**Biogeosciences
Discussions**

Phosphorus status of soils from contrasting forested ecosystems in Southwestern Siberia: combined effects of plant species and climate

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BGD

9, 6365–6408, 2012

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Abstract

The Russian boreal forest, which mainly consists of extensive forests in Siberia, is the largest continuous forest region on Earth and represents 70 % of the world's boreal forest. 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 deeper to increase access to mineral P. Improved understanding and quantification of the processes controlling P availability in surface and deep soil layers of forest ecosystems are thus required. Relative contributions of organic and inorganic P and, consequently, P availability in forest ecosystems depend on decomposition processes, which could be strongly affected by vegetation composition, temperature, precipitation, and their changes due to a warming climate. The objectives of the present study were to (1) evaluate P status of surface and deep forest soil horizons from two contrasted biomes in Southwestern Siberia (i.e. forest steppe in the West Siberian plain and blackish ("chernevaya" in Russian) taiga in the low Salair mountains) and (2) assess the effects of vegetation (siberian fir stand, common aspen stand and herbs in a forest gap) and local climate on soil P fractions. Results revealed high contents in total P (645–1042 $mg\,kg^{-1}$ in the surface mineral soils) and available inorganic P (diffusive phosphate ions in one week = 83–126 $mg\,kg^{-1}$). In addition, there was an accumulation of diffusive phosphate ions in the subsoils resulting from differences between soil horizons in total inorganic P and soil properties. Consequently, deeper root systems may mine substantial amounts of available P for the trees and the potential enhanced growth and C sequestration due to climate change should thus a priori not be P-limited. High proportions of total organic P (47–56 % of total P in the surface mineral soils) show that decomposition processes potentially play a significant role in P availability. Results show that decomposition processes are affected by vegetation (deciduous broadleaved trees, evergreen coniferous, herbs) and local climate (precipitations; snow cover with its isolating effect on soil). Results on the effects

of plant species and local climate improved our understanding of the potential effects of climate change on P availability through warming and vegetation redistribution.

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 fertility level, moisture and soil 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 (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 it is often as limiting as N (Elser et al., 2007) and low P availability can constrain N_2 fixation (Wang et al., 2007; Vitousek et al., 2010). 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, in response to P scarcity, trees may mine the soil deeper to take up more nutrients (Thomas et al., 1999; Iversen, 2010). 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, from which a large part consists of extensive coniferous forests in Siberia (i.e. the taiga), 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, at least during the next century (MEA, 2005; Luo et al., 2006; IPCC, 2007). However, soil fertility (e.g. P availability in the surface and deep soils), which may limit C sequestration (Reich et al., 2006), has to be evaluated in this region.

⁵ Decomposition processes are assumed to play a significant role in P availability in forest soils, since organic P fractions generally represent high proportions of total P in such ecosystems with permanent vegetation (Attiwill and Adams, 1993; Achat et al., 2009). Temperature and precipitation are low and winter periods long in Siberia, and this hampers microbial activity, organic matter decomposition (Huston and Wolverton, ¹⁰ 2009) and consequently soil P availability. Future climate scenarios show that this region will warm by 2° to 10 °C during the next century (IPCC, 2007; Soja et al., 2007) and, consequently, decomposition processes may be stimulated. A warming climate and an increase in annual precipitation will also affect vegetation distribution and composition in Siberian forests (Soja et al., 2007; Shuman et al., 2011), and decomposition pro- ¹⁵ cesses are known to be strongly affected by (dominant) tree species (e.g., Voriskova et al., 2011). Therefore, in addition to an assessment of soil P status in surface and deep soil layers, our knowledge basis on the effects of vegetation, environmental conditions and their changes on decomposition processes in Siberian forests has to be improved. Together this will permit to quantify P availability for trees and to enable us ²⁰ to assess the extent to which C sequestration will potentially occur.

The low Salair mountains (400–500 m a.s.l.) 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, which represent a natural combination of forest islands (mostly white birch and com- ²⁵ mon aspen) and dry meadows. In contrast, vegetation of the humid areas of the Salair mountains is blackish ("chernevaya" in Russian) taiga with Siberian fir and common aspen as main dominant trees (Chytry et al., 2008; http://www.terrestrial-biozones.net/index.html). Precipitations are twice as high in the Salair mountains, as compared to the surrounding forest steppe biomes (Lashchinskiy, 2009). It results in thicker snow

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cover and higher isolating effect on soils in the blackish taiga than in the forest steppe. This region is thus an appropriate model system to assess the effects of vegetation and local climate on decomposition processes and P availability in Southwest Siberian forest ecosystems. Furthermore, information on the effects of vegetation and local cli-
5 mate would help to elucidate the effects of climate change on P availability through warming and vegetation redistribution.

The objectives of the present study were to (1) evaluate P status (total P, relative contributions of total organic and total inorganic P, available inorganic P: phosphate ions (iP) in soil solution and diffusive iP) of surface and deep forest soil horizons from
10 two contrasted biomes in Southwestern Siberia (i.e. one site in the forest steppe, in the West Siberian plain, referred as "lowland site" in this study; one site in the blackish taiga, in the low Salair mountains, referred as "upland site" in this study) and (2) assess the effects of vegetation and local climate on soil P fractions. We studied forest plots with different dominant vegetation, which are common in the studied region, i.e.
15 common aspen (*Populus tremula*), siberian fir (*Abies sibirica*) and herbs in forest gaps. Our first initial hypothesis was that vegetation affects soil P status (distribution of total P in organic and inorganic P forms, and consequently P availability) through litter quality (e.g. lignin and C/N and C/P ratio), physical-chemical soil properties (e.g. soil pH), microbiological activity, and therefore decomposition processes (e.g., Augusto et al.,
20 2002; Ushio et al., 2010; Voriskova et al., 2011). Our second hypothesis was that local climate in Southwestern Siberia also affects the distribution of total P in organic and inorganic P forms, and therefore P availability, through direct effects on litter decomposition and indirect effects on litter quality and microbial community (Aerts, 2006). The blackish taiga sites feature twice higher productivity than the lowland forest-steppe sites
25 and we suggested that higher precipitations and a thicker snow cover (and its isolating effect on soils) in the upland sites would enable higher activity of soil microbial communities, faster decomposition processes and higher nutrient availability. Therefore, in addition to an evaluation of the P status, we also assessed stocks of forest floor, thickness of the humus accumulation horizon, physical-chemical and microbiological soil

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properties (microbial biomass and enzyme activity), quality of organic matter and soil respiration.

2 Material and methods

2.1 Study sites, description of soil profiles and soil sampling

We studied three adjacent plots located in the blackish taiga in the Salair mountains (one with a deciduous broadleaved species dominating the canopy (*P. tremula*); one with an evergreen needle leaved species dominating the canopy (*A. sibirica*); one 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. One additional plot (with *P. tremula* dominating the canopy) was located in the northern part of 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.

Soils of the Salair mountain site are Orthieutric Albeluvisols (WRB, 2006), also known as soddy deeply podzolic soils in the Russian soil classification, whereas Albic Luvisols (grey forest soils) characterize the lowland site. All soils have been developed from loess deposits (Chlachula, 2011) and have comparable particle size distribution (1–7 % sand, 73–84 % loam, 13–21 % clay). 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 Salair mountains, average annual precipitation reaches 700–1000 mm at the southwest macroslope 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 isolating effect of a permanent snow cover, which reaches 100–250 cm depth during 160–180 days. For the lowland site, average annual precipitation is only 450 mm and average temperatures are −18.5 °C in January and +18.9 °C

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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 Salair mountain site, soils in the lowland forest site are frozen in winter down to 60–80 cm.

We compared the three adjacent plots in the Salair mountain site (*P. tremula*, *A. sibirica*, forest gap with herbaceous plants) to evaluate the effect of vegetation types on P status, and we compared the two sites with *P. tremula* (Salair mountain vs. lowland site) to evaluate the effects of climate and soil freezing. All studied stands with *P. tremula* and *A. sibirica* were mature and displayed close 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 yr) and densities (150–230 tree ha^{-1}). For the upland site and the lowland site, respectively, tree height was 22–26 and 16–18 m, stand basal area was 3.5–5.5 and 2.4 m^2 ha^{-1} and mean tree diameter at breast height was 18–20 and 14–15 cm.

Soil sampling was carried out in June and July 2010. In each plot, three representative zones were chosen. 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 thickness of each soil horizon was measured. 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 replicates per plot and per soil horizon). A second soil sampling was carried out for further soil analyses. Subsamples of forest floors and subsamples of 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 physical-chemical soil properties and P status (total P, total organic P, total inorganic P, diffusive iP and iP in soil solution). All analyses on dried mineral soils were carried out on each individual soil replicates (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.

2.2   Main physical-chemical and microbiological soil properties

Total organic C and N 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 (20 g : 50 ml). 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 Alef et al.'s (1995) procedure.

2.3   Soil P status

2.3.1   Total, total organic, total inorganic and microbial P

Total P content of soil samples was determined by wet digestion with concentrated fluoric (HF) and perchloric acids after calcination at 450 °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 studied mineral soils and forest floors (total P-HF = 1.00 × P-H_2SO_4 + 163.98; r^2 = 0.99; $P < 0.0001$; n_{obs} = 54).

Total soil organic P was determined using the Saunders and Williams' (1955) procedure, 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 was subsequently calculated as total P-HF minus total organic P. Microbial P was quantified in moist soils using a fumigation-sorption-extraction method (Morel et al., 1996), which accounts for the rapid sorption reactions of iP 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).

2.3.2 Available phosphate ions: diffusive iP and iP in soil solution

In this study, we quantified the diffusive iP at the solid-to-solution interface (Pr), resulting from molecular agitation. This mechanism of diffusion leads to a transfer of iP from the solid constituents to the soil solution under a gradient of concentration (Jungk and Claassen, 1997). Diffusive iP was quantified as a function of time using an isotopic labelling and dilution procedure during batch experiments with soil suspensions at steady state (e.g. constant concentration of iP in soil solution; Fardeau, 1996; Frossard and Sinaj, 1997; Morel, 2007).

