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Drying and rewetting of forest floors: dynamics of soluble phosphorus, microbial biomass-phosphorus, and the composition of microbial communities

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Abstract

Drying and rewetting (D/W) of soils often leads to a pulse of total dissolved phosphorus (TDP) by lysis of sensitive microorganisms. The relevance of D/W on the P cycle in ecosystems depends on the duration of the TDP release. In forest soils, the forest floor represents a hotspot of microbial activity and is often prone to D/W. Here, we investigated the dynamics of TDP, the microbial P pool (Pmic), and the composition of microbial communities after D/W. Samples were taken from Oi and Oe layers of a European beech and a Norway spruce site and desiccated up to − 100 MPa (pF 6) at 20 °C, while controls were kept moist. TDP and Pmic were measured 0, 1, 3, 7, and 14 days after rewetting and the composition of microbial communities was analyzed by automated ribosomal intergenic spacer analysis after 14 days. After D/W, the largest TDP net release (D/W-control) was from Oe layers with 40–50 mg P kg^{-1} and inorganic P as the dominant fraction. The TDP concentrations decreased strongly in Oi layers within 1 (beech) to 4 (spruce) days, while remaining stable in Oe layers. The TDP dynamics were linked to the decrease and recovery of Pmic after D/W. Pmic dynamics differed between layers and stand types, suggesting the influence of microbial communities with different D/W sensitivities. The composition of microbial communities varied strongly among sites and layers, while D/W only affected the composition of bacterial and fungal communities in the spruce Oe layer. D/W of forest floors increases the plant available P and affects the P cycle in forest ecosystems.

Keywords Drying–rewetting · Inorganic dissolved phosphorus · Soil microbial biomass · Soil microbial communities · Total dissolved phosphorus

Introduction

Drying and rewetting (D/W) of soils represents a stress to soil microorganisms (Blackwell et al. 2010; Fierer and Schimel 2002). Rewetting of desiccated soil can cause a pulse of soluble N and P and an increase in soil respiration (Borken and Matzner 2009; Butterly et al. 2009; Bünemann et al. 2013; Gordon et al. 2008). The release of soluble N and P after rewetting is often attributed to the lysis of soil microorganisms, their biomass representing a significant pool of organic N and P in soils (Achat et al. 2012; Bünemann et al. 2013; Dinh et al. 2016; Turner and Haygarth 2001). The microbial biomass pools of N and P may decline by D/W up to 50% (Chen et al. 2016; Gordon et al. 2008; Mondini et al. 2002; Yevdokimov et al. 2016). The released N and P due to the lysis of microorganisms in turn of D/W may be used by plants and surviving microorganisms.

The uptake by plants or leaching of the released soluble nutrients depends on the change of their concentrations following the rewetting. Investigations on the dynamics of soluble N and P after D/W are sparse for mineral soils and even more scarce for forest floors, despite the latter being hotspots of microbial activity in forest soils. In experiments with mineral soils, highest concentrations of dissolved P were observed 2 h after rewetting and concentrations decreased by about 50% after 50 h (Blackwell et al. 2009). In contrast, Butterly

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et al. (2011) showed that dissolved P concentrations can remain constant in some mineral soils for 50 h after rewetting.

An important sink of released N and P might be the immobilization into the recovering microbial biomass after D/W. Intensive microbial immobilization of dissolved P into the microbial biomass was reported in a ^{33}P labeling experiment with mineral soils within 12 h after rewetting (Yevdokimov et al. 2016). In addition, several studies reported a recovery of the microbial biomass within 1 to 9 days after rewetting of desiccated mineral soils (Chen et al. 2016; Hamer et al. 2007; Wu and Brookes 2005).

In the forest floor, the effect of D/W on the release of P directly after D/W differed between the layers, with larger release from Oe layers than from Oi layers despite similar microbial biomass (Dinh et al. 2016). As the different forest floor layers are inhabited by different microbial communities (Kohl et al. 2015; Voříšková et al. 2014), the soil microbial community composition might influence the effects of D/W cycles. Moreover, different groups of soil microorganisms reacted differently to D/W and soil fungi are considered to be more resistant to desiccation than bacteria (Bapiri et al. 2010; Sheik et al. 2011; Yuste et al. 2011). Hence, D/W might reduce the ratio of bacteria to fungi (Kakumanu et al. 2013) and change the composition of bacterial communities (Fierer and Schimel 2002).

Here, we investigated the dynamics of soluble P, microbial biomass P, and the changes in microbial community composition following the drying and rewetting of forest floors. We hypothesized that after rewetting, (1) the soluble P will decrease with time due to the recovering of the soil microbial biomass, (2) the desiccation and recovery of the soil microbial biomass goes along with changes in its community composition, and (3) the impact of D/W on microbial biomass and the community composition depends on the initial microbial community in the different layers of forest floors. To test these hypotheses, we conducted a D/W batch experiment using forest floor samples from a European beech and a Norway spruce forest to measure water-soluble and microbial biomass P over 14 days as well as the composition of microbial communities after D/W.

Materials and methods

Study sites and sample preparation

Samples were collected from a European beech stand near Bayreuth (N 49° 58.23′, E 11° 35.8′) and from a Norway spruce site at Waldstein (N 50° 8.33′, E 11° 32.20′) in Germany. Both sites have a loamy texture and the parent material is upper Triassic Sandstone at Bayreuth and Granite at Waldstein. Samples were collected from Oi (intact needles and leaves) and Oe layers (moderately decomposed needles and leaves) in late autumn 2016. Samples were homogenized by hand, roots, and twigs were removed, and the Oi samples were cut into pieces of 1–2 cm. The initial litter properties of beech and spruce forest are presented in Table 1.

Experimental design

Moist samples were arranged as a 1-cm layer in petri-dishes with 200 mm diameter. All samples were adjusted to a water content equivalent to 50% of the maximum water holding capacity (WHC) and pre-incubated for 3 weeks in a climate chamber at 20 °C to allow the microbial activity to adjust. At the end of the pre-incubation period, the D/W experiment was started by opening the petri-dishes. The control petri-dishes were kept closed. Soil water potentials were measured daily by a dew point potentiometer (WP4C, Decagon Devices, USA) until a water potential of about − 100 MPa (pF 6) was reached. At this point of desiccation, the D/W samples were rewetted to 50% WHC by spraying with deionized water. Following rewetting, the D/W samples were maintained at 50% WHC throughout.

Analytical methods

The D/W treatment and controls were sampled at 0 h (directly after rewetting), 3 h, 8 h 1, 3, 7, and 14 days after rewetting. At each time point, 4 D/W and 4 control petri dishes were destructively harvested. Subsamples of 8 g were extracted in deionized water (soil:water ratio of 1:10) by shaking for 140 min on a horizontal shaker to measure the total water-soluble P (TDP) and water-soluble inorganic P (DIP). Water extracts were filtered through a cellulose membrane acetate filter (0.45 μm, Sartorius AG, Göttingen, Germany). DIP was measured spectrophometrically by using the colorimetric molybdate-ascorbic acid method (Murphy and Riley 1962). TDP was determined by ICP-OES (Jobin-Yvon Horiba Group, JY2000, Varian Inc., Palo Alto, California, USA). Water-soluble organic P (DOP) was calculated as the difference between TDP and DIP. The net release P was determined as the difference between the P release from the D/W and the control samples.

Microbial biomass P (Pmic) was measured immediately after rewetting (time 0) and at days 1, 3, 7, and 14 by the chloroform fumigation-extraction method (Brookes et al. 1982; Oberson et al. 1997; Vance et al. 1987). The samples were extracted with Bray 1 solution (0.025 M HCl + 0.03 M NH_4F) with a sample:solution ratio of 1:10 (Aponte et al. 2010; Bray and Kurtz 1945). Pmic was calculated as difference of inorganic P in the fumigated and non-fumigated extracts using a conversion factor of 2.5 (Brookes et al. 1982; Jenkinson et al. 2004). Inorganic P in the solutions was measured spectrophotometrically using the colorimetric molybdate-ascorbic acid method (Murphy and Riley 1962).

Table 1 Properties of the forest floor layers

Site	Layer	TOC	TN	TP	TOC: TN	TOC: TP	pH_{H2O}
		[g kg^{-1}]					
Beech	Oi	491	9	0.6	54.5	877	7.0
	Oe	493	20	0.7	24.7	704	5.3
Spruce	Oi	503	17	1.0	29.6	484	5.5
	Oe	493	20	1.2	24.7	411	4.7

TOC total organic C, *TN* total N, *TP* total P

Forest floor samples were dried at 60 °C for 48 h prior to total C, total N, and total P measurements. Total P was determined after digestion with HNO_3 using an ICP-OES (Jobin-Yvon Horiba Group, JY2000, Varian Inc., Palo Alto, CA, USA). Total C and total N were determined using an elemental analyzer (Vario MAX, Elementar, Hanau, Germany).

Microbial community analysis

Microbial communities of the Oi and Oe layers were characterized using an automated ribosomal intergenic spacer analysis (ARISA; Fisher and Triplett 1999) as previously described (Weig et al. 2013). Community profiles were determined from samples collected prior to D/W as well as D/W and control samples from day 14 after rewetting. Ribosomal intergenic spacers and internal transcribed sequences were PCR-amplified in two separate reactions using bacteria-specific (ITSF and ITSReub; Cardinale et al. 2004) and fungi-specific primers (ITS1F-Z; Weig et al. 2013 and ITS2; White et al. 1990), respectively. Bacterial and fungal specific amplification products were separated on a fragment Analyzer equipped with the 55-cm long capillary array using the DNF-910 reagent kit (Advanced Analytical, https://www.aati-us.com/). A primary data matrix (sample vs. peak size) of absolute peak height of the bacterial and fungal fragments in the range from 200 to 1000 base pairs was used for further analysis.

Data analyses

Primary data matrices based on the bacterial and fungal fragments were analyzed in PRIMER 7 (Plymouth Routines in Multivariate Ecological Research, v. 7.0.13, PRIMER-E Ltd., UK): Raw peak height values were standardized as percentage of the sample total and sample-specific ARISA profiles were created by cumulating the values of each sample in fragment size order. Resemblance matrices of bacterial and fungal ARISA profiles were created by using the Manhattan distance for resemblance measure. Non-metric multidimensional scalings (NMDS) were performed using a maximum of 50 restarts and a minimum stress threshold of 0.01. Differences between specific sample groups were tested by Analysis of similarities (ANOSIM) using a maximum of 999 restarts. No differences were found between samples collected prior to D/W and control samples collected 14 days after rewetting of the D/W samples (bacteria = ANOSIM: $r = 0.059$, $p = 0.079$; d: fungi = ANOSIM: $r = 0.001$, $p = 0.389$). Therefore, only D/W and control samples were included in further analyses. The whole fungal and bacterial community datasets were analyzed for differences among sites and layers by ANOSIM (one factor with four levels: spruce Oi, spruce Oe, beech Oi, and beech Oe). Further, the communities in each layer were tested independently for variations among the treatments (D/W and controls).

All other statistical analyses and graphics were done in R environment for statistical computing (R Core Team 2014). Normality and homogeneity of the data were tested using Shapiro-Wilk test and Levene's test, respectively. Student's *t* test was used to test for statistical differences among groups. Wilcoxon rank-sum tests were used if data were not normal and/or variances were not homogeneously distributed.

Results

The concentrations of TDP in the controls were generally lowest in the beech Oi samples and highest in spruce Oe samples (Fig. 1). The rewetting of dried organic layers caused a significant increase of TDP in all samples ($p < 0.05$). The increase of TDP was always largest immediately after rewetting. The maximum TDP concentrations after rewetting were observed in spruce Oe reaching up to 118 mg TDP kg^{-1}, while concentrations of 20 mg TDP kg^{-1} were observed in beech Oi after rewetting.

The net release of TDP (D/W – control) decreased with time in all samples, but differences between the forest floor layers emerged: In beech and spruce Oi, the net release decreased with time from 12 mg TDP kg^{-1} to near zero after day 1 (beech) and from 55 to 10 mg TDP kg^{-1} in spruce, with a sharp decline at day 4 (Fig. 2). In contrast, the net release of TDP from Oe layers decreased much less. For beech Oe, the net release of TDP decreased continuously from 50 immediately after rewetting to 30 mg kg^{-1} at day 14. For spruce Oe, the net release of TDP decreased from 47 to about 40 mg kg^{-1} after 8 h and remained constant from then on.

In all samples, the net release of TDP was mostly in form of DIP (Fig. 2). DOP amounted to about 25% of TDP in spruce Oi and Oe and in beech Oi, but only to about 7.5% of TDP in beech Oe. The time trends of the net release of DIP and DOP were both similar to those observed for TDP. The maximum net release of both compounds was at time 0. Like with TDP, the net release DIP and DOP decreased stronger in Oi than in Oe samples.

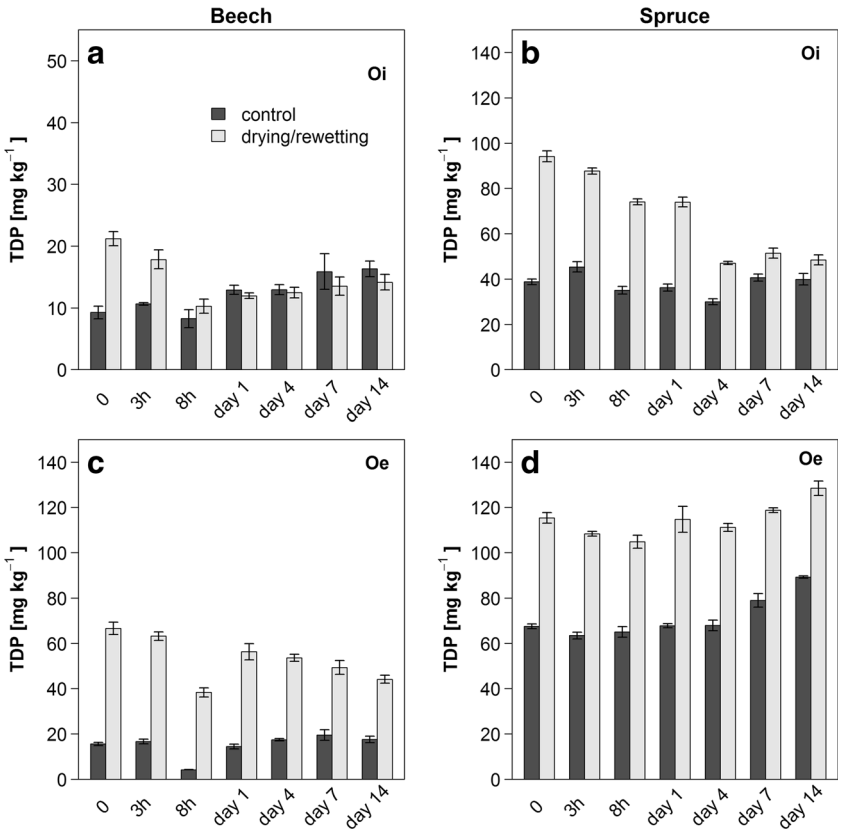

Fig. 1 Total dissolved P (TDP) following drying and rewetting of Oi and Oe layers of beech (**a**, **c**) and spruce forest floors (**b**, **d**) (Mean ± SEM; $n = 4$)

In the controls, the amount of Pmic was in the range of 400 to 700 mg kg^{-1} in beech Oi, Oe, and in spruce Oi, but Pmic was less (around 350 mg kg^{-1}) in spruce Oe (Fig. 3). After rewetting (time 0), the D/W treatment caused a reduction in Pmic in spruce Oi and Oe. In spruce Oi, Pmic decreased by about 6% (32 mg kg^{-1}) in comparison to the controls. In spruce Oe the difference of Pmic to the controls immediately after rewetting was 94 mg kg^{-1}. While Pmic recovered in spruce Oi already at day 1, the reduction of Pmic by D/W in spruce Oe persisted until day 14. In contrast to spruce, the effect of D/W on Pmic of beech Oi and Oe was not statistically significant. However, for beech Oe, there was a tendency for a decrease of Pmic immediately after rewetting by about 16% (92 mg kg^{-1}) in comparison to the controls. This tendency was no longer observed at day 1.

The ARISA revealed that the composition of bacterial as well as fungal communities differed significantly among all 4 layers (spruce Oe, spruce Oi, beech Oe, and beech Oi; all pairwise-tests: $p < 0.05$; Fig. 4a, b). In the spruce Oe layer, the composition of bacterial and fungal communities of the D/W samples differed significantly from the controls 14 days after rewetting (Fig. 4c, d). In the beech Oe layer, similar patterns were observed for the composition of bacterial communities, but the differences were not significant at the $p < 0.05$ level. D/W had no effect on the microbial community composition in the spruce as well as the beech Oi layers.

Discussion

Drying and rewetting caused a release of TDP from the forest floors of both tree species. The largest net release of TDP was from the Oe layer with 50 and 40 mg kg^{-1} for beech and spruce, respectively. The net TDP release in the present study was more than 30 times higher than the reported release of TDP after D/W from mineral soils (Butterly et al. 2011). This is not surprising, considering that differences in microbial biomass between organic layers and mineral horizons are in a similar range (e.g., Dinh et al. 2016). In agreement with Butterly et al. (2009) and Blackwell et al. (2013), DOP release decreased with incubation time after rewetting and DOP concentrations were smaller than DIP concentrations. DOP may be rapidly mineralized during the 2 h of rewetting (Bünemann et al. 2013; Macklon et al. 1997) and converted to DIP (Zhang et al. 2016).

The TDP released after rewetting strongly decreased probably due to immobilization with incubation time in the Oi layers of both tree species to very low levels after day 1 in beech and day 4 in spruce. In contrast, TDP release after rewetting was rather stable in Oe layers and still observable at day 14. In mineral soils, Blackwell et al. (2009) reported a sharp decline of the TDP release already 1 day after rewetting. The continuing TDP net release in the Oe layers for more than 14 days indicates that the D/W might have a high relevance

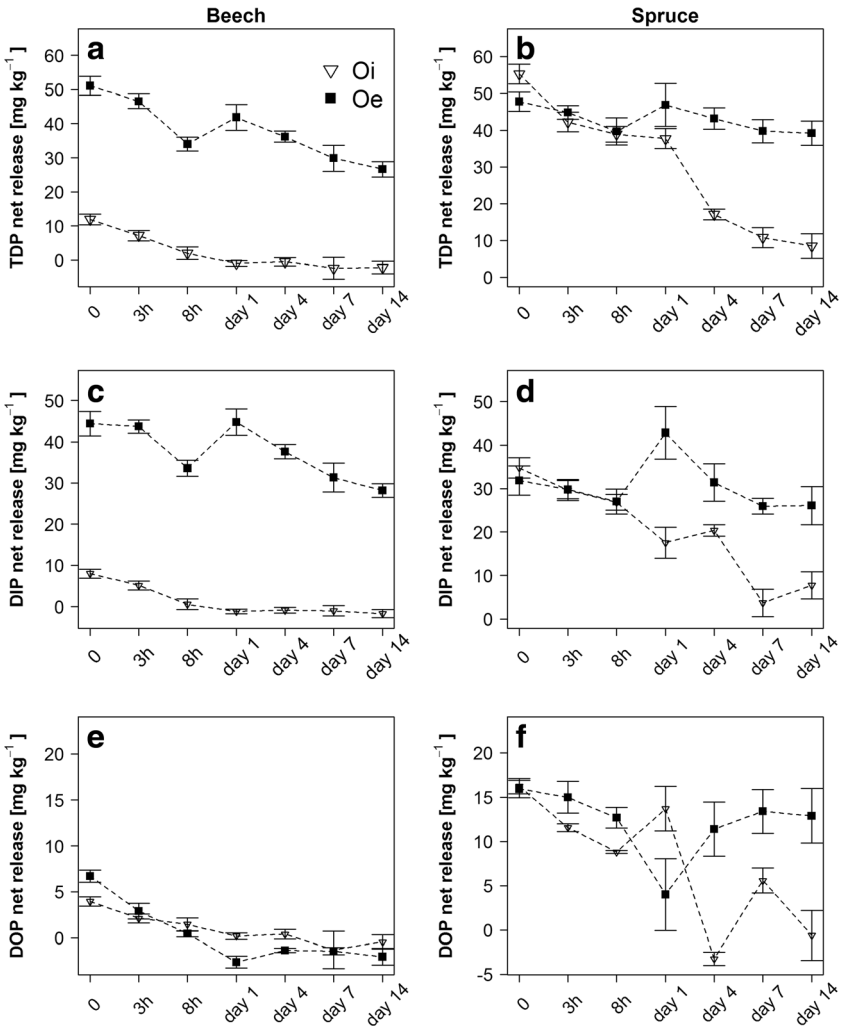

Fig. 2 Net release (D/W – controls) of total dissolved P (TDP), dissolved inorganic P (DIP) and dissolved organic P (DOP) after drying and rewetting in Oi and Oe layers of beech (**a**, **c**, **e**) and spruce forest floors (**b**, **d**, **f**) (Mean ± SEM; $n = 4$)

for the P transport from the forest floor into the mineral soil by leaching and for the uptake of P by plant roots. We extrapolated the potential release of P after D/W from forest floors (data on forest floor stocks from Gerstberger et al. 2004) based on the net releases from this experiment. The total TDP net release from Oi + Oe layers ranges from 1.4 kg P ha^{-1} (beech stands) to 2.0 kg P ha^{-1} (spruce stands) immediately after rewetting and from 0.7 kg P ha^{-1} (beech stands) to 1 kg P ha^{-1} (spruce stands) 14 days after rewetting. This release may provide a substantial pool of available P, as the total annual P uptake of trees in temperate forest (litterfall + increment) is in the range of 4–7 kg P ha^{-1} a^{-1} (Ilg et al. 2009). Bünemann et al. (2013) reported that plant roots took up about 30% of the P released by D/W in a grassland soil, emphasizing the relevance of D/W cycles for the P cycling in the soil-plant system. However, as the rewetting in our laboratory experiment was fast and massive, the P net release after rewetting of a forest floor under field conditions might be less due to only a partial rewetting based on the hydrophobicity of surfaces and preferential flow paths (Bogner et al. 2008; Borken and Matzner 2009). Hence, the P release in the laboratory experiment likely represents the upper limit of D/W effects.

The dynamic of Pmic is suggested to be a driver of the TDP net release after D/W and the subsequent immobilization of TDP by the growing and previously declined microbial biomass (Zhang et al. 2016). Relating the dynamics of Pmic to those of the TDP net release in forest floors is hampered as the amount of TDP released after D/W was less than 10% of the Pmic pool in our experiment. However, the observed decrease of Pmic after drying in spruce Oe (by 90 mg kg^{-1}) and spruce Oi (by 30 mg kg^{-1}) was in a similar range to the net TDP release. This supports the conclusion that Pmic is a major source of the TDP release. The relative reduction of Pmic in Oe layers was similar to studies with grassland or arable mineral soils. Chen et al. (2016) found a decrease of Pmic by 21% after drying, and a full recovery 7 days after rewetting. Nguyen and Marschner (2005) observed that Pmic decreased by 25% after drying followed by a rapid increase after 1 day rewetting.

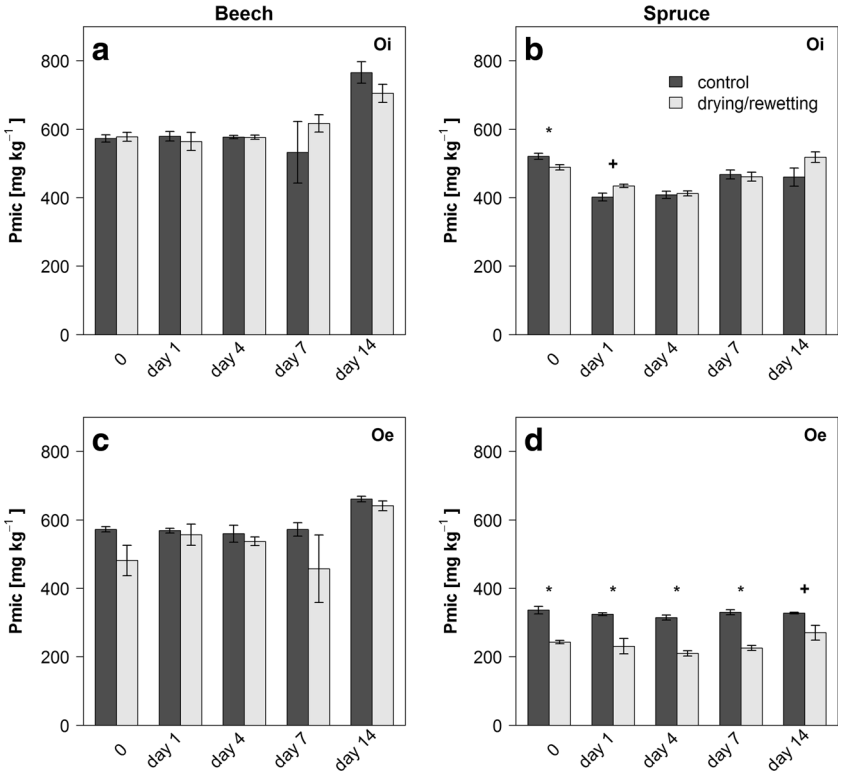

Fig. 3 Microbial biomass P (Pmic) following drying and rewetting of Oi and Oe layers of beech (**a**, **c**) and spruce forest floors (**b**, **d**) (Mean ± SEM; $n = 4$, * = $p < 0.05$; + = $p < 0.1$)

The spruce Oe layer showed not only the most pronounced but also stable reduction of Pmic, coinciding with the dynamics of the net TDP release and indicating a minor immobilization of released P in the microbial biomass. In contrast, no clear change in microbial biomass was seen in the beech Oi layer following D/W which coincided to the small TDP net release.

In accordance with the Pmic data, the ARISA revealed that D/W only affected the microbial community composition in the spruce Oe layer 14 days after D/W. In all other layers, D/W had minor or no effects on the microbial community composition. Therefore, and since Pmic had fully recovered 14 days after D/W, the proportion of microorganisms being sensitive to D/W in forest floor Oi layers seems to be less than in Oe

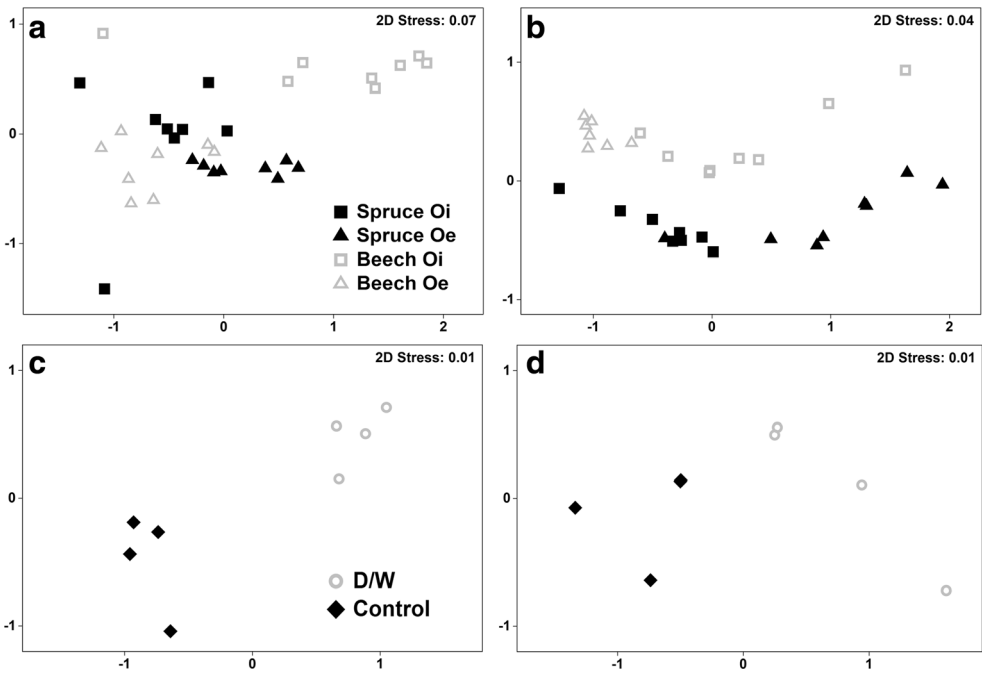

Fig. 4 Non-metric multidimensional scaling ordination (NMDS) of the microbial communities among organic layers of the spruce and the beech site (**a**: bacteria = ANOSIM: $r = 0.588$, $p = 0.001$, all pairwise-tests: $p < 0.05$; **b**: fungi = ANOSIM: $r = 0.627$, p = 0.001, all pairwise-tests: $p < 0.05$) and in the spruce Oe layer between D/W and control samples 14 days after rewetting (**c**: bacteria = ANOSIM: $r = 1.000$, $p = 0.029$; d: fungi = ANOSIM: $r = 0.635$, $p = 0.029$). Microbial communities were characterized by automated ribosomal intergenic spacer analysis (ARISA)

layers and in grassland or arable soils. The frequent exposition of Oi layers to D/W seems to shift the community compositions towards resistant species with low responses in P release. These community shifts require further attention and a more direct approach like high-resolution sequencing is necessary to enable a detailed taxonomic determination of the microbial community composition in future studies (cf. Schöler et al. 2017; Vestergaard et al. 2017).

In a previous study, we showed that the net release of TDP after D/W varies among microbial groups and was in the order gram-negative bacteria >> gram-positive bacteria = fungi (Dinh et al. 2017). This suggests that the effect of D/W on Pmic largely depends on the microbial community composition, with fungi and gram-positive bacteria being less susceptible to D/W than gram-negative bacteria. Schmitt and Glaser (2011) and Kohl et al. (2015) observed that the ratio of fungi to bacteria was much larger in Oi layers than in Oe and Oa layers. This is supported by Yevdokimov et al. (2016) who observed a strong reduction of Pmic after D/W in pH neutral Chernozem and Phaeozem soils, but not in an acidic Podzol with soil microbial communities likely dominated by fungi. Moreover, a slower recovery of declined Pmic is to be expected in fungi dominated than in bacteria dominated soils. Therefore, differences in the TDP release between Oi and Oe layers in our experiment are likely based on variations in fungi to bacteria ratios as supported by the variation of the composition of microbial communities between the layers.

Overall, the dynamics of Pmic and the composition of microbial communities in our experiment support the postulated role of microbial biomass for the TDP net release and its temporal development after rewetting.

Conclusions

This study demonstrated that D/W can increase the pool of water soluble and plant available P for at least 14 days. The release of soluble P and its temporal dynamics seem to be matched by the decline and recovery of the Pmic pool. The effect of D/W on the release of P from the forest floor was layer and tree stand specific. This suggests that the degree of decline and recovery of the Pmic pool after D/W is specific for the soil microbial communities inhabiting the different layers of the forest floor.

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References

Achat DL, Augusto L, Gallet-Budynek A, Bakker MR (2012) Drying-induced changes in phosphorus status of soils with contrasting soil organic matter contents—implications for laboratory approaches. Geoderma 187-188:41–48

Aponte C, Marañón T, García LV (2010) Microbial C, N and P in soils of Mediterranean oak forests: influence of season, canopy cover and soil depth. Biogeochemistry 101:77–92

Bapiri A, Bååth E, Rousk J (2010) Drying-rewetting cycles affect fungal and bacterial growth differently in an arable soil. Microb Ecol 60: 419–428

Blackwell MSA, Brookes PC, de La F-MN, Murray PJ, Snars KE, Williams JK, Haygarth PM (2009) Effects of soil drying and rate of re-wetting on concentrations and forms of phosphorus in leachate. Biol Fertil Soils 45:635–643

Blackwell M, Brookes PC, de la Fuente-Martinez N, Gordon H, Murray PJ, Snars KE, Williams JK, Bol R, Haygarth PM (2010) Phosphorus solubilization and potential transfer to surface waters from the soil microbial biomass following drying–rewetting and freezing–thawing. In: Sparks DL (Ed) Advances in agronomy. Elsevier Academic Press Inc, San Diego, pp 1–35

Blackwell MSA, Carswell AM, Bol R (2013) Variations in concentrations of N and P forms in leachates from dried soils rewetted at different rates. Biol Fertil Soils 49:79–87

Bogner C, Wolf B, Schlather M, Huwe B (2008) Analysing flow patterns from dye tracer experiments in a forest soil using extreme value statistics. Eur J Soil Sci 59:103–113

Borken W, Matzner E (2009) Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Glob Chang Biol 15: 808–824

Bray RH, Kurtz LT (1945) Determination of total, organic, and available forms of phosphorus in soils. Soil Sci 59:39–46

Brookes PC, Powlson DS, Jenkinson DS (1982) Measurement of microbial biomass phosphorus in soil. Soil Biol Biochem 14:319–329

Bünemann EK, Keller B, Hoop D, Jud K, Boivin P, Frossard E (2013) Increased availability of phosphorus after drying and rewetting of a grassland soil. Processes and plant use. Plant Soil 370:511–526

Butterly CR, Bünemann EK, McNeill AM, Baldock JA, Marschner P (2009) Carbon pulses but not phosphorus pulses are related to decreases in microbial biomass during repeated drying and rewetting of soils. Soil Biol Biochem 41:1406–1416

Butterly CR, McNeill AM, Baldock JA, Marschner P (2011) Rapid changes in carbon and phosphorus after rewetting of dry soil. Biol Fertil Soils 47:41–50

Cardinale M, Brusetti L, Quatrini P, Borin S, Puglia AM, Rizzi A, Zanardini E, Sorlini C, Corselli C, Daffonchio D (2004) Comparison of different primer sets for use in automated ribosomal intergenic spacer analysis of complex bacterial communities. Appl Environ Microbiol 70:6147–6156

Chen H, Lai L, Zhao X, Li G, Lin Q (2016) Soil microbial biomass carbon and phosphorus as affected by frequent drying–rewetting. Soil Res 54:321

Dinh M-V, Schramm T, Spohn M, Matzner E (2016) Drying-rewetting cycles release phosphorus from forest soils. J Plant Nutr Soil Sci 179:670–678

Dinh M-V, Guhr A, Spohn M, Matzner E (2017) Release of phosphorus from soil bacterial and fungal biomass following drying/rewetting. Soil Biol Biochem 110:1–7

Fierer N, Schimel JP (2002) Effects of drying–rewetting frequency on soil carbon and nitrogen transformations. Soil Biol Biochem 34:777–787

Fisher MM, Triplett EW (1999) Automated approach for ribosomal intergenic spacer analysis of microbial diversity and its application

to freshwater bacterial communities. Appl Environ Microbiol 65: 4630–4636

Gerstberger P, Foken T, Kalbitz K (2004) The Lehstenbach and Steinkreuz Catchments in NE Bavaria, Germany. In: Matzner E (ed) Biogeochemistry of forested catchments in a changing environment. Springer Berlin Heidelberg, Berlin, pp 15–41

Gordon H, Haygarth PM, Bardgett RD (2008) Drying and rewetting effects on soil microbial community composition and nutrient leaching. Soil Biol Biochem 40:302–311

Hamer U, Unger M, Makeschin F (2007) Impact of air-drying and rewetting on PLFA profiles of soil microbial communities. J Plant Nutr Soil Sci 170:259–264

Ilg K, Wellbrock N, Lux W (2009) Phosphorus supply and cycling at long-term forest monitoring sites in Germany. Eur J For Res 128: 483–492

Jenkinson D, Brookes PC, Powlson DS (2004) Measuring soil microbial biomass. Soil Biol Biochem 36:5–7

Kakumanu ML, Cantrell CL, Williams MA (2013) Microbial community response to varying magnitudes of desiccation in soil. A test of the osmolyte accumulation hypothesis. Soil Biol Biochem 57:644–653

Kohl L, Laganière J, Edwards KA, Billings SA, Morrill PL, van Biesen G, Ziegler SE (2015) Distinct fungal and bacterial $\delta^{13}C$ signatures as potential drivers of increasing $\delta^{13}C$ of soil organic matter with depth. Biogeochemistry 124:13–26

Macklon A, Grayston SJ, Shand CA, Sim A, Sellars S, Ord BG (1997) Uptake and transport of phosphorus by *Agrostis capillaris* seedlings from rapidly hydrolysed organic sources extracted from ^{32}P-labelled bacterial cultures. Plant Soil 190:163–167

Mondini C, Contin M, Leita L, de NM (2002) Response of microbial biomass to air-drying and rewetting in soils and compost. Geoderma 105:111–124

Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. Anal Chim Acta 27: 31–36

Nguyen BT, Marschner P (2005) Effect of drying and rewetting on phosphorus transformations in red brown soils with different soil organic matter content. Soil Biol Biochem 37:1573–1576

Oberson A, Friesen DK, Morel C, Tiessen H (1997) Determination of phosphorus released by chloroform fumigation from microbial biomass in high P sorbing tropical soils. Soil Biol Biochem 29:1579–1583

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL https://www.R-project.org/

Schmitt A, Glaser B (2011) Organic matter dynamics in a temperate forest soil following enhanced drying. Soil Biol Biochem 43:478–489

Schöler A, Jacquiod S, Vestergaard G, Schulz S, Schloter M (2017) Analysis of soil microbial communities based on amplicon sequencing of marker genes. Biol Fertil Soils 53:485–489

Sheik CS, Beasley WH, Elshahed MS, Zhou X, Luo Y, Krumholz LR (2011) Effect of warming and drought on grassland microbial communities. ISME J 5:1692–1700

Turner BL, Haygarth PM (2001) Biogeochemistry. Phosphorus solubilization in rewetted soils. Nature 411:258

Vance ED, Brookes PC, Jenkinson DS (1987) Microbial biomass measurements in forest soils. The use of the chloroform fumigation-incubation method in strongly acid soils. Soil Biol Biochem 19: 697–702

Vestergaard G, Schulz S, Schöler A, Schloter M (2017) Making big data smart—how to use metagenomics to understand soil quality. Biol Fertil Soils 53:479–484

Voříšková J, Brabcová V, Cajthaml T, Baldrian P (2014) Seasonal dynamics of fungal communities in a temperate oak forest soil. New Phytol 201:269–278

Weig AR, Peršoh D, Werner S, Betzlbacher A, Rambold G (2013) Diagnostic assessment of mycodiversity in environmental samples by fungal ITS1 rDNA length polymorphism. Mycol Prog 12:719–725

White T, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications. Academic Press, London, pp 315–322

Wu J, Brookes PC (2005) The proportional mineralisation of microbial biomass and organic matter caused by air-drying and rewetting of a grassland soil. Soil Biol Biochem 37:507–515

Yevdokimov I, Larionova A, Blagodatskaya E (2016) Microbial immobilisation of phosphorus in soils exposed to drying-rewetting and freeze-thawing cