4.3.1 Vertical stratification

Owing to the biological sinks (i.e. plant roots and microbial biomass) and the continuous input of organic materials from litter and root turnover (Walbridge et al., 1991; Attiwill and Adams, 1993; Achat et al., 2009; De Schrijver et al., 2012), total organic P fractions represented high proportions of total P in the surface soil layers (e.g. 47–56 % in the A or A + AE horizon; Fig. 3). This indicated that microbiological processes potentially play a key role in P cycle and availability in the studied forest soils, through mineralization of soil organic matter (Walbridge et al., 1991; Attiwill and Adams, 1993). Microbial P, which generally displays fast turnover (Achat et al., 2010), represents up to 16 % of total P in the study surface soil layers. Therefore, micro-organisms can also act as a significant source of available phosphate ions through

the remineralization process (i.e. release of microbial P after cell death; Achat et al., 2010; Richardson and Simpson, 2011). However, the contribution of the organic and microbial P fractions to total P (relatively to the fractions of total inorganic P and diffusive phosphate ions) and therefore the potential contribution of the microbiological processes to P availability decreased with increasing soil depth (Figs. 3, 4). The decrease in total organic P with increasing soil depth is consistent with the decreases in total C or N (see correlations coefficients in Table 2). The vertical stratification of the relative contribution of organic versus inorganic P in forest soils is in agreement with previous studies (e.g. Walbridge et al., 1991; Achat et al., 2009). Nevertheless, in opposition with the same authors who reported major contributions of organic P fractions in the forest floor (≈80 % of total P), comparable contributions of both organic and inorganic P could be found in the study forest floors (Fig. 3). Following Walbridge et al. (1991), inorganic P fractions in the forest floor can be due to the presence of a geochemical sink, i.e. surface sites (Al and Fe oxides) that are reactive with the phosphate ions. However, the large inorganic P fractions observed in the studied forest floors may not be only attributed to a geochemical sink. Indeed, as explained before, Al and Fe oxide concentrations are low and the geochemical sink may thus be small in the studied forest floors.

4.3.2 Relationships between soil P fractions, microbiological activity and decomposition processes: comparison between the study plots

Large organic P fractions were found in the surface soil layers, suggesting potentially significant role of the decomposition processes in P availability. However, microbiological activity and decomposition processes varied between the study plots. Forest floor accumulation was lower in plot 1 than in the other forested plots. In addition, in plot 1, the humus accumulation soil horizon (A + AE) tended to be thinner and the C stocks in the entire soil profile lower than in the three other plots. Following previous observations (Fisher and Binkley, 2000; Augusto et al., 2002; Guckland et al., 2009; Hansen et al., 2009), such differences in organic material accumulation result more from different decomposition rates (higher in plot 1) than from differences in litter production, since the study sites are located in the same climatic region (i.e. at the same latitude). Litterfall was not determined in the present study. However, based on stand characteristics and productivity, litter production may be similar or even lower in plot 4. Therefore, high accumulation of organic materials would imply that decomposition rates are low in this plot. In addition, the incubation experiment showed that the forest floor from plot 1 displayed the lowest proportion of the readily available organic pool (see Fig. 1), suggesting that a larger part of this organic pool had decomposed before soil sampling in this plot. Based on these results and also data obtained on the mineral soils (microbiological

activity including microbial biomass, soil respiration; enzymatic activity), we assume that decomposition and recycling processes were highest in plot 1. This is in agreement with the results on the P status: considering the three adjacent plots 1 to 3, probably due to high microbiological activity and fast decomposition processes, plot 1 displayed in general the lowest fractions of total organic P and consequently the highest fractions of available phosphate ions (in absolute numbers or as a percentage of total P; see Tables 3, 5, 6 and Figs. 3 and 4). Despite similar parent material (loess), plot 4 displayed lower total P concentrations, compared with the three adjacent plots 1 to 3. To account for this variability and to assess the effects of microbiological activity and decomposition processes on the different organic and inorganic P fractions, P fractions are not discussed in absolute numbers but are considered relative to the total P concentration (De Schrijver et al., 2012). Although plot 4 had generally low microbial and enzymatic activities and slow recycling processes (e.g. high stocks of forest floor), total organic P in this plot (in % of total P) was similar or lower than those in the three other plots (Fig. 4). However, in addition to the microbiological activity, P fractions could also be affected by the soil properties (see an example in Fig. 4). Owing to differences in Al and Fe oxides concentrations and soil pH, stabilization of organic P and protection from microbial and enzymatic biodegradation may be less important in plot 4 than in the three other plots (Giesler et al., 2004; Celi and Barberis, 2005; Turner et al., 2005; Vincent et al., 2012). Accordingly, positive relationships between total organic P and Al and Fe oxides were found in the entire mineral soil profile (Table 2) or in a given soil layer (e.g. A + AE or A horizon; $r^2 = 0.68$; $P < 0.0001$).

4.3.3 Possible effects of vegetation and climate

Differences between plots in the decomposition processes and therefore P status (Sect. 4.3.2.) may be explained as an effect of vegetation and an effect of local climate. However, our experiment was not designed to statistically test these effects of vegetation and climate directly, and we here discuss our emerging trends in our results in the context of other studies.

We found no significant differences in any soil characteristics in the Bt horizon among the three adjacent plots in the low Salair mountain site (Table 1), and differences found in top soil characteristics may be due to an effect of vegetation (Augusto et al., 2003). Compared to plot 2 (under *A. sibirica*), plot 1 (under *P. tremula*) displayed faster decomposition processes, higher microbiological activity, and soil pH and organic matter quality more favourable to microbial activity and decomposition (higher soil pH, higher concentrations of N, P, Ca, and K in the forest floor and lower lignin/N, C/N and C/P ratios). All these results are in agreement with the differences generally observed between evergreen coniferous and deciduous broadleaf trees (e.g. Cornwell et al., 2008;

Guckland et al., 2009). In plot 3 (forest gap), the lack of forest floor accumulation may result from fast litter decomposition of the herbaceous forbs (Cornwell et al., 2008). However, microbiological activity was low in the mineral soil. This may be explained by low root density and an absence of ectomycorrhizal fungi (in the absence of trees) and consequently low exudation of C available for the microorganisms and of phosphatase exoenzymes (Read et al., 2004; Lambers et al., 2008; Richardson and Simpson, 2011).

Decomposition processes were higher in plot 1 (plot under *P. tremula* in the low Salair mountains) than in plot 4 (plot under *P. tremula* in the forest steppe site), and this difference may be explained by different local climate (higher precipitation and insulating effect of the snow cover in the low Salair mountains; Groffman et al., 2001; Nobrega and Grogan, 2007). Soil freezing was shown to strongly reduce rate of soil respiration (Mikan et al., 2002), and we speculate that microbiological activity and decomposition processes during the winter period may be lower in the frozen soils of the forest steppe site than in the unfrozen soils of the low Salair mountain site. Also, precipitation is lower in the forest steppe site (Lashchinskiy, 2009), and this may result in lower soil moisture and consequently lower decomposition rates (Aerts, 2006). Climate may also affect decomposition processes indirectly through effects on plant litter quality (phenotypic responses) and decomposer communities (Aerts, 2006). Accordingly, plot 4 displayed low microbiological and enzyme activities and low organic matter quality (low nutrient concentration, high lignin/N, C/N and C/P ratio), which is consistent with the low decomposition rates in this plot. In addition to a potential effect of local climate, differences between plots 1 and 4 may also be explained by different soil properties (e.g. total P, pH, Al and Fe oxides) which may also influence decomposition processes (Fisher and Binkley, 2000; Giesler et al., 2004; Celi and Barberis, 2005; Guckland et al., 2009). Consequently, both local climatic conditions and soil properties may explain the differences observed between plots 1 and 4 in the decomposition processes.

5 Conclusions

Concentrations of total P (879–1042 μg g^{-1} in the surface mineral soils) and plant-available phosphate ions (e.g. diffusive phosphate ions in one week = 83–126 μg g^{-1}) of the studied Siberian forest soils were high compared with other ecosystems with permanent vegetation. In addition, there was an accumulation of diffusive phosphate ions in the subsoil. Therefore, whenever root systems can go deeper into the soils in our studied ecosystems, this would permit accessing a substantial amount of available phosphate ions. Any potential stimulation of growth and C sequestration due to climate change seems thus not P-limited. High proportions of total organic P (up to 47–56 % of total P) show that decomposition
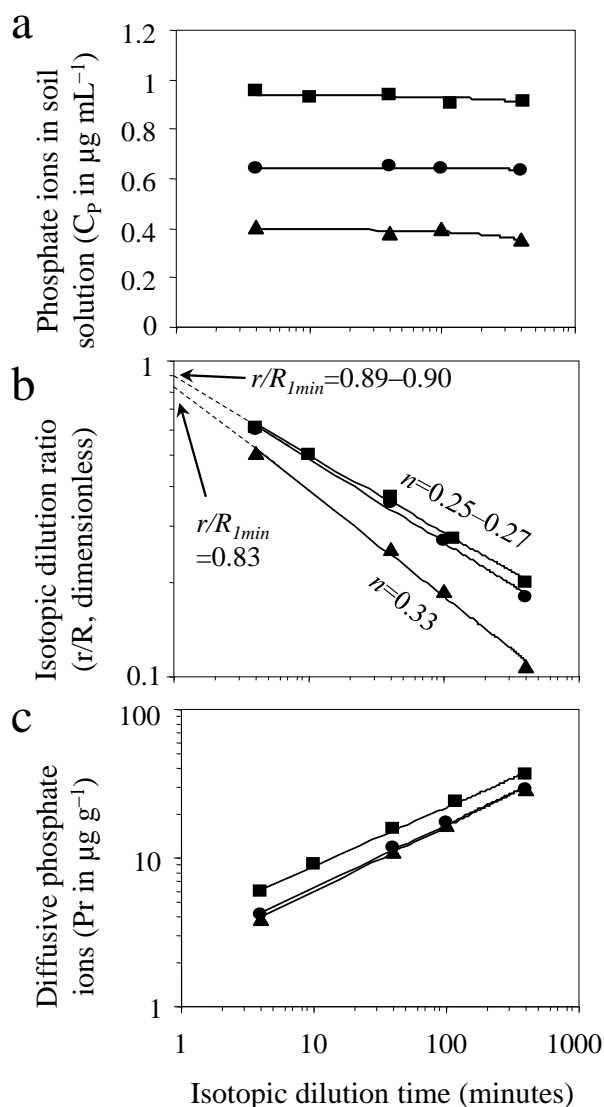
Fig. A1. Concentration of phosphate ions in soil solution (C_P in **a**), isotopic dilution ratio (r/R in **b**) and diffusive phosphate ions (Pr in **c**) as a function of isotopic dilution time. Example for the A + AE soil horizon of plot 1. The different symbols represent the different soil sub-replicates or zones. No time dependence of C_P in (**a**) (linear regression: $P > 0.05$). Adjustment of Eq. (5) in (**b**): $r^2 > 0.994$; $P < 0.0001$. Adjustment of Eq. (6) in (**c**): $r^2 > 0.998$; $P < 0.0001$. Mean concentrations of phosphate ions in soil solution and parameters of Eqs. (5) and (6) are given in Table 6.

processes, P dynamics and availability in the study acidic forest soils were also affected by the soil properties, namely Al and Fe oxides and soil pH. To our knowledge, the present study enabled a first extensive assessment of soil P status in relation to microbiological and physicochemical soil properties in Siberian forest sites. The Siberian forest is however huge, and relationships between soil P status, decomposition processes and soil properties should be studied over larger ranges of site conditions.

processes potentially play a significant role in P availability, particularly in the surface soil horizons. However, results also point out that microbiological activity and decomposition processes varied between the study plots. In the present study, higher microbiological activity and decomposition processes generally resulted in lower contributions of organic P fractions to total P and consequently larger available inorganic P fractions. In addition to the decomposition

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