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 °C. The amount of iP in soil solution (P_W in mg kg^{-1}) 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 the concentration of iP in the soil solution (C_P in mg l^{-1}) 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 colori-metric 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):

$$P_W = C_P \cdot \frac{V}{M} \qquad (1)$$

During the 400 min-period of isotopic dilution with pre-equilibrated soil suspensions, C_P was constant (see examples in Fig. 1a). In such a steady state, the gross rate of iP desorption from the soil solid phase to solution is equal to the gross rate of iP sorp-tion onto the solid phase. We further assumed that no isotopic discrimination occurs between the two P isotopes ($^{31}PO_4$ and $^{32}PO_4$) during the exchange between the solu-tion and the solid constituents. The amount of unlabeled iP newly transferred from the solid constituents to the solution (Pr) was thus calculated from P_W and r values, using the principle of isotopic dilution and the isotopic composition ratio:

$$\text{Isotopic composition ratio} = \frac{r}{P_W} = \frac{R - r}{Pr} \qquad (2)$$

Rearranging Eq. (2) gives:

$$Pr = \frac{P_W \cdot (R - r)}{r} = P_W \left(\frac{1}{r/R} - 1 \right) \qquad (3)$$

where r/R is the isotopic dilution ratio.

The theoretical Eq. (4) adapted by Fardeau (1996) was used to closely fit the exper-imental values of r/R as a function of time (see examples in Fig. 1b).

$$r/R = r/R_{1\text{min}} \cdot (\text{time}^{-n}) \quad \text{for} \quad r/R \geq r_\infty/R \qquad (4)$$

where r_∞/R 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

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calculated as the ratio of P_W to total inorganic P (Fardeau, 1993). The r/R_{1min} and n parameters account for the immediate and the slow physical–chemical reactions, respectively. Parameter r/R_{1min} describes the rate of disappearance of the tracer from the solution after 1 min (Frossard and Sinaj, 1997). The n parameter ranges from 0 to 0.5 (Fardeau, 1993). When n parameter is zero, there is no time dependence of diffusion at the solid-to-solution interface whereas when 0.5 is reached, diffusion is theoretically the greatest. These parameters enable evaluation of iP reactivity with the solid constituents or phosphate mobility in the soil-water system (Frossard et al., 1989).

For a given soil sample, measured values of Pr were described by the kinetic Eq. (5) (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 Fig. 1c):

$$P_r = Pr_{1min} \cdot time^p \tag{5}$$

Where parameter Pr_{1min} is the amount of diffusive iP in one minute and parameter p accounts for the time dependence. These parameters were used to extrapolate Pr to more relevant time scales (up to one year in the present study).

Values of C_P, isotopic dilution parameters and Pr varied between soils (see Fig. 1). We thus tested whether differences between soil samples in C_P and Pr values resulted from different physical-chemical soil properties and therefore different iP dynamics 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. (5) used for each individual soil sample (see Fig. 1), we also tested whether a kinetic Freundlich equation could be used to describe the dynamics of the iP transfer kinetics at different C_P levels, providing that physical-chemical soil properties are similar between soil samples:

$$P_r = v \cdot C_P^w \cdot time^p \tag{6}$$

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Where v, w and p are adjusted parameters: v is the Pr value after one minute for a concentration of iP in soil solution of $1\,mg\,l^{-1}$; w accounts for the changes in Pr with increasing C_P values; p accounts for the changes in Pr with time.

2.4 Soil respiration and quality of organic matter

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 ($0.33–0.38\,ml\,g^{-1}$ for the mineral soils; $1.51–1.97\,ml\,g^{-1}$ for the forest floors) and incubated at 20 °C. Moist fresh 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 (C-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 C-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, 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 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. 7; Li et al., 2003).

$$\text{Cumulative net C mineralization} = AO \cdot (1 - e^{-k_{AO} \cdot time}) + k_{RO} \cdot time \qquad (7)$$

Where AO and k_{AO} represent the pool size and the first-order rate of mineralization of the readily available organic pool, respectively, and k_{RO} is the rate of mineralization of the recalcitrant organic pool.

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In addition to an assessment of soil respiration, we also evaluated organic matter quality (contents in C, N, P, K, Ca, Mg, Mn and lignin and lignin/N ratio for the forest floors; calculations of C/N and C/P for all forest floor and mineral soil samples; Hättenschwiler and Gasser, 2005; Berg et al., 2010; Blanco et al., 2011). Aliquots of
5 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
10 acid hydrolysis of the residue remaining after extraction with acetone (Vazquez et al., 1995).

2.5 Data processing and statistics

In addition to the contents of C, N and P in soils, stocks were calculated using the masses of forest floor and the thickness of the mineral soil horizons with their bulk
15 density.

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. Linear and non-linear procedures were also used to assess the relationships between the isotopic dilution parameters ($r/R_{1\text{min}}$ and n), iP concentration in soil solution and
20 physical-chemical soil properties. For a given soil horizon, differences between plots (or composite samples) in the different physical-chemical soil properties and P status variables were tested using one-way ANOVA and the Bonferroni t-test. Differences between stocks in the entire soil profile and between surface mineral soils (i.e. A + AE horizon for the upland site and A horizon for the lowland site) were also tested. Prior
25 to this, quantity variables were log-transformed and proportion variables were arc-sine transformed to comply with model conditions. All statistics were preformed with SYSTAT software (2000).

3 Results

3.1 Soil profiles, physical-chemical and microbiological properties

3.1.1 General description

Beneath the forest floors (F), soil profiles were differentiated between humus accumu-
lation, eluvial and illuvial soil horizons (A + AE, E, EBt and Bt in the upland site; A, AE
and Bt in the lowland site) and, in general, the physical-chemical soil properties were
significantly different between soil layers. Total C, total N and Al and Fe oxides contin-
ually decreased with increasing soil depth, while the surface mineral horizons (A + AE
or A) displayed the most acidic soil pH (Table 1). The microbial biomass and the acid
phosphatase activity were also significantly affected by the soil depth and were higher
in the composite samples of forest floor (Table 1).

3.1.2 Comparison among vegetation types in the Salair mountains

Stocks of forest floor were higher with *A. sibirica* than with *P. tremula*, while there was
no forest floor in the forest gap (Table 1). In contrast, the thicknesses of humus accu-
mulation soil horizon (A + AE) and total C and N in a given soil layer (Table 1) or in the
entire soil profile (stocks in Table 2a) were in general not significantly different between
plots. It was also the case for the contents in Al and Fe oxides. The soil pH was more
acidic with *A. sibirica*, with significant differences in the forest floor (composite sample)
and the surface mineral soil (Table 1). Concerning the microbiological soil properties,
moist composite samples from the plot with *P. tremula* displayed the highest values of
microbial biomass, and those from the forest gap the lowest. Acid phosphatase activity
was also lower in the composite samples from the forest gap and was not different
between composite samples from the two other plots (Table 1).

3.1.3 Comparison between Salair mountains and lowland site with *P. tremula*

Considering the stands with *P. tremula*, the stock of forest floor was higher and the humus accumulation soil horizon (A + AE horizons) thicker in the lowland site than in the upland site (Table 1). For a given soil layer, contents in total C and total N were in general not different between plots (excepted for the composite samples of forest floor; Table 1). However, owing to thicker humus accumulation horizon, stocks of total C in the entire soil profile tended to be higher in the lowland site (Table 2a). Contents in Al + Fe oxides were significantly lower and the soil pH significantly less acidic in the lowland site than in the upland site (Table 1). The microbial biomass and phosphatase activity were also lower in the moist composite samples from the lowland site than those from the upland site (Table 1).

3.2 Soil P status

3.2.1 General description, depth effect and relationships with soil properties

Total P ranged from 645 to 1042 mg kg^{-1} in the mineral soils and was up to 2380 mg kg^{-1} in the forest floors (Table 3). The different P fractions were significantly affected by the soil horizons. Total P and total organic P continually decreased with increasing soil depth, while total inorganic P was higher in the subsoil (Bt horizon) than in the surface soil horizons. Up to 56 % of total P was in organic forms (mean of 53 % for the surface mineral soils and the four plots) and this proportion decreased with increasing soil depth (Table 3). 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 available iP, experimental values of C_P and Pr in 400 min in surface mineral soils were 0.24–0.65 mg l^{-1} and 23–32 mg kg^{-1}, respectively (Table 4). Using parameters Pr_{1min} and p, extrapolated Pr values were 83–126 mg kg^{-1} after one week, 145–233 mg kg^{-1} after one month and 379–466 mg kg^{-1} after one year, which

was equivalent to total inorganic P (405–472 mg kg^{-1}). Values of C_P, parameters of the equations describing the isotopic dilution ratio and Pr as a function of time, and Pr in 400 min were affected by the soil horizons. For instance, parameter r/R_{1min} decreased, parameter n increased, and therefore reactivity of iP with the solid constituents in-
5 creased with increasing soil depth. The C_P and Pr values could also vary between sites (Table 4). In general, variability in the isotopic dilution parameters was mainly re- lated to the variability in the C_P values (less reactivity with high C_P values; Fig. 2a, b). However, these relationships were also affected by the soil horizons (see arrows in Fig. 2a, b), owing to differences in physical-chemical soil properties, namely Al and Fe
10 oxides, soil pH and total C (Fig. 3a, b). Because, in a given soil horizon, soil properties were generally similar between the three adjacent plots in the upland site (*P. tremula*, *A. sibirica* and forest gap; see Table 1), iP dynamics was similar between plots and Pr could be closely described as a function of time and C_P according to a single Freundlich kinetic equation (Fig. 2c, d).

15 ### 3.2.2 Comparison among vegetation types in the Salair mountains

All P fractions were higher in the forest floor from the *P. tremula* plot than the forest floor from the *A. sibirica* plot (Table 3). Considering the mineral soils (Table 3) or the entire soil profile (Table 2b, c), total P was not significantly different between plots, while total organic P (in mg kg^{-1} or in % of total P) could be significantly lower and total inorganic
20 P and microbial P significantly higher in the plot with *P. tremula* than in the plot with *A. sibirica* and the forest gap.
    For the forest floor and the surface mineral soil horizon (A + AE), available iP (C_P, Pr$_{1min}$ and Pr$_{400min}$) was significantly higher with *P. tremula* than with *A. sibirica*, values for the forest gap being intermediate (Table 4). However, there was no significant dif-
25 ference between plots in available iP in the deep soil horizons (excepted C_P in the Bt horizon; Table 4) and consequently in the entire soil profile (Table 2b).

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3.2.3 Comparison between Salair mountains and lowland sites with *P. tremula*

All P fractions in a given soil horizon (total P, total organic, total inorganic P and microbial P in Table 3; available iP: diffusive iP in Table 4) or in the entire soil profile (Table 2b) were in general significantly lower in the lowland site than in the upland site. However, the proportion of total P that was in organic forms was not significantly different between the two sites (Tables 3, 2c).

3.3 Soil respiration and quality of organic matter

3.3.1 Comparison among vegetation types in the Salair mountains

Compared with the *A. sibirica* plot, the composite sample of forest floor from the *P. tremula* plot displayed higher cumulative and daily soil respirations and lower contributions of the readily available organic fraction (% AO) to the total amount of mineralized C (Fig. 4a, b). However, these differences in daily soil respiration were only visible during the first 20 days of incubation (Fig. 4b). Concerning the surface mineral soil horizon, composite sample from the *P. tremula* plot displayed higher soil respiration and higher contributions of the readily available organic fraction than the composite samples from the *A. sibirica* plot and the forest gap (Fig. 4c, d). However, differences in soil respiration between samples from *P. tremula* and *A. sibirica* occurred only during the first 55 days of incubation (Fig. 4d). In addition to differences in soil respiration, there were also differences in organic matter quality: generally lower contents in nutrients (excepted Mg and Mn in forest floors), higher lignin contents, and higher lignin/N, C/N and C/P ratios with *A. sibirica* and higher C/N and C/P ratio in the microbial biomass with *A. sibirica* and the forest gap (Table 5; see also Tables 1 and 3 for N and P contents in the forest floors).

3.3.2 Comparison between Salair mountains and lowland sites with *P. tremula*

Considering the stands with *P. tremula* and the forest floors, soil respiration and the contributions of the readily available organic fraction (% AO) to the total amount of mineralized C were lower in the composite sample from the upland site than that from the lowland site (Fig. 4a, b). Inversely, for the surface mineral soils, soil respiration and contributions of the readily available organic fraction were higher in the composite sample from the upland site than that from the lowland site (Fig. 4c, d). There were also differences between sites or composite samples in organic matter quality and C/N and C/P ratio in the microbial biomass (in general, lower ratio in the upland site; Table 5).

4 Discussion

4.1 First objective: general P status of surface and deep Siberian forest soils

Total P in the surface mineral soils (645–1042 mg kg^{-1}) was in the upper ranges of values reported in other ecosystems with permanent vegetation (e.g. mean of 30 forest soils = 557 mg kg^{-1}; mean of 71 grassland soils = 919 mg kg^{-1}; in Achat et al., 2009). In addition, values for available iP (diffusive iP in one week = 83–126 mg kg^{-1}) were comparable to mean values reported in the literature for grasslands (mean of 20 soils = 126 mg kg^{-1}) and agricultural croplands (mean of 31 soils = 75 mg kg^{-1}) and high compared with one P-deficient forest ecosystem in Southwestern France (mean of 18 soils = 17 mg kg^{-1} in Achat et al., 2009; no data for other forest contexts available for comparison), suggesting that the studied Siberian forest soils are probably not P-deficient. Similarly to other forest ecosystems under the same latitude (Hedin et al., 2009), the studied forest floors displayed low $N : P$ ratio ($N : P$ ratio = 10–12). This shows that P is abundant relative to N. According to Huston and Wolverton (2009), great concentrations of P can be explained by low temperature and/or relatively low

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precipitation at latitude 54–55°, and therefore low rates of nutrient loss through mineral leaching and, for the lowland site, low 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).

⁵ Owing to differences between soil horizons in total inorganic P and soil properties (poorly crystalline Al and Fe oxides, soil pH and total C, see Figs. 2, 3; Strauss et al., 1997; Achat et al., 2011), diffusive iP varied with soil depth and accumulated in the sub-soils. Consequently, deeper root systems (Thomas et al., 1999; Iversen, 2010) would lead to substantial amounts of available iP for the trees. This suggests that the poten-
¹⁰ tial for enhanced growth and C sequestration would a priori not be P-limited. However, further studies should focus on the potential N limitations in these ecosystems (Reich et al., 2006).

Similarly to other context with permanent vegetation (Attiwill and Adams, 1993; Achat et al., 2009) and owing to the continuous input of organic materials from litter and
¹⁵ root turnover (De Schrijver et al., 2012), total organic P fractions represented high proportions of total P in the surface soil layers (47–56 % in the A or A + AE horizon) and these proportions of total organic P decreased with increasing soil depth. This shows that microbiological processes potentially play a key role in P cycle and iP availability in the studied forest soils, especially in surface soil layers, through mineralization of
²⁰ soil organic matter (Attiwill and Adams, 1993). However, decomposition processes and therefore iP availability in the studied forest sites depend on the vegetation types and environmental conditions (see next sections). Microbial P, which generally displays fast turnover (Achat et al., 2010), represents up to 16 % of total P in the present study. Therefore, micro-organisms can also act as a significant source of available iP through
²⁵ the remineralization process (i.e. release of microbial P after cell death; Achat et al., 2010; Richardson and Simpson, 2011).

4.2 Second objective: effects of vegetation and local climate on soil P status (conceptual diagram in Fig. 5).

4.2.1 Comparing adjacent plots in the Salair mountains: effects of vegetation

The main problem in studying the effect of vegetation is to determine if the soil chemical properties are the consequence or the cause of the spatial distribution of plant species. To overcome this drawback, common garden are suitable but are not easily available. In "natural" forests, like in our context, one has to check for any relationship between soil properties and vegetation distribution, all over in deep soil layers where the effect of vegetation is often nil (Augusto et al., 2003). We compared on this purpose the properties of the Bt horizon among the three plots. It appeared that there were no difference in total contents in C, N and P or pH value and only slight differences in oxides content (see Tables 1 and 3). We consequently assumed that the studied plots were comparable.

Compared to the plot with *A. sibirica*, the plot with *P. tremula* displayed lower accumulations of forest floor, which can be explained by higher decomposition rates (e.g., in this study, higher C mineralization during the incubation experiments). This explanation agrees with Fisher and Binkley (2000), Augusto et al. (2002), Guckland et al. (2009) and Hansen et al. (2009) who found that tree species growing under similar soil and climatic conditions do not influence the amount of litterfall inputs to the forest floor and that large variability in forest floor accumulation are primarily attributed to differences in litter decomposition. The composite sample of forest floor from the *P. tremula* plot also displayed the lowest proportion of readily available organic pool (%AO), suggesting that a larger part of this organic pool has decomposed before soil sampling in this plot. This is in agreement with previous observations, which suggest that evergreen coniferous litters decompose in general more slowly than litters from deciduous broadleaf trees (Cornwell et al., 2008; Voriskova et al., 2011). Different decomposition rates between plant species are generally attributed to different chemical composition of dead litter (e.g. contents in nutrients, especially N and P; lignin content), which affects

fungal community composition and biomass and enzyme production (Hättenschwiler and Gasser, 2005; Cornwell et al., 2008; Treseder, 2008; Gusewell and Gessner, 2009; Berg et al., 2010; Ushio et al., 2010; Voriskova et al., 2011). In the present study, differences between composite samples in forest floor quality (lower contents in N, P, Ca, and K and higher lignin/N, C/N and C/P ratios with *A. sibirica*) and microbial biomass (lower with *A. sibirica*) were in general consistent with differences in decomposition rates (lower with *A. sibirica*). Soil fauna, with its significant roles in the acceleration of organic matter decomposition (Xin et al., 2012), is also differently influenced by tree species (Augusto et al., 2002; Xin et al., 2012). For instance, earthworm density is in general lower under conifers than under hardwood species (Augusto et al., 2002), and is positively correlated with Ca contents in litters (Reich et al., 2005). In the present study, results on the samples of forest floors suggest that Ca contents could be higher beneath *P. tremula* than *A. sibirica*, and this may be in line with the lower decomposition rate and higher forest floor accumulation beneath *A. sibirica*. A difference of 0.5–0.7 pH unit in the forest floor and the top mineral was also found between the studied tree species, which agrees with previous observations (Augusto et al., 2002). Soil was more acidic with *A. sibirica* and this probably affected faunal composition (Augusto et al., 2002) and hampered organic matter decomposition (Guckland et al., 2009). Decomposition processes and enzyme activities also depend on soil moisture (Ushio et al., 2010), which can be affected by tree species due to differences in interception loss (evaporation of precipitation from the canopy without entering the soil or trees), transpiration and rooting depth (Augusto et al., 2002; Shugalei, 2005). In the present study, soil moisture was not monitored. However, topsoil moisture content may be higher under hardwoods compared to conifers (Augusto et al., 2002), and this may partly explain the higher decomposition rates under *P. tremula* in the present study.

In the forest gap, the lack of forest floor accumulation probably resulted from fast litter decomposition of the herbaceous forbs (Cornwell et al., 2008) and fast litter incorporation in the mineral soil. However, in the mineral soils, results suggest that microbial biomass, phosphatase activity and decomposition processes (in this study, C

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mineralization) were lower in the forest gap than in the two forest stands. This could be explained by differences in root density, and consequently root exudation and C available for the microorganisms (lower in the absence of aspen or fir overstory and their roots; Richardson and Simpson, 2011). In addition, trees could have ectomycorrhizal fungi which have great abilities to utilize organic nutrient pools, owing to exudation of phosphatases (Read et al., 2004, Lambers et al., 2008).

In agreement with our first hypothesis and with previous studies (e.g., Ushio et al., 2010; Voriskova et al., 2011), results suggest that vegetation types affect organic matter quality, soil pH, microbial biomass, enzyme activity and decomposition of soil organic matter in the Salair mountains, and this probably explains the significant differences between sites in P status (see conceptual diagram in Fig. 5). Owing to higher decomposition rates, the contribution of organic P fractions to total organic P were in general lower in the plot with *P. tremula* than in the two other plots. The Freundlich kinetic equation (see Fig. 2c, d) showed that differences in available iP (diffusive iP and iP in soil solution) between plots in a given soil horizon resulted more from different amounts of inorganic P in soils than from different physical-chemical soil properties and therefore different amounts of reactive surface and iP dynamic at the solid-to-solution interface (Morel et al., 2000; Achat et al., 2011). In other words, the vegetation affected iP availability in the Salair mountain site through the decomposition processes of organic matter and the distribution of total P in the different P fractions (higher inorganic fraction and consequently higher iP availability with *P. tremula*; higher organic fraction for *A. sibirica* and the forest gap).

4.2.2 Comparing the Salair mountain and lowland sites: effect of local climate

Stocks of forest floor and humus accumulation in the top mineral soil beneath *P. tremula* were higher in the lowland site than in the upland site. Such differences in organic material accumulation can result from differences in litter production and decomposition rates (Fisher and Binkley, 2000; Liski et al., 2003; Aerts, 2006). Litterfall was not determined in the present study, but the two sites were located in the same climatic region

(i.e. at the same latitude) and this might result in comparable litter production (Fisher and Binkley, 2000). However, based on stand characteristics and productivity, litter production may be higher in the upland site, due to local climate differences. Therefore, higher accumulation of organic materials in the lowland site implies that decomposition rates are lower in this site. This is in agreement with the results of the incubation experiment, which suggest that C mineralization rates in the top mineral soil are lower in the lowland site. Also, rates of C mineralization and contribution of the readily available organic pool to total mineralized C during the incubation with the composite samples of forest floor suggest that most of the readily available organic compounds in the lowland site have not been mineralized before soil sampling and that litter and forest floor decomposition processes are faster in the upland site.

Differences between lowland and upland sites in decomposition processes can be explained by different local climate (higher precipitation and isolating effect of the snow cover in the upland site; Groffman et al., 2001; Nobrega and Grogan, 2007). Soil microorganisms can survive and grow below $0\,^\circ$C because small amounts of water remain unfrozen and diffusion of microbial substrates and waste products are possible (Ostroumov and Siegert, 1996), and microbial respiration was shown in frozen soils even at $-10\,^\circ$C (Mikan et al., 2002) or $-16\,^\circ$C (Panikov, 1999). Therefore, although soils of the studied lowland site are frozen during the winter, microbiological activity and decomposition processes probably occur during this period. However, soil freezing strongly reduces rate of soil respiration (Mikan et al., 2002) and we conclude that microbiological activity and decomposition processes during the winter period are lower in the frozen soils of the lowland site than in the unfrozen soils of the upland site (due to the heating effect of the snow cover). Also, precipitations are lower in the lowland site, and this results in lower soil moisture and consequently lower decomposition rates (Aerts, 2006). In addition to the direct effects due to the high sensitivity of biological processes to temperature and water availability, climate also affects decomposition processes indirectly through effects on plant litter quality (phenotypic responses) and decomposer communities (Aerts, 2006). Results suggest that the lowland site displayed low microbiological

and enzyme activities and low organic matter quality (e.g., high lignin/N, C/N and C/P ratio), which is consistent with the low decomposition rates. However, we can not conclude that differences in organic matter quality and microbial activity result only from indirect effects of climate. Indeed, mineral soils of the lowland site display lower total P

5 contents and this may also affect litter and forest floor quality (Fisher and Binkley, 2000), and consequently fungal community composition and biomass and enzyme production (Voriskova et al., 2011). Inversely, soils of the lowland site displayed higher soil pH (of 0.2–0.5 pH unit) and lower contents in Al and Fe oxides, which favour in general degradation of organic compounds (Giesler et al., 2004; Celi and Barberis, 2005; Turner

10 et al., 2005; Guckland et al., 2009). To summarize: decomposition processes were lower and consequently organic material accumulation higher in the lowland site than in the upland site, and different decomposition processes resulted from local climatic conditions and to a lesser extent soil properties (see conceptual diagram in Fig. 5).

Despite similar parent material (loess), the two sites significantly differed in total P.

15 To account for this variability and to assess the effects of environmental conditions (mainly climate) 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). Contrarily to our second hypothesis, results showed that total organic P (in % of total P) was not significantly different between the lowland

20 and the upland sites. However, we can not conclude that different climatic conditions between the two sites (heating effect of the snow cover and precipitation) do not affect soil P status, since the different P fractions were also affected by the soil properties. Owing to differences in Al and Fe oxides contents and soil pH, stabilization of organic P was probably less important in the lowland site (Celi and Barberis, 2005; Turner et al.,

25 2005) and iP reactivity with the solid constituents and consequently diffusive iP were also affected (see comparison between the surface mineral soils of the two sites in Figs. 2a, b, 3; A + AE for the upland site, A and AE for the lowland site; Strauss et al., 1997; Achat et al., 2011). Further studies are thus needed to separately assess the

effects of climate and soil substrate on P status of forest soils in Southwestern Siberia (see Fig. 5).

4.2.3 Implications of vegetation redistribution and local climate change

Results of the present study show that relative contributions of organic and inorganic P fractions and therefore iP availability are affected by plant species, through several effects on organic matter decomposition. Consequently, changes in vegetation distribution (e.g. expansion of the transitional lowland forest-steppe biome, expansion of the blackish taiga across the Altai-Sayan mountains) and composition, due to a warming climate (Soja et al., 2007; Shuman et al., 2011), is also expected to affect soil P availability. Nutrient availability is also expected to be affected by the climate change through an effect of temperature and moisture on decomposition processes. In the lowland forest-steppe, decomposition rates are probably limited because soils remain frozen during long winter periods and precipitations are low. However, increases in temperature and precipitations are predicted in West Siberia and South Siberian mountains (IPCC, 2007; Soja et al., 2007) and higher precipitations could lead to thicker snow cover in winter, while the comparison between lowland and upland sites in the present study suggests that higher soil temperature (due to the isolating effect of the snow cover) and/or higher precipitations stimulate decomposition processes and probably nutrient availability. Higher precipitations and temperatures, and consequently, higher soil moisture and nutrient availability could lead to an increase in tree growth and C sequestration (Loustau et al., 2005; de Graaff et al., 2006; Dijkstra and Cheng, 2008), particularly in the forest steppe zone. Future researches should focus on the possible implications of vegetation redistribution and local climate change on nutrient availability and on the relationships between the present results and the future climate changes (see Fig. 5).

5   Conclusions

Contents in total P (645–1042 mg kg^{-1} in the surface mineral soils) and available iP (diffusive iP in one week = 83–126 mg kg^{-1}) of the studied Siberian forest soils were high compared with other ecosystems with permanent vegetation. In addition, there was an accumulation of diffusive iP in the subsoils, owing to differences between soil horizons in total inorganic P and soil properties. Consequently, deeper root systems would lead to substantial amounts of available iP for the trees and the potential stimulation of growth and C sequestration due to climate change may a priori not be P-limited. High proportions of total organic P (47–56 % of total P in the surface mineral soils) show that decomposition processes probably play a significant role in iP availability, but results also point out that decomposition processes are affected by dominant plant species (deciduous broadleaved trees, evergreen coniferous, herbs) and local climate (precipitations; snow cover and its isolating effect on soil). Results on the effects of plant species and local climate improved our understanding on the potential effects of climate change on iP availability through warming and vegetation redistribution.

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Achat, D. L., Bakker, M. R., Augusto, L., Saur, E., Dousseron, L., and Morel, C.: Evaluation of the phosphorus status of P-deficient podzols in temperate pine stands: combining isotopic dilution and extraction methods, Biogeochemistry, 92, 183–200, 2009.

Achat, D. L., Morel, C., Bakker, M. R., Augusto, L., Pellerin, S., Gallet-Budynek, A., and Gonzalez, M.: Assessing turnover of microbial biomass phosphorus: combination of an isotopic dilution method with a mass balance model, Soil Biol. Biochem., 42, 2231–2240, 2010.

Achat, D. L., Augusto, L., Morel, C., and Bakker, M. R.: Predicting available phosphate ions from physical-chemical soil properties in acidic sandy soils under pine forests, J. Soils Sediments, 11, 452–466, 2011.

Aerts, R.: The freezer defrosting: global warming and litter decomposition rates in cold biomes, J. Ecol., 94, 713–724, 2006.

AFNOR: Qualité des sols, in: Recueil de Normes, vol. 1, AFNOR, Paris, 1999.

Alef, K.: Soil respiration, in: Methods in Applied Soil Microbiology and Biochemistry, edited by: Alef, K. and Nannipieri, P., Academic Press, London, 214–219, 1995.

Alef, K., Nannipieri, P., and Trazar-Cepeda, C.: Phosphatase activity, in: Methods in Applied Soil Microbiology and Biochemistry, edited by: Alef, K. and Nannipieri, P., Academic Press, London, 338–339, 1995.

Attiwill, P. M. and Adams, M. A.: Nutrient cycling in forests, New Phytol., 124, 561–582, 1993.

Augusto, L., Ranger, J., Binkley, D., and Rothe, A.: Impact of several common tree species of European temperate forests on soil fertility, Ann. For. Sci., 59, 233–253, 2002.

Augusto, L., Dupouey, J. L., and Ranger, J.: Effects of tree species on understory vegetation and environmental conditions in temperate forests, Ann. For. Sci., 60, 823–831, 2003.

Berg, B., Davey, M. P., De Marco, A., Emmett, B., Faituri, M., Hobbie, S. E., Johansson, M. B., Liu, C., McClaugherty, C., Norell, L., Rutigliano, F. A., Vesterdal, L., and Virzo De Santo, A.: Factors influencing limit values for pine needle litter decomposition: a synthesis for boreal and temperate pine forest systems, Biogeochemistry, 100, 57–73, 2010.

Blanco, J. A., Imbert, J. B., and Castillo, F. J.: Thinning affects *Pinus sylvestris* needle decomposition rates and chemistry differently depending on site conditions, Biogeochemistry, 106, 397–414, 2011.

Brookes, P. C., Landman, A., Pruden, G., and Jenkinson, D. S.: Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil, Soil Biol. Biochem., 17, 837–842, 1985.

Celi, L. and Barberis, E.: Abiotic stabilization of organic phosphorus in the environment, in: Organic Phosphorus in the Environment, edited by: Turner, B. L., Frossard, E., and Baldwin, D. S., CABI Publishing, Cambridge, USA, 113–132, 2005.

Chlachula, J.: Climate History and Early Peopling of Siberia, in: Earth and Environmental Sciences, edited by: Dar, I. A. and Dar, M. A., InTech Europe, Rijeka, Croatia, 495–538, available online: http://www.intechopen.com/articles/show/title/climate-history-and-early-peopling-of-siberia, last access: 17 May 2012, 2011.

Chytry, M., Danihelka, J., Kubesova, S., Lustyk, P., Ermakov, N., Hajek, M., Hajkova, P., Koci, M., Otypkova, Z., Rolecek, J., Reznickova, M., Smarda, P., Valachovic, M., Popov, D., and Pisut, I.: Diversity of forest vegetation across a strong gradient of climatic continentality: Western Sayan Mountains, Southern Siberia, Plant Ecol., 196, 61–83, 2008.

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Perez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Diaz, S., Garnier, E., Gurvich, D. E., Kazakou, E., Klein, J. A., Read, J., Reich, P. B., Soudzilovskaia, N. A., Victoria Vaieretti, M., and Westoby, M.: Plant species traits are the predominant control on litter decomposition rates within biomes worldwide, Ecol. Lett., 11, 1065–1071, 2008.

De Graaff, M. A., van Groenigen, K. J., Six, J., Hungate, B., and van Kessel, C.: Interactions between plant growth and soil nutrient cycling under elevated CO_2: a meta-analysis, Glob. Change Biol., 12, 2077–2091, 2006.

De Schrijver, A., Vesterdal, L., Hansen, K., De Frenne, P., Augusto, L., Achat, D. L., Staelens, J., Baeten, L., De Keersmaeker, L., De Neve, S., and Verheyen, K.: Four decades of post-agricultural forest development have caused major redistributions of soil phosphorus fractions, Oecologia, 169, 221–234, 2012.

Dijkstra, F. and Cheng, W.: Increased soil moisture content increases plant N uptake and the abundance of ^{15}N in plant biomass, Plant Soil, 302, 263–271, 2008.

Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B., and Smith, J. E.: Global analysis of nitrogen and

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phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems, Ecol. Lett., 10, 1135–1142, 2007.

Fardeau, J. C.: Le phosphore assimilable des sols: sa représentation par un modèle fonctionnel à plusieurs compartiments, Agronomie, 13, 317–331, 1993.

Fardeau, J. C.: Dynamics of phosphate in soils: an isotopic outlook, Fert. Res., 45, 91–100, 1996.

Fisher, R. F. and Binkley, D.: Ecology and Management of Forest Soils, 3 Edn., John Wiley & Sons, Inc., New York, USA, 489 pp., 2000.

Food and Agriculture Organization: Global Forest Resources Assessment 2005, Progress towards sustainable forest management, FAO Forestry paper 147, Food and Agriculture Organization of the United Nations, Rome, 2006.

Frossard, E. and Sinaj, S.: The isotope exchange kinetic technique: a method to describe the availability of inorganic nutrients, applications to K, P, S and Zn, Isot. Environ. Healt. S., 33, 61–77, 1997.

Frossard, E., Stewart, J. W. B., and St. Arnaud, R. J.: Distribution and mobility of phosphorus in grassland and forest soils of Saskatchewan, Can. J. Soil Sci., 69, 401–416, 1989.

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

Gilbert, N.: The disappearing nutrient, Nature, 461, 716–718, 2009.

Groffman, P. M., Driscoll, C. T., Fahey, T. J., Hardy, J. P., Fitzhugh, R. D., and Tierney, G. L.: Colder soils in a warmer world: a snow manipulation study in a northern hardwood forest ecosystem, Biogeochemistry, 56, 135–150, 2001.

Guckland, A., Jacob, M., Flessa, H., Thomas, F. M., and Leuschner, C.: Acidity, nutrient stocks, and organic-matter content in soils of a temperate deciduous forest with different abundance of European beech (*Fagus sylvatica* L.), J. Plant Nutr. Soil Sc., 172, 500–511, 2009.

Güsewell, S. and Gessner, M. O.: $N : P$ ratios influence litter decomposition and colonization by fungi and bacteria in microcosms, Funct. Ecol., 23, 211–219, 2009.

Hansen, K., Vesterdal, L., Schmidt, I. K., Gundersen, P., Sevel, L., Bastrup-Birk, A., Pedersen, L. B., and Bille-Hansen, J.: Litterfall and nutrient return in five tree species in a common garden experiment, Forest Ecol. Manag., 257, 2133–2144, 2009.

Hättenschwiler, S. and Gasser, P.: Soil animals alter plant litter diversity effects on decomposition, Proc. Natl. Acad. Sci., 102, 1519–1524, 2005.

Hedin, L. O., Jack Brookshire, E. N., Menge, D. N. L., and Barron, A. R.: The nitrogen paradox in tropical forest ecosystems, Annu. Rev. Ecol. Evol. S., 40, 613–35, 2009.

Huston, M. A. and Wolverton, S.: The global distribution of net primary production: resolving the paradox, Ecol. Monogr., 79, 343–377, 2009.

IPCC, Fourth Assessment Report: Climate Change, Geneva, Switzerland, available online: http://www.ipcc.ch/publications_and_data/publications_and_data_reports.shtml, last access: 17 May 2012, 2007.

Iversen, C. M.: Digging deeper: fine-root responses to rising atmospheric CO_2 concentration in forested ecosystems, New Phytol., 186, 346–357, 2010.

Jungk, A. and Claassen, N.: Ion diffusion in the soil-root system, Adv. Agron., 63, 53–110, 1997.

Lambers, H., Raven, J. A., Shaver, G. R., and Smith, S. E.: Plant nutrient-acquisition strategies change with soil age, Trends Ecol. Evol., 23, 95–103, 2008.

Lashchinskiy, N. N.: Vegetation of Salair mountain range, Academic Press Geo, Novosibirsk, 263 pp., 2009 (in Russian).

Li, H., Han, Y., and Cai, Z.: Nitrogen mineralization in paddy soils of the Taihu Region of China under anaerobic conditions: dynamics and model fitting, Geoderma, 115, 161–175, 2003.

Liski, J., Nissinen, A., Erhard, M., and Taskinen, O.: Climatic effects on litter decomposition from artic tundra to tropical rainforest, Glob. Change Biol., 9, 575–584, 2003.

Loustau, D., Bosc, A., Colin, A., Ogée, J., Davi, H., François, C., Dufrêne, E., Déqué, M., Cloppet, E., Arrouays, D., Le Bas, C., Saby, N., Pignard, G., Hamza, N., Granier, A., Bréda, N., Ciais, P., Viovy, N., and Delage, F.: Modeling climate change effects on the potential production of French plains forests at the sub-regional level, Tree Physiol., 25, 813–823, 2005.

Luo, Y., Hui, D., and Zhang, D.: Elevated CO_2 stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis, Ecology, 87, 53–63, 2006.

McKeague, J. A. and Day, J. H.: Dithionite and oxalate-extractable Fe and Al as aids in differentiating various classes of soils, Can. J. Soil Sci., 46, 13–22, 1966.

Millennium Ecosystem Assessment, Ecosystems and Human Wellbeing: Current State and Trends, edited by: Hassan, R., Scholes, R., and Ash, N., Vol. 1, Island Press, Washington, DC, 838 pp., 2005.

Mikan, C. J., Schimel, J. P., and Doyle, A. P.: Temperature controls of microbial respiration in arctic tundra soils above and below freezing, Soil Biol. Biochem., 34, 1785–1795, 2002.

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Morel, C.: Mobilité et biodisponibilité du phosphore dans les sols cultivés: mécanismes, modélisation et diagnostic, Oceanis, 33, 51–74, 2007.

Morel, C., Tiessen, H., and Stewart, J. W. B.: Correction for P-sorption in the measurement of soil microbial biomass P by $CHCl_3$ fumigation, Soil Biol. Biochem., 28, 1699–1706, 1996.

Morel, C., Tunney, H., Plénet, D., and Pellerin, S.: Transfer of phosphate ions between soil and solution: perspectives in soil testing, J. Environ. Qual., 29, 20–59, 2000.

Nobrega, S. and Grogan, P.: Deeper snow enhances winter respiration from both plant-associated and bulk soil carbon pools in Birch Hummock Tundra, Ecosystems, 10, 419–431, 2007.

Norby, R. J., DeLucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., Ledford, J., McCarthy, H. R., Moore, D. J. P., Ceulemans, R., De Angelis, P., Finzi, A. C., Karnosky, D. F., Kubiske, M. E., Lukac, M., Pregitzer, K. S., Scarascia-Mugnozza, G. E., Schlesinger, W. H., and Oren, R.: Forest response to elevated CO_2 is conserved across a broad range of productivity, Proc. Natl. Acad. Sci., 102, 18052–18056, 2005.

Oren, R., Ellsworth, D. S., Johnsen, K. H., Phillips, N., Ewers, B. E., Maier, C., Schafer, K. V. R., McCarthy, H., Hendrey, G., McNulty, S. G., and Katul, G. G.: Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere, Nature, 411, 469–472, 2001.

Ostroumov, V. E. and Siegert, C.: Exobiological aspects of mass transfer in microzones of permafrost deposits, Adv. Space Res., 18, 79–86, 1996.

Panikov, N. S.: Fluxes of CO_2 and CH_4 in high latitude wetlands: measuring, modelling and predicting response to climate change, Polar Res., 18, 237–244, 1999.

Read, D. J., Leake, J. R., and Perez-Moreno, J.: Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes, Can. J. Bot., 82, 1243–1263, 2004.

Reich, P. B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S. E., Eissenstat, D. M., Chorover, J., Chadwick, O. A., Hale, C. M., and Tjoelker, M. G.: Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species, Ecol. Lett., 8, 811–818, 2005.

Reich, P. B., Hobbie, S. E., Lee, T., Ellsworth, D. S., West, J. B., Tilman, D., Knops, J. M. H., Naeem, S., and Trost, J.: Nitrogen limitation constrains sustainability of ecosystem response to CO_2, Nature, 440, 922–925, 2006.

Richardson, A. E. and Simpson, R. J.: Soil Microorganisms mediating phosphorus availability, Plant Physiol., 156, 989–996, 2011.

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Saunders, W. M. H. and Williams, E. G.: Observations on the determination of total organic phosphorus in soils, J. Soil Sci., 6, 247–267, 1955.

Shugalei, L. S.: The Siberian afforestation experiment: history, methodology, and problems, in: Tree Species Effects on Soils: Implications for Global Change, edited by: Binkley, D. and Menyailo, O., NATO Science Series, Series IV: Earth and Environmental Sciences, Springer, Netherlands, 257–268, 2005.

Shuman, J. K., Shugart, H. H., and O'Halloran, T. L.: Sensitivity of Siberian larch forests to climate change, Glob. Change Biol., 17, 2370–2384, 2011.

Soja, A. J., Tchebakova, N. M., French, N. H. F., Flannigan, M. D., Shugart, H. H., Stocks, B. J., Sukhinin, A. I., Parfenova, E. I., Stuart Chapin III, F., and Stackhouse Jr., P. W.: Climate-induced boreal forest change: predictions versus current observations, Global Planet. Change, 56, 274–296, 2007.

Strauss, R., Brümmer, G. W., and Barrow, N. J.: Effects of crystallinity of goethite: II. rates of sorption and desorption of phosphate, Eur. J. Soil Sci., 48, 101–114, 1997.

SYSTAT: Software, Inc., Version 10, Chicago, IL, 2000.

Terrestrial biozones: available online: http://www.terrestrial-biozones.net/index.html, last access: 28 March 2012.

Thomas, S. M., Whitehead, D., Reid, J. B., Cook, F. J., Adams, J. A., and Leckie, A. C.: Growth, loss, and vertical distribution of *Pinus radiata* fine roots growing at ambient and elevated CO_2 concentration, Glob. Change Biol., 5, 107–121, 1999.

Treseder, K. K.: Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies, Ecol. Lett., 11, 1111–1120, 2008.

Trichet, P., Bakker, M. R., Augusto, L., Alazard, P., and Merzeau, D.: Fifty years of pine fertilization experiments in the Landes of Gascogne (France), Forest Sci., 55, 390–402, 2009.

Turner, B. L., Cade-Menun, B. J., Condron, L. M., and Newman, S.: Extraction of soil organic phosphorus, Talanta, 66, 294–306, 2005.

Ushio, M., Kitayama, K., and Balser, T. C.: Tree species effects on soil enzyme activities through effects on soil physicochemical and microbial properties in a tropical montane forest on Mt. Kinabalu, Borneo, Pedobiologia, 53, 227–233, 2010.

Vance, E. D., Brookes, P. C., and Jenkinson, D. S.: An extraction method for measuring soil microbial biomass C, Soil Biol. Biochem., 19, 703–707, 1987.

Vazquez, G., Antorrena, G., Gonzalez, J., and Freire, S.: Studies on the composition of *Pinus Pinaster* foliage, Bioresource Technol., 51, 83–87, 1995.

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van Veldhoven, P. P. and Mannaerts, G. P.: Inorganic and organic phosphate measurements in the nanomolar range, Anal. Biochem., 161, 45–48, 1987.

Vitousek, P. M., Porder, S., Houlton, B. Z., and Chadwick, O. A.: Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions, Ecol. Appl., 20, 5–15, 2010.

Voriskova, J., Dobiasova, P., Snajdr, J., Vanek, D., Cajthaml, T., Santruckova, H., and Baldrian, P.: Chemical composition of litter affects the growth and enzyme production by the saprotrophic basidiomycete Hypholoma fasciculare, Fungal Ecol., 4, 417–426, 2011.

Wang, Y. P., Houlton, B. Z., and Field, C. B.: A model of biogeochemical cycles of carbon, nitrogen, and phosphorus including symbiotic nitrogen fixation and phosphatase production, Global Biogeochem. Cy., 21, GB1018, 15 pp., doi:10.1029/2006GB002797, 2007.

WRB: World Reference Base For Soil Resources, Ed. FAO, IUSS, ISRIC, Rapport FAO 103, Rome, 132 pp., 2006.

Xin, W. D., Yin, K. Q., and Song, B.: Contribution of soil fauna to litter decomposition in Songnen sandy lands in Northeastern China, J. Arid Environ., 77, 90–95, 2012.

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Table 1. Stocks of forest floor, description of the soil profiles and main physical-chemical and microbiological soil properties.

| | Upland site in the Salair mountains | | | | Lowland site | |
	P. tremula	*A. sibirica*	Forest gap			*P. tremula*
Stocks of forest floor (Mgha^{-1})						
F	2.4 ± 0.2**b**	18.6 ± 4.4**a**	0 [¶]	F		10.0 ± 1.6**a**
Thickness of the soil horizons (cm)						
A + AE	18.5 ± 2.4**a**	20.0 ± 0.4**a**	24.7 ± 0.9**a**	A		31.3 ± 1.4
E	39.1 ± 2.5**a**	38.0 ± 3.3**a**	34.0 ± 3.9**a**	AE		23.0 ± 5.6
EBt	12.9 ± 1.9**a**	15.7 ± 4.4**a**	12.3 ± 3.4**a**			
Bt	28.5 ± 2.8+	27.0 ± 2.7+	29.1 ± 1.0+	Bt		40.8 ± 8.7+
Total C (gkg^{-1})						
F[#]	451.9 ± 3.6**(b)**	408.8 ± 4.6**(c)**	–[¶]	F[#]		468.6 ± 4.0**(a)**
A + AE	34.8 ± 3.4**a**	31.7 ± 2.6**a**	31.2 ± 2.9**a**	A		39.3 ± 2.3**a**
E	6.9 ± 0.8**a**	9.1 ± 1**a**	7.1 ± 0.7**a**	AE		7.9 ± 1.1
EBt	3.6 ± 0.01**a**	3.9 ± 0.3**a**	3.3 ± 0.3**a**			
Bt	2.2 ± 0.3**a**	3.0 ± 0.1**a**	2.2 ± 0.3**a**	Bt		3.2 ± 0.2**a**
Total N (gkg^{-1})						
F[#]	25.91 ± 0.05**(a)**	18.25 ± 0.06**(b)**	–[¶]	F[#]		17.13 ± 0.26**(a)**
A + AE	3.14 ± 0.28**a**	2.75 ± 0.21**a**	2.60 ± 0.02**a**	A		2.60 ± 0.10**a**
E	0.83 ± 0.07**a**	0.95 ± 0.06**a**	0.77 ± 0.06**a**	AE		0.75 ± 0.06
EBt	0.62 ± 0.02**a**	0.60 ± 0.05**a**	0.49 ± 0.02**a**			
Bt	0.43 ± 0.04**a**	0.44 ± 0.002**a**	0.43 ± 0.02**a**	Bt		0.47 ± 0.01**a**

Table 1. Continued.

| | Upland site in the Salair mountains | | | | Lowland site | |
	P. tremula	*A. sibirica*	Forest gap		*P. tremula*	
Al + Fe oxides (mmol kg^{-1})						
F[#]	24.1	57.4	–[¶]	F[#]	19.5	
A + AE	145.4 ± 6.6**a**	142.3 ± 4.9**a**	149.7 ± 3.7**a**	A	105.2 ± 3.2**b**	
E	133.2 ± 8.0**a**	131.1 ± 4.7**a**	136.2 ± 1.7**a**	AE	97.1 ± 3.1	
EBt	125.0 ± 6.1**a**	115.2 ± 0.7**a**	117.5 ± 1.5**a**			
Bt	115.2 ± 3.1**a**	106.2 ± 0.9**ab**	104.9 ± 2.5**ab**	Bt	101.3 ± 1.2**b**	
Soil pH						
F[#]	6.04 ± 0.003**(b)**	5.79 ± 0.01**(c)**	–[¶]	F[#]	6.58 ± 0.003**(a)**	
A + AE	5.56 ± 0.02**a**	5.02 ± 0.07**b**	5.47 ± 0.04**a**	A	5.73 ± 0.09**a**	
E	5.51 ± 0.05**a**	5.46 ± 0.06**a**	5.53 ± 0.03**a**	AE	6.23 ± 0.09	
EBt	5.75 ± 0.06**a**	5.82 ± 0.13**a**	5.74 ± 0.04**a**			
Bt	5.84 ± 0.11**b**	5.75 ± 0.06**b**	5.99 ± 0.03**ab**	Bt	6.26 ± 0.1**a**	
Microbial C (g kg^{-1})						
F[#]	5.2 ± 0.8**(b)**	5.6 ± 1**(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 (g kg^{-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)**	
Acid phosphatase activity (phosphomonoesterase; mg p – nitrophenol kg^{-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)**	

Means ± standard errors (n_{obs} = 3 soil profiles or 3–4 aliquots of each composite sample[#]). Different small letters denote significant ($P < 0.05$) differences between plots in a given soil horizon. Different small 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.

Table 2. Stocks of C, N, and P and P fractions as a % of total P in the entire forest floor + mineral soil profile (100 cm).

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

Means ± standard errors ($n_{\mathrm{obs}} = 3$ soil profiles). Different small letters denote significant ($P < 0.05$) differences between plots.

Stocks were calculated using the masses of forest floor (0–$19\,\mathrm{Mg\,ha^{-1}}$) and the thickness of the mineral soil layers (0.12–$0.41\,\mathrm{m}$; see Table 1) with their bulk density (0.70–$1.56\,\mathrm{g\,cm^{-3}}$).

[¶] Extrapolated values of diffusive iP using Eq. (5).

Table 3. Total, total organic, total inorganic and microbial P.

| | Upland site in the Salair mountains | | | | Lowland site |
	P. tremula	A. sibirica	Forest gap		P. tremula
Contents in mg kg^{-1}					
Total P					
F[#]	2379.6 ± 71.9**(a)**	1576.2 ± 46.3**(b)**	–[¶]	F[#]	1720.3 ± 13.5**(b)**
A + AE	1042.1 ± 37.9**a**	899.4 ± 41.5**ab**	991.1 ± 25.6**ab**	A	879.1 ± 12.9**b**
E	714.6 ± 69.6**a**	753.9 ± 56.8**a**	771.4 ± 34.4**a**	AE	708.8 ± 21.4
EBt	644.7 ± 27.8**a**	697.1 ± 32.5**a**	717.5 ± 26.7**a**		
Bt	686.9 ± 13.9**a**	703.0 ± 17.5**a**	753.9 ± 14.6**a**	Bt	700.0 ± 13.9**a**
Total organic P					
F[#]	1008.6 ± 18.9**(a)**	812.7 ± 46.2**(b)**	–[¶]	F[#]	825.5 ± 0.3**(b)**
A + AE	570.2 ± 3.0**a**	494.8 ± 35.0**ab**	554.5 ± 28.5**a**	A	415.7 ± 25.2**b**
E	220.7 ± 28.7**a**	284.6 ± 23.3**a**	320.6 ± 23.1**a**	AE	155.9 ± 20.6
EBt	137.4 ± 7.4**b**	239.7 ± 35.5**a**	156.1 ± 14.2**ab**		
Bt	102.2 ± 2.4**b**	198.1 ± 6.7**a**	108.8 ± 2.5**b**	Bt	81.4 ± 6.4**c**
Total inorganic P					
F[#]	1371.0 ± 18.9**(a)**	763.5 ± 46.2**(b)**	–[¶]	F[#]	894.8 ± 0.3**(b)**
A + AE	471.9 ± 39.7**a**	404.6 ± 18.3**a**	436.6 ± 9.8**a**	A	463.3 ± 12.4**a**
E	493.9 ± 41.1**a**	469.3 ± 36.6**a**	450.7 ± 13.2**a**	AE	552.9 ± 5.9
EBt	507.3 ± 21.7**a**	457.4 ± 30.2**a**	561.4 ± 15.9**a**		
Bt	584.8 ± 11.8**a**	504.9 ± 12.2**b**	645.1 ± 15.2**a**	Bt	618.7 ± 20.1**a**
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 ± 2**a**	55 ± 2**a**	56 ± 2**a**	A	47 ± 2**a**
E	31 ± 1**b**	38 ± 1**a**	41 ± 1**a**	AE	22 ± 2
EBt	21 ± 1**b**	34 ± 4**a**	22 ± 1**b**		
Bt	15 ± 0.2**b**	28 ± 0.5**a**	14 ± 0.5**b**	Bt	12 ± 1**b**

Means ± standard errors (n_{obs} = 3 soil profiles or 3–4 aliquots of each composite sample[#]). Different small letters denote significant ($P < 0.05$) differences between plots in a given soil horizon. Different small 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.

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Table 4. Phosphate concentration in soil solution (C_P), isotopic dilution parameters[§] (r/R_{1min} and n) and diffusive phosphate ions (parameters[†] Pr_{1min} and p; Pr_{400min}).

| | Upland site in the Salair mountains | | | | Lowland site |
	P. tremula	A. sibirica	Forest gap		P. tremula
C_P (mg l^{-1})					
F[#]	30.4 ± 0.6**(a)**	10.3 ± 0.6**(b)**	–¶	F[#]	25.6 ± 0.5**(a)**
A + AE	0.65 ± 0.16**a**	0.24 ± 0.01**b**	0.31 ± 0.04**ab**	A	0.49 ± 0.11**ab**
E	0.035 ± 0.011**a**	0.035 ± 0.005**a**	0.040 ± 0.003**a**	AE	0.044 ± 0.012
EBt	0.029 ± 0.002**ab**	0.034 ± 0.002**a**	0.026 ± 0.001**b**		
Bt	0.031 ± 0.002**a**	0.032 ± 0.004**a**	0.032 ± 0.001**a**	Bt	0.026 ± 0.002**a**
r/R_{1min}					
F[#]	1.02 ± 0.01**(a)**	1.00 ± 0.01**(a)**	–¶	F[#]	1.01 ± 0.01**(a)**
A + AE	0.87 ± 0.02**a**	0.77 ± 0.04**a**	0.80 ± 0.01**a**	A	0.73 ± 0.05**a**
E	0.32 ± 0.03**a**	0.39 ± 0.02**a**	0.36 ± 0.02**a**	AE	0.21 ± 0.04
EBt	0.13 ± 0.006**a**	0.17 ± 0.02**a**	0.12 ± 0.01**a**		
Bt	0.10 ± 0.004**a**	0.11 ± 0.01**a**	0.11 ± 0.01**a**	Bt	0.09 ± 0.004**a**
n					
F[#]	0.024 ± 0.003**(ab)**	0.036 ± 0.001**(b)**	–¶	F[#]	0.017 ± 0.003**(a)**
A + AE	0.28 ± 0.03**ab**	0.35 ± 0.004**b**	0.33 ± 0.01**ab**	A	0.24 ± 0.03**a**
E	0.40 ± 0.002**a**	0.40 ± 0.008**a**	0.40 ± 0.01**a**	AE	0.33 ± 0.02
EBt	0.39 ± 0.004**a**	0.39 ± 0.001**a**	0.39 ± 0.01**a**		
Bt	0.40 ± 0.008**a**	0.39 ± 0.02**a**	0.40 ± 0.01**a**	Bt	0.37 ± 0.01**a**
Pr_{1min} (mg kg^{-1})					
F[#]	11.6 ± 5.2**(a)**	7.9 ± 1.9**(a)**	–¶	F[#]	12.51 ± 2.93**(a)**
A + AE	2.71 ± 0.46**a**	1.53 ± 0.06**b**	1.74 ± 0.18**ab**	A	2.49 ± 0.31**ab**
E	0.82 ± 0.17**a**	0.63 ± 0.02**a**	0.89 ± 0.07**a**	AE	1.57 ± 0.23
EBt	2.15 ± 0.16**a**	1.76 ± 0.10**a**	1.89 ± 0.17**a**		
Bt	3.04 ± 0.21**a**	2.55 ± 0.08**a**	3.04 ± 0.36**a**	Bt	3.13 ± 0.45**a**
p					
F[#]	0.40 ± 0.12**(a)**	0.34 ± 0.04**(a)**	–¶	F[#]	0.24 ± 0.04**(a)**
A + AE	0.42 ± 0.02**ab**	0.46 ± 0.004**a**	0.45 ± 0.01**a**	A	0.38 ± 0.02**b**
E	0.44 ± 0.004**a**	0.46 ± 0.01**a**	0.43 ± 0.01**a**	AE	0.37 ± 0.03
EBt	0.39 ± 0.01**a**	0.42 ± 0.009**a**	0.41 ± 0.002**a**		
Bt	0.39 ± 0.01**a**	0.41 ± 0.01**a**	0.39 ± 0.02**a**	Bt	0.35 ± 0.01**a**
Pr_{400min} (mg kg^{-1})					
F[#]	83.2 ± 6.9**(a)**	53.9 ± 5.7**(b)**	–¶	F[#]	51.8 ± 1.3**(b)**
A + AE	31.9 ± 2.5**a**	22.8 ± 0.7**b**	25.6 ± 1.6**ab**	A	23.8 ± 0.4**b**
E	10.8 ± 2**a**	10.2 ± 1.1**a**	12.2 ± 0.6**a**	AE	13.9 ± 0.6
EBt	21.1 ± 0.1**a**	20.2 ± 1.8**a**	22.2 ± 1.5**a**		
Bt	31.4 ± 2**a**	28.2 ± 2.3**a**	30.9 ± 2.7**a**	Bt	24.9 ± 1.9**a**

Means ± standard errors (n_{obs} = 3 soil profiles or 3 aliquots for each composite sample[#]). Different small letters denote significant ($P < 0.05$) differences between plots in a given soil horizon. Different small letters in parentheses denote significant ($P < 0.05$) differences between composite samples.

Significant depth effect in each plot ($P < 0.04$), excepted for parameter p in the upland site with P. tremula ($P = 0.84$).

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

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

¶ No forest floor in the forest gap.

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Table 5. Contents in K, Ca, Mg, Mn and lignin and lignin/N ratio for the forest floors, C/N and C/P ratio for the forest floors and mineral soils.

| | Upland site in the Salair mountains | | | | Lowland site |
	P. tremula	A. sibirica	Forest gap		P. tremula
Contents in total K, Ca, Mg, Mn and lignin ($g\,kg^{-1}$)					
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 ± 0.1**b**	11.5 ± 0.1**b**	12.0 ± 1.0**b**	A	15.1 ± 0.3**a**
E	8.4 ± 0.5**a**	9.5 ± 0.4**a**	9.2 ± 0.3**a**	AE	10.4 ± 0.6
EBt	5.8 ± 0.2**a**	6.7 ± 1.2**a**	6.8 ± 0.4**a**		
Bt	5.1 ± 0.2**b**	6.8 ± 0.1**a**	5.2 ± 0.5**b**	Bt	6.8 ± 0.5**ab**
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 ± 4.3**a**	35.1 ± 1.4**a**	31.6 ± 3.6**a**	A	44.7 ± 2.2**a**
E	9.7 ± 0.3**b**	12.0 ± 0.4**a**	9.2 ± 0.5**b**	AE	11.1 ± 1.2
EBt	5.6 ± 0.2**a**	5.6 ± 0.2**a**	4.7 ± 0.4**a**		
Bt	3.2 ± 0.3**ab**	4.2 ± 0.2**ab**	3.0 ± 0.4**b**	Bt	4.6 ± 0.4**a**
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**(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)**

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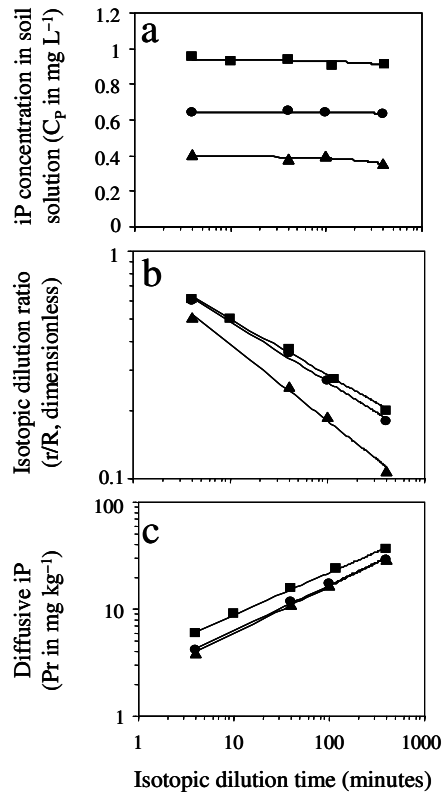[¶] No forest floor in the forest gap.

Fig. 1. Concentration of iP in soil solution (C_P; **a**), isotopic dilution ratio (r/R; **b**) and diffusive iP (Pr; **c**) as a function of isotopic dilution time. Example for the A + AE soil horizon of the *P. tremula* plot in the Salair mountain site. The different symbols represent the different soil replicates. No time dependence of C_P in **(a)** (linear regression: $P > 0.05$). Adjustment of Eq. (4) in **(b)**: $r^2 > 0.994$; $P < 0.0001$. Adjustment of Eq. (5) in **(c)**: $r^2 > 0.998$; $P < 0.0001$. Mean concentrations of iP in soil solution and parameters of Eqs. (4) and (5) are given in Table 4.

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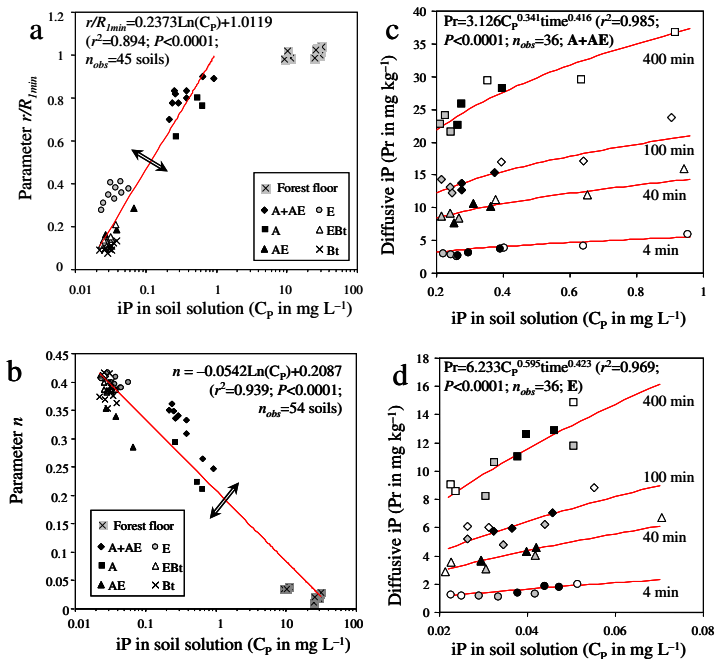Printer-friendly Version

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Fig. 2. Isotopic dilution parameters (r/R_{1min} in **a**; n in **b**) as a function of the concentration of iP in soil solution (C_P), considering all plots, soil profiles and soil horizons; diffusive iP (Pr) as a function of time and C_P in a given mineral soil horizon of the three adjacent plots in the Salair mountain site (A + AE horizon in **c**; E horizon in **d**). Arrows in **(a)** and **(b)**: effects of soil horizons and soil properties (see relationships between residual values of parameter n and soil properties in Fig. 3). Parts **(c)** and **(d)**: *open symbols*, *P. tremula*; *gray symbols*, *A. sibirica*; *black symbols*, forest gap (three replicates per plot); *solid lines*, adjustments of the Freundlich kinetics Eq. (6).

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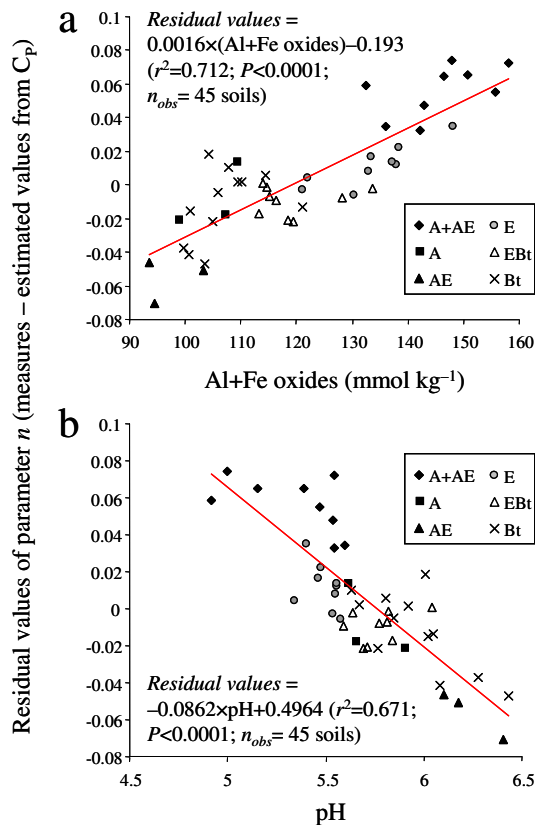Printer-friendly Version

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Fig. 3. Effects of soil horizons and soil properties on isotopic dilution parameters for the mineral soils: Relationships between residual values of parameter n (measures – estimated values with iP concentration in soil solution; see Fig. 2b) and Al + Fe oxides extracted with ammonium oxalate (**a**) and soil pH (**b**). *Solid lines*, non-linear adjustments. Stepwise procedure: residual values on parameter $n = 0.108 + 0.000937 \cdot (\text{Al} + \text{Fe oxides}) - 0.039 \cdot \text{pH} + 0.000416 \cdot \text{total C}$ ($r^2 = 0.816$; $P < 0.0001$; $n_{\text{obs}} = 45$ mineral soils).

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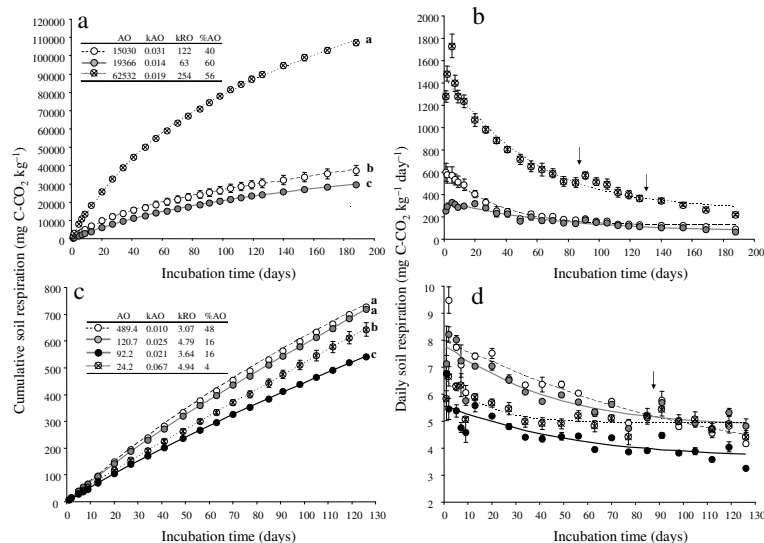Printer-friendly Version

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Fig. 4. Cumulative and daily soil respiration of incubated forest floors (**a**, **b**) and surface mineral soils (horizon A or A + AE) (**c**, **d**). Means ± standard error (n_{obs} = 4 aliquots and jars for each composite sample). Salair mountains: *open symbols*, *P. tremula*; *gray symbols*, *A. sibirica*; *black symbols*, forest gap. Lowland site with *P. tremula*: *hatched symbols*. Solid lines, adjustments (two-pool model; Eq. (7); 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 small 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.
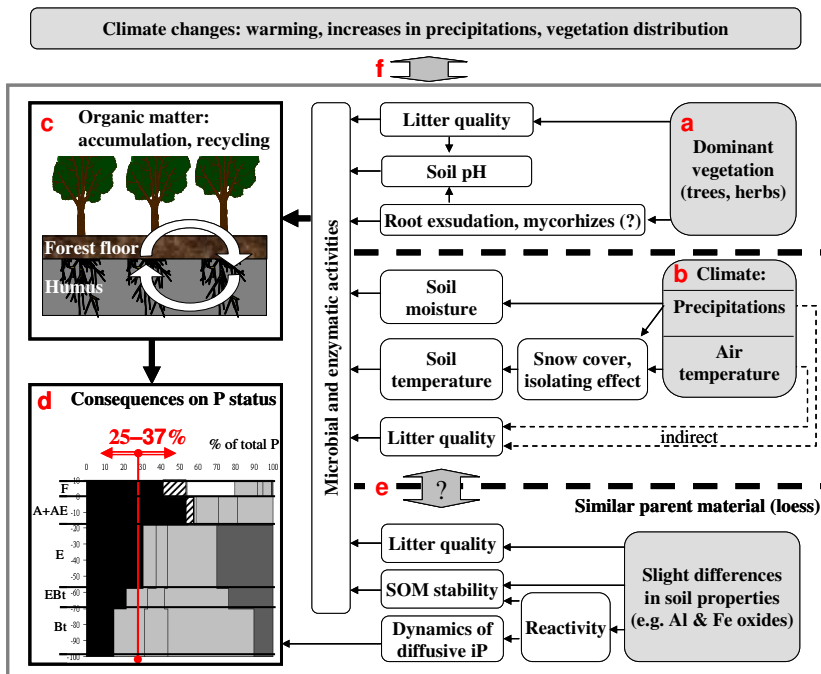
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Fig. 5. Conceptual diagram of the results of the present study: effects of dominant vegetation (**a**) and local climate (**b**) on organic matter accumulation and recycling (**c**), and subsequent consequences on soil P fractions (relative contributions of organic and inorganic P) and therefore available P (**d**). Future researches in the west Siberian forest ecosystems should focus on the interactions between climate and soil substrate (**e**) and the relationships between the present results and the future climate changes (**f**). P fractions (**d**): *black colour*, total organic P; *hatched*, microbial P; *white*, iP in soil solution; *grey*, diffusive iP (in one week, one month and one year); *dark grey*, not diffusive inorganic P; *arrow*, effect of organic matter recycling on the relative proportion of total organic P in the entire soil profile.