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Phosphorus mineralization can be driven by microbial need for carbon

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ABSTRACT

Despite the importance of phosphorus (P) mineralization to maintain soil fertility, little is known about the mechanisms that regulate microbial P mineralization. We tested the hypothesis that microbial P mineralization can be driven by microbial need for carbon (C). For this purpose, net microbial uptake kinetics of ^{14}C and ^{33}P from glucose-6-phosphate were studied in a Leptosol depending on availability of C, nitrogen (N), and P. After 60 h of incubation, 16.4% of the ^{14}C from glucose-6-phosphate was recovered in the microbial biomass, while ^{33}P incorporation into the microbial biomass was a third less. The higher net uptake of ^{14}C than of ^{33}P from the glucose-6-phosphate indicates that soil microorganisms use the organic moiety of phosphorylated organic compounds as a C source, but only use a small proportion of the P. Hence, they mineralize P without incorporating it. Our finding that the net uptake of ^{14}C and ^{33}P in the soils amended with inorganic P did not differ from the control treatment indicates that P mineralization was not driven by microbial need for P but rather for C. In a second experiment with three temperate forest soils we found that the activity of ^{14}C from glucose-6-phosphate in soil solution decreased faster than the activity of ^{33}P from glucose-6-phosphate. This might suggest that higher net uptake of C than of P from glucose-6-phosphate can also be observed in other temperate forest soils differing in C, N, and P contents from the Leptosol of the main experiment. In conclusion, the experiments show that microbial P mineralization can be a side-effect of microbial C acquisition from which plants potentially can benefit.

1. Introduction

One important measure to mitigate decreasing rock phosphate resources suitable for fertilizer production is to remobilize phosphorus (P) stocks already present in soil (Cordell et al., 2009). Total P contents in top soils (0–15 cm) typically range from 50 to 500 mg kg^{-1} (Sims and Pierzynski, 2005). However, only a small percentage of this P is bioavailable due to the high sorption capacity of the phosphate ions. The chemical forms of P in soils differ with parent material, soil pH and vegetation cover, and pedogenesis. The organic P pool increases with soil development, but tends to decline again in highly weathered soils (Walker and Syers, 1976). A large proportion of P in soils of the temperate zone is present in organic forms, and has to be mineralized to become available for plants (Stutter et al., 2012). Despite the importance of P mineralization to maintain soil fertility, little is known about the factors that drive microbial P mineralization.

Microorganisms can mineralize organic P inside and outside their cells. Many genera of bacteria are able to take up intact phosphorylated organic compounds (Heath, 2005; Winkler, 1973). Hexose phosphates can be taken up via a transport system called Uhp, which is induced exclusively by glucose-6-phosphate, but transports various hexose phosphates (Dietz, 1976). It has been pointed out that this transport system might become important for bacterial energy and carbon (C) metabolism once C becomes limited and hexose phosphates are abundant (Dietz, 1976; Kadner et al., 1994). While bacterial transport systems for phosphorylated compounds have been described at a molecular scale and in physiological studies with defined culture media (Dietz, 1976; Winkler, 1973; Kadner et al., 1994), little is known about microbial uptake of phosphorylated compounds in soils. However, it has been reported that C-limited microorganisms in deep strata of the ocean and in marine sediments use the organic moiety of phosphorylated compounds as a C source (Hoppe and Sören, 1999; Hoppe, 2003; Steenbergh et al., 2011). In soils, microbes are commonly C limited because organic matter is stabilized against decomposition by various mechanisms such as sorption, spatial inaccessibility or recalcitrance (De Nobili et al., 2001; Demoling et al., 2007; Blagodatskaya et al., 2009). Yet, according to a conceptual model proposed by McGill and Cole (1981) P mineralization in soils is decoupled from C mineralization. The model states that while nitrogen (N) is mineralized during SOM

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decomposition driven by bacterial need for C or energy, P mineralization is strongly controlled by the organisms' need for this element.

We tested the hypothesis that microbial P mineralization can be driven by microbial demand for C. More precisely, we tested the hypothesis that microorganisms use the organic moiety of phosphorylated organic compounds, but do not incorporate the P. This would mean that P mineralization can be a side effect of microbial C acquisition. To test this hypothesis we studied net microbial uptake kinetics of C and P from glucose-6-phosphate either uniformly labeled with ^{14}C or with ^{33}P. Phosphate monoesters represent a significant part of P in soils (Stutter et al., 2012). Glucose-6-phosphate is a common form of P in microorganisms, and therefore part of the highly cycled P pool in soils (Kadner et al., 1994; Oberson and Joner, 2005). Both ^{33}P- and ^{14}C-labeled glucose-6-phosphate was incubated with a Leptosol, and net microbial uptake kinetics of ^{33}P and ^{14}C were analyzed. In order to decrease potential limitations and allow microbial growth, the Leptosol was amended with C, N or P. To estimate whether we can find indications that the obtained results also hold true for temperate soils that differ in terms of C, N, and P contents, a further incubation experiment was carried out. In this experiment, the decreases in the contents of C and P of glucose-6-phosphate in the soil solution were studied.

2. Material and methods

2.1. Soils and sampling

The soils chosen for the experiments differ in C and P contents (Table 1). The soils are located in central Germany, in forests around the city of Göttingen. The mean annual temperature in the study area is 8.7 °C and the mean annual precipitation is approximately 640 mm. The Leptosol is located in the east of Göttingen (51°33′23 N, 9°58′25 E) in the Göttinger Wald. The soils in Göttinger Wald are largely developed from shell limestone and a mixed deciduous forest can be found featuring *Fagus sylvatica*, *Acer* sp., and *Sorbus aucuparia*. The Podzol and the Cambisol are located in the Bramwald in the southwest of Göttingen. The Podzol (51°31′01 N, 9°39′15 E) was formed on tertiary sands, while the Cambisol (51°30′51 N, 9°39′08 E) has developed from basalt. The vegetation on the Podzol is strongly dominated by *Picea abies*, while *F. sylvatica* is the dominant species on the Cambisol.

Soils were sampled in May 2012. Three profiles were dug in each soil. From each soil profile, we collected one sample from the subsoil below the A horizon at a depth of 21–25 cm. Subsoil was chosen because it is assumed that here C limitation of microorganisms is especially severe. The sampled horizons were classified as rendzic (Leptosol), spodic (Podzol), and cambic (Cambisol) according to WRB. One sample per horizon was taken from each profile. The soils were sieved (2 mm) and pre-incubated at 20 °C and 40% water holding capacity for 4 weeks prior to the incubation experiments in order to let them reach equilibrium under laboratory conditions after sampling and sieving disturbance.

2.2. Microbial uptake kinetics of C and P

Microbial net uptake kinetics of C and P from D-glucose-6-phosphate in a Leptosol amended with C, N or P were studied in an incubation experiment. The experiment was comprised of 120 experimental units. Each experimental unit consisted of 8.55 g of pre-incubated dry mass equivalent soil in a glass jar. One quarter of them received C, the second quarter N, the third quarter P, and the last quarter did not receive any amendment and served as a control. The C, N, and P amendments were designed according to Aldén et al. (2001) and Demoling et al. (2007). The soils received 2 mg g^{-1} C as glucose, 0.1 mg g^{-1} N as NH_4NO_3 or 0.1 mg g^{-1} P as KH_2PO_4 in 1 ml distilled H_2O. The control units received 1 ml distilled H_2O. The addition of KH_2PO_4 increased the content of $NaHCO_3$-extractable P to 8.1 (±0.1) μg g^{-1}, while the other treatments did not affect the content of $NaHCO_3$-extractable P. The soils were incubated at 20 °C in the dark for 48 h. Subsequently, 64 units were labeled with 20 kBq ^{14}C(U)-D-glucose-6-phosphate (specific ^{14}C activity: 9.0 GBq $mmol^{-1}$), and 60 units were labeled with 90 kBq ^{33}P-D-glucose-6-phospahate (specific ^{33}P activity: 111.0 GBq $mmol^{-1}$) in 1 ml distilled H_2O. The labeling led to an addition of 0.1 nmol glucose-6-phosphate per gram soil in the units labeled with ^{14}C and to 2.9 nmol glucose-6-phosphate per gram soil in the units labeled with ^{33}P. All experimental units were incubated at 20 °C in the dark throughout the experiment. Four parallel units of every treatment labeled with ^{14}C-glucose-6-phosphate were equipped with small glass vessels with 2 ml 0.2 M NaOH in order to trap the respired CO_2. The NaOH was renewed every day and ^{14}C activity in the NaOH was determined with a multi-purpose scintillation counter (Beckman–Coulter) using the scintillation cocktail RotiszintEcoplus (Roth).

At regular intervals three parallel units of each treatment were destructively harvested and the fumigation extraction method was applied to determine the uptake of ^{14}C and ^{33}P into the microbial biomass (Brookes et al., 1982; Wu et al., 1990). The units labeled with ^{14}C-glucose-6-phosphate were harvested 2, 7, 27, and 64 h after the labeling. The samples labeled with ^{33}P-glucose-6-phosphate were harvested 7, 26, 53, 168, and 240 h after the labeling. Each sample was split into two equal parts. One half was directly extracted. The other half was fumigated with chloroform for 24 h, and subsequently extracted. In order to analyze C uptake, 4.25 g soil labeled with ^{14}C-glucose-6-phosphate were extracted with 25 ml 0.5 M K_2SO_4 according to Wu et al. (1990). To analyze the P uptake 4.25 g soil labeled with ^{33}P-glucose-6-phosphate were extracted with 80 ml 0.5 M $NaHCO_3$ according to Brookes et al. (1982). The extracts of the non-fumigated soils are called soil extracts in the following. In order to determine the recovery efficiency of inorganic P, the 4.25 g of the same soil used in the experiment soil was spiked with 25 μg g^{-1} P and extracted with 0.5 M $NaHCO_3$

Table 1
Texture, pH, total organic carbon (C), total nitrogen (N), total phosphorus (P), C/P ratio, and $r_{1\ min}/R$ in the Leptosol, Podzol, and Cambisol. TOC and N were determined with an element analyzer. Total P was measured with ICP-AES (Spectroflame, Spectro). $r_{1\ min}/R$ is the percentage of ^{33}P orthophosphate that can be recovered from the soil 1 min after its addition to the soil. The values depict means that were calculated from independent analyses of three soil profiles per soil type. Values in brackets depict standard deviations.

Soil type	Texture [%]			pH_{H_2O}	C [g kg^{-1}]	N [g kg^{-1}]	P [g kg^{-1}]	C/P [mol mol^{-1}]	$r_{1\ min}/R$ [%]
	Sand	Silt	Clay						
Leptosol	1.1 (±0.1)	53.9 (±1.9)	45.0 (±1.9)	4.8 (±0.0)	15.6 (±3.9)	1.2 (±0.1)	0.32 (±0.01)	126	6
Podzol	65.0 (±1.3)	22.4 (±5.2)	12.6 (±6.1)	4.0 (±0.0)	28.1 (±3.5)	0.9 (±0.2)	0.13 (±0.01)	558	64
Cambisol	24.8 (±0.9)	55.1 (±1.1)	20.1 (±2.0)	5.0 (±0.0)	7.9 (±2.3)	0.6 (±0.1)	0.20 (±0.03)	102	3

as the other samples (Bünemann et al., 2007). C in the K_2SO_4-extracts was analyzed by a Dohrmann C analyzer (Dohrmann). Inorganic P in the $NaHCO_3$ extracts was determined with the ammonium molybdate assay using a spectrophotometer Specord 40 (Analytik Jena). Both ^{33}P and ^{14}C activity were determined with a multi-purpose scintillation counter (Beckman–Coulter) using the scintillation cocktail RotiszintEcoplus (Roth). Microbial C contents and ^{14}C activities were calculated by subtracting the C concentration or the ^{14}C activity in the soil extract from the C concentration or the ^{14}C activity in the extract of the fumigated sample. Microbial P contents and ^{33}P activities were calculated in the same way, but with a correction for the P recovery efficiency. The recovery of P in the $NaHCO_3$ extracts of the P-spiked Leptosol was 51%. Consequently, to correct for the extraction efficiency, the P contents and ratios of ^{33}P recovery in the extracts were multiplied by 1.96.

2.3. C and P in soil solution

A second incubation experiment was performed, in order to compare the decrease in the contents of C and P of glucose-6-phosphate in soil solution. The experiment was carried out with the Leptosol as well as with a Podzol and a Cambisol (Table 1). Two grams dry mass equivalent were pre-incubated in 19 ml distilled H_2O on a temperature-regulated shaker (Gallenkamp) at 20 °C and 100 rpm in the dark. After 16 h, three parallels of each soil received 5.0 kBq uniformly labeled ^{14}C D-glucose-6-phosphate, and three parallels received 5.0 kBq ^{33}P labeled D-glucose-6-phospahate each in 1 ml of distilled H_2O. After 40, 70, 120, 180, 240, and 300 min, 1 ml was taken and centrifuged at 20 000 × *g* at 4 °C for 3 min (Centrifuge 5417R, Eppendorf). The supernatant was centrifuged again at 20 000 × *g* at 4 °C for 3 min. Immediately afterward, ^{14}C and ^{33}P activities in the supernatant were determined with a multi-purpose scintillation counter (Beckman–Coulter) using the scintillation cocktail RotiszintEcoplus (Roth).

2.4. Statistics

The significance of differences in ^{14}C and ^{33}P recovery, C and P contents and specific activities were tested by ANOVA followed by Duncan-test using the software SPSS 18.0. $\alpha < 0.05$ was considered as the threshold value for significance.

3. Results

3.1. Microbial uptake kinetics of C and P

After 24 h, 20.7% of the ^{14}C from glucose-6-phosphate was already released as CO_2 from the control soil (Fig. 1). The soils amended with N and P behaved similarly to the control. The high release of ^{14}C as CO_2 from the C amended soil after 4 days of incubation indicates that even under C saturation, C from P containing organic compounds is taken up by microorganisms.

Two hours after labeling, only 2.2% of the added ^{14}C remained in the extracts from the control soil (Fig. 2A). In contrast to the ^{14}C activity, the ^{33}P activity (Fig. 2B) in the extracts decreased strongly during the first two days (Fig. 2B). The C, N, and P amended soils behaved similarly. As much as 21.7% of the ^{14}C was recovered in the microbial biomass of the non-amended soil after only 2 h of incubation. The ^{14}C recovery in the microbial biomass was similar in the C, N, and P amended soils (Fig. 3A), showing that nutrient addition did not change microbial uptake of ^{14}C from glucose-6-phosphate. ^{14}C recovery in the microbial biomass did not change significantly during the incubation (Fig. 3A). Increases in microbial C were found exclusively due to the C amendment, but not due to N or P addition (Fig. 3C).

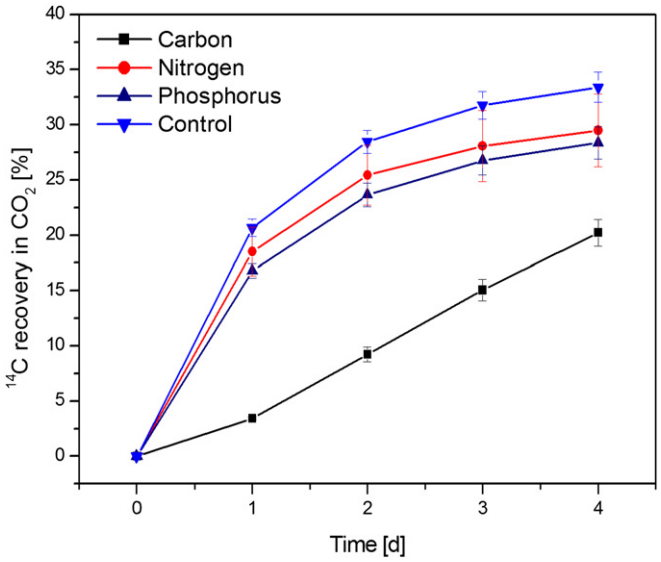

Fig. 1. Recovery of ^{14}C in CO_2 from ^{14}C-glucose-6-phosphate during the first four days of incubation of a Leptosol. Besides the control, the results for carbon-, nitrogen-, and phosphate-amended soil are shown.

In contrast to ^{14}C recovery, ^{33}P recovery in the microbial biomass increased continuously with time (Fig. 3B). During the first 26 h negative ^{33}P recoveries in the microbial biomass were observed (Fig. 3B). The reason for this is that ^{33}P in the fumigated soils had 24 h more to exchange with ^{31}P than in the non-fumigated soils. The longer duration of isotopic exchange lead to lower ^{33}P activities in the extracts of the fumigated soils than in the extracts of the non-fumigated soils. This resulted in negative ^{33}P recoveries in the in microbial biomass during the first 26 h of the experiment. Since the exchange of ^{33}P against ^{31}P proceeds exponentially, changes in ^{33}P activity in the extracts became marginal after 2 days (Fig. 2B), and positive ^{33}P recoveries in the microbial biomass were measured (Fig. 3B). After 60 h, 16.4% of the ^{14}C was recovered in the microbial biomass and 33.4% in the respired CO_2, while only 5.6% of the ^{33}P was found in the microbial biomass in the control treatment (Fig. 4). After 10 d, ^{33}P recovery in the microbial biomass increased only up to 13.8% (Figs. 3B and 4), while microbial P remained constant (Fig. 3C).

3.2. C and P in soil solution

During the first 50 min or – in case of the Cambisol – 180 min the decrease in ^{14}C and ^{33}P activity proceeded simultaneously (Fig. 5). After this period, more ^{33}P than ^{14}C was recovered in the soil solution of all three soils. After 300 min, the ^{33}P recovery exceeded the ^{14}C recovery by a factor of 2.0 in the Leptosol, 5.2 in the Podzol, and 2.2 in the Cambisol (Fig. 5). The higher recovery of both ^{14}C and ^{33}P from the soil solution of the Podzol (Fig. 5) can be attributed to the lower P sorption capacity of this soil, which can be seen from the higher $r_{1\ min}/R$ value of the Podzol (Table 1). The lower ^{33}P recovery in the soil solution of the Leptosol compared to the extract (Fig. 2A) is due to the much lower P extraction efficiency of water compared to $NaHCO_3$.

4. Discussion

Microbial C contents increased exclusively due to C amendment, but not due to N or P additions (Fig. 3C), indicating that microorganisms in the Leptosol were most likely C limited or co-limited by C in combination with other nutrients. This result is in accordance

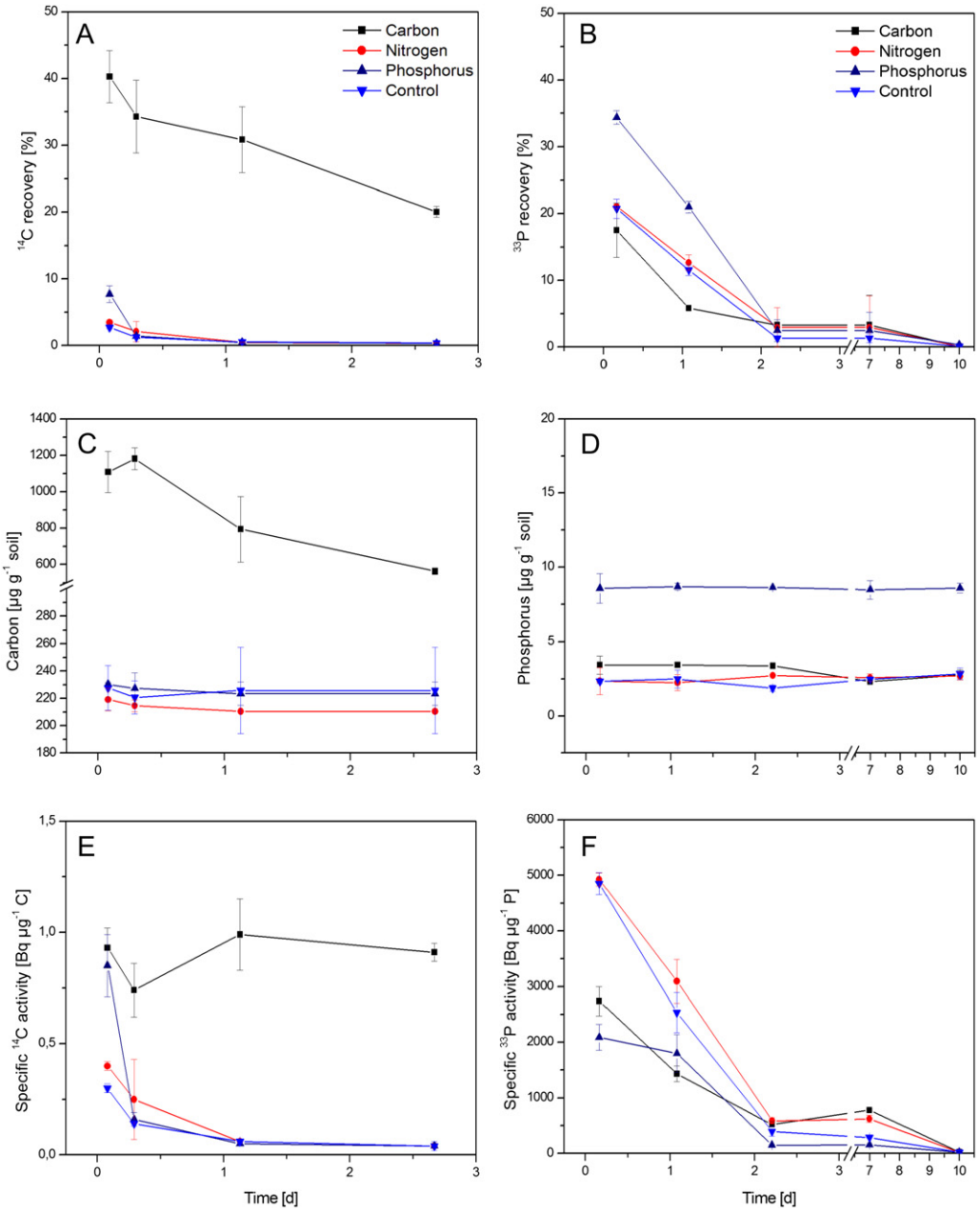

Fig. 2. Carbon and phosphorus in the extracts of a Leptosol labeled with ^{14}C- or ^{33}P-glucose-6-phosphate as dependent on incubation time. We compared the ^{14}C recovery (A), the total carbon content (C), and the specific ^{14}C activity (E) to the recovery of the ^{33}P (B), the phosphorus content (D), and the specific ^{33}P activity (F). Besides the control, the results for the carbon-, nitrogen-, and phosphorus-amended soil are shown.

with studies that reported limitation of microorganisms in temperate forest soils by C (Joergensen et al., 1990; De Nobili et al., 2001; Ekblad and Nordgren, 2002). However, in light of recent studies on multielement limitation it seems possible that microorganisms were not just limited by C, but by C in combinations with other nutrients (Kaspari et al., 2008; Townsend et al., 2011).

The respired 20.6% of the ^{14}C of glucose-6-phosphate after the first 24 h (Fig. 1) is in accordance with Fransson and Jones (2007) who studied the mineralization of ^{14}C-labeled organic phosphoric compounds in comparison to their non-phosphorylated counterparts in the Ah horizon of a grassland soil. The authors found that after 24 h of incubation 23% of the glucose-6-phosphate-C as well as of the glucose-C was mineralized. They concluded that phosphatase activity does not limit microbial use of C of low molecular weight organic-P substrates in soil.

Higher net uptake rates of C than of P from glucose-6-phosphate – indicated by the differences in ^{14}C and ^{33}P recovery in the microbial biomass (Figs. 3A, B and 4) – can be interpreted in two ways. It could be that the microbes took up glucose-6-phosphate as an intact molecule, kept the C, and released P in order to maintain their C/P stoichiometry. The other possible interpretation is that the glucose-6-phosphate was dephosphorylated before it was taken up. The question whether the glucose-6-phosphate was dephosphorylated before the uptake or inside the microbial cells cannot be answered based on our results. To our knowledge, studies about microbial uptake of C and P from phosphorylated organic compounds in soil do not exist. The finding that the net uptake of ^{14}C was three times higher than the net uptake of ^{33}P together with the observation that the addition of inorganic P did not change the net uptake of ^{14}C and ^{33}P from

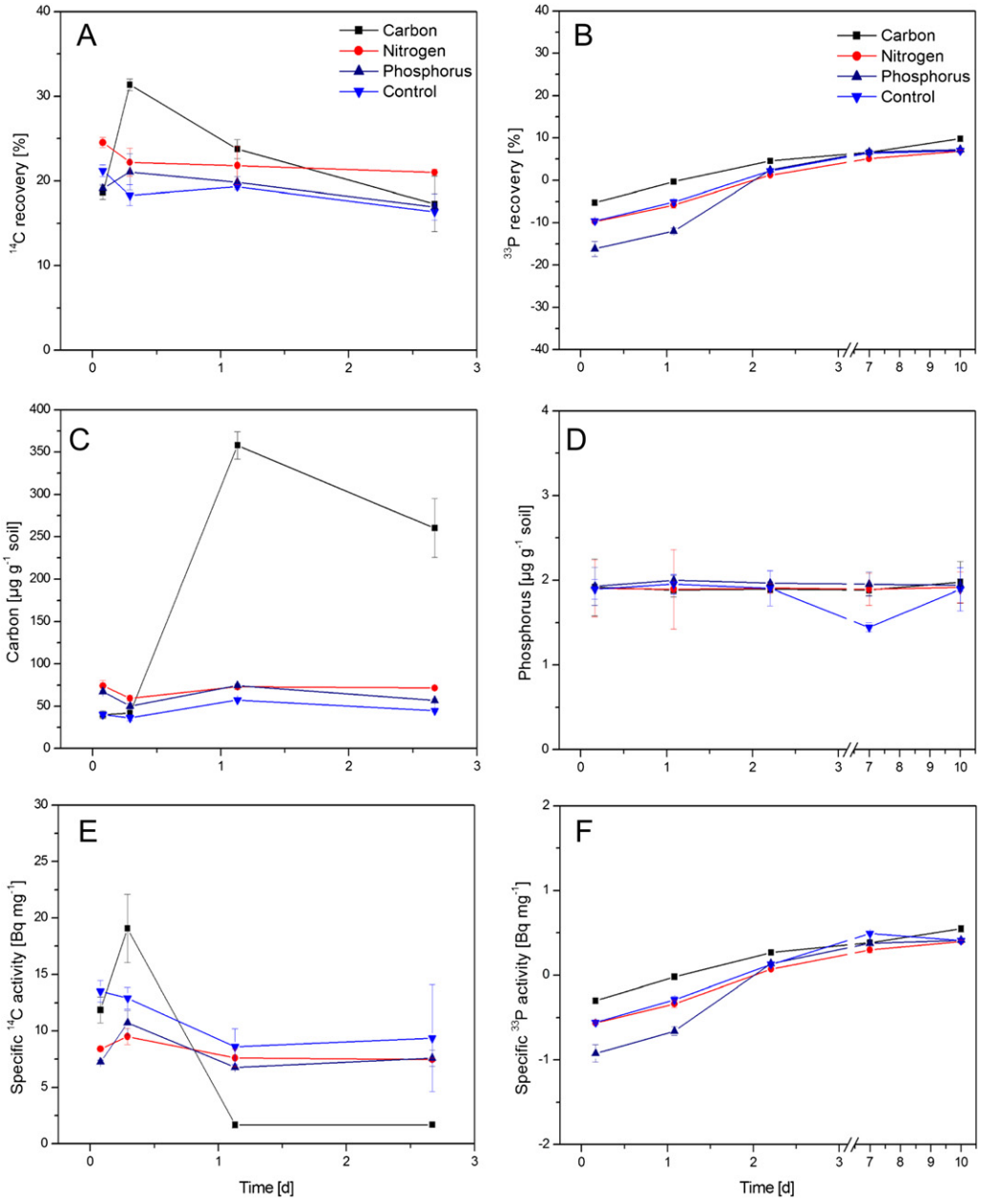

Fig. 3. Carbon and phosphorus in the microbial biomass of a Leptosol labeled with ^{14}C- or ^{33}P- glucose-6-phosphate as dependent on incubation time. We compared the ^{14}C recovery (A), the total carbon content (C), and the specific ^{14}C activity (E) to the recovery of the ^{33}P (B), the phosphorus content (D), and the specific ^{33}P activity (F).

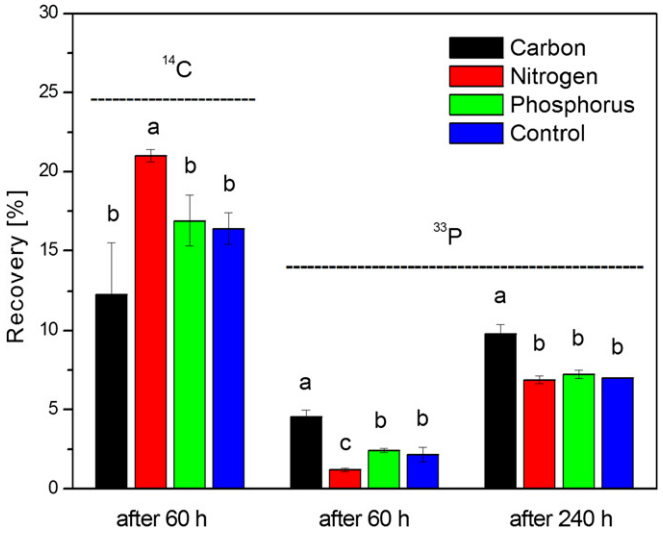

Fig. 4. Recovery of ^{14}C in the microbial biomass after 60 h, and recovery of ^{33}P in the microbial biomass after 60 and 240 h. Besides the control, the results for the carbon-, nitrogen-, and phosphorus-amended soil are shown. Letters indicate differences between amendments.

the glucose-6-phosphate (Figs. 3A, B and 4) indicates that the microorganisms used glucose-6-phosphate mainly as a C source. Thus, the P mineralization seems to have been driven by the microorganisms' need for C. However, we cannot exclude that the microorganisms were co-limited by C in combination with P, and that their C and P uptake was driven by the need for both elements. The C:P ratio of glucose-6-phosphate (6) is significantly lower than the C:P ratio of microorganisms, which during the experiment in the control was 59.6 8 (±10.4). However, the added glucose-6-phophate did not significantly change the C:P ratio of the soil, because it was only added in trace amounts (<3 nmol g^{-1}). The observed partitioning of C and P most likely reflects the common partitioning of C and P from hexose phosphates in this soil.

Our interpretation that microbial mineralization of P of glucose-6-phosphate was driven by microbial need for C seems to be confirmed by the short-term experiment. The higher recovery of ^{33}P than of ^{14}C in the soil solution after 50–180 min is remarkable considering the higher potential of P than of C to adsorb to the solid soil phase, and the dilution of ^{33}P by unlabeled ^{31}P from the soil. The simultaneous decrease in ^{14}C and ^{33}P activity during the first 50–180 min could be interpreted that glucose-6-phosphate was adsorbed to the soil solid phase or that it was taken up by microorganisms as an intact molecule. While – following this interpretation – the higher recovery of ^{33}P in the soil solution after 50 or 180 min can be interpreted as a release of ^{33}P by the microbes. However, it is equally possible that glucose-6-phosphate was dephosphorylated outside the microbial cells prior to the uptake of the organic moiety. The short term experiment seems to confirm that microorganisms in temperate forest soils that differ from the Leptosol in terms of C, N, and P contents (Table 1) also use phosphorylated organic compounds mainly as a C source. Our findings are in accordance with studies showing that microorganisms in the sea use dissolved organic P compounds to satisfy their C demand (Hoppe and Sören, 1999; Nausch and Nausch, 2007; Steenbergh et al., 2011).

Taken together, our experiments suggest that soil microorganisms in some temperate forest soils use the organic moiety of phosphorylated organic compounds as a C source, and only incorporate a small proportion of the P. Hence, they mineralize P without

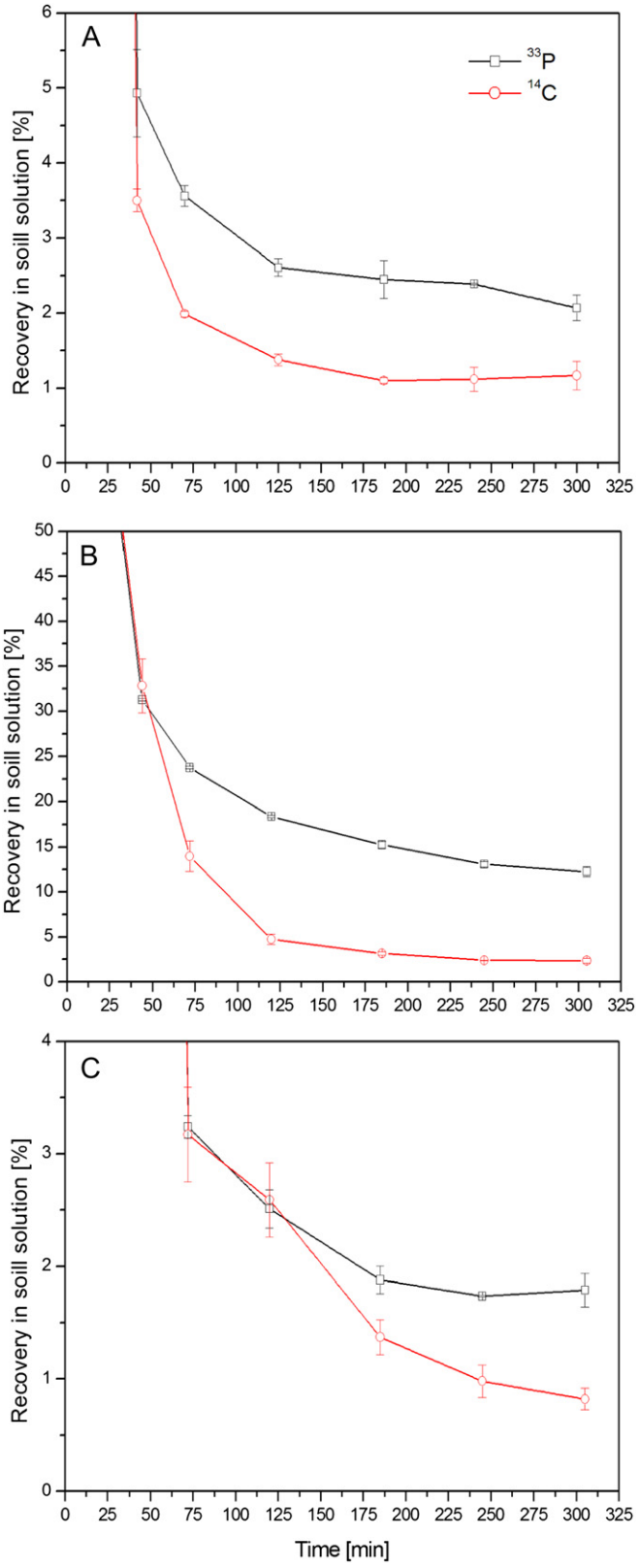

Fig. 5. Recovery of ^{14}C and ^{33}P from glucose-6-phosphate in the soil solution during a short term incubation of three subsoils; a Leptosol (A), a Podzol (B), and a Cambisol (C).

incorporating it. This P mineralization, which seems to be driven by microbial demand for C can potentially be beneficial for plants. It is well known that mycorrhiza provide plants with P. Our study indicates that also non-mycorrhizal soil microorganisms might

facilitate P acquisition for plants as suggested by Richardson et al. (2009). Finally, the study indicates that microbial C demand does not only drive N and S mineralization, as stated by McGill and Cole (1981), but seems to also be able to drive P mineralization.

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References

Aldén, L., Demoling, F., Baath, E., 2001. Rapid method of determining factors limiting bacterial growth in soil. Applied & Environmental Microbiology 67, 1830–1838.
Brookes, P.C., Powlson, D.S., Jenkinson, D.S., 1982. Measurement of microbial biomass phosphorus in soil. Soil Biology and Biochemistry 14, 319–329.
Blagodatskaya, V., Blagodatsky, S., Anderson, T.-H., Kuzyakov, Y., 2009. Contrasting effects of glucose, living roots and maize straw on microbial growth kinetics and substrate availability in soil. European Journal of Soil Science 60, 186–197.
Bünemann, E.K., Marschner, P., McNeill, A.M., McLaughlin, M.J., 2007. Measuring rates of gross and net mineralisation of organic phosphorus in soils. Soil Biology and Biochemistry 39, 900–913.
Cordell, D., Drangert, J.O., White, S., 2009. The story of phosphorus: global food security and food for thought. Global Environmental Change 19, 292–305.
De Nobili, M., Contin, M., Mondini, C., Brookes, P.C., 2001. Soil microbial biomass is triggered into activity by trace amounts of substrate. Soil Biology and Biochemistry 33, 1163–1170.
Demoling, F., Figueroa, D., Bååth, E., 2007. Comparison of factors limiting bacterial growth in different soils. Soil Biology and Biochemistry 39, 2485–2495.
Dietz, G.W., 1976. The hexose phosphate transport system by Escherichia coli. Advances in Enzymology and Related Areas of Molecular Biology 44, 237–259.
Ekblad, A., Nordgren, A., 2002. Is growth of soil microorganisms in boreal forests limited by carbon or nitrogen availability? Plant and Soil 242, 115–122.
Fransson, A.M., Jones, D.L., 2007. Phosphatase activity does not limit the microbial use of low molecular weight organic-P substrates in soil. Soil Biology and Biochemistry 39, 1213–1217.
Heath, R.T., 2005. Microbial turnover of organic phosphorus in aquatic systems. In: Turner, B.L., Frossard, E., Baldwin, D.S. (Eds.), Organic Phosphorus in the Environment. Cabi Publishing, Wallingford, UK.
Hoppe, H.-G., Sören, U., 1999. Profiles of ectoenzymes in the Indian Ocean: phenomena of phosphatase activity in the mesopelagic zone. Aquatic Microbial Ecology 19, 139–148.
Hoppe, H.-G., 2003. Phosphatase activity in the sea. Hydrobiologia 493, 187–200.
Joergensen, R.G., Brookes, P.C., Jenkinson, D.S., 1990. Survival of the soil microbial biomass at elevated temperatures. Soil Biology and Biochemistry 22, 1129–1136.
Kadner, R.J., Island, M.D., Merkel, T.J., Webber, C.A., 1994. Transmembrane control of the Uhp sugar-phosphate transport system; the sensation of Glu6P. In: Torriani-Gorini, A., Yagil, E., Silver, S. (Eds.), Phosphate in Microorganisms: Cellular and Molecular Biology. American Society of Microbiology Press, Washington DC, pp. 78–84.
Kaspari, et al., 2008. Multiple nutrients limit litterfall and decomposition in a tropical forest. Ecology Letters 11, 35–43.
McGill, W.B., Cole, C.V., 1981. Comparative aspects of cycling of organic C, N, S and P through soil organic matter. Geoderma 26, 267–286.
Nausch, M., Nausch, G., 2007. Bioavailable dissolved organic phosphorus and phosphorus use by heterotrophic bacteria. Aquatic Biology 1, 151–160.
Oberson, A., Joner, E.J., 2005. Microbial turnover of phosphorus in soil. In: Turner, B.L., Frossard, E., Baldwin, D. (Eds.), Organic Phosphorus in the Environment. CABI, Wallingford, Oxon, UK, pp. 133–164.
Richardson, A., Barea, J.-M., McNeill, A., Prigent-Combaret, C., 2009. Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. Plant and Soil 321, 305–339.
Sims, J.T., Pierzynski, G.M., 2005. Chemistry of phosphorus in soil. In: Tabatabai, A.M., Sparks, D.L. (Eds.), Chemical Processes in Soil. SSSA Book Series 8. SSSA, Madison.
Steenbergh, A.K., Bodelier, P.L.E., Hoogveld, H.L., Slomp, C.P., Laanbroek, H.J., 2011. Phosphatases relieve carbon limitation of microbial activity in Baltic Sea sediments along a redox-gradient. Journal Limnology and Oceanography 56, 2018–2026.
Stutter, M.I., Shand, C.A., George, T.S., Blackwell, M.S.A., Bol, R., MacKay, R.L., Richardson, A.E., Condron, L.M., Turner, B.L., Haygarth, P.M., 2012. Recovering phosphorus from soil: a root solution? Environmental Science & Technology 46, 1977–1978.
Townsend, A.R., Cleveland, C.C., Houlton, B.Z., Alden, B.A., White, J.W.Z., 2011. Multielement regulation of the tropical forest carbon cycle. Frontiers in Ecology and the Environment 9, 9–17.
Walker, T.W., Syers, J.K., 1976. Fate of phosphorus during pedogenesis. Geoderma 15, 1–19.
Winkler, H.H., 1973. Distribution of an inducible hexose-phosphate transport system among various bacteria. Journal of Bacteriology 116, 1079–1081.
Wu, J., Joergensen, R.G., Pommerening, B., Chaussod, R., Brookes, P.C., 1990. Measurement of soil microbial biomass C – an automated procedure. Soil Biology and Biochemistry 22, 1167–1169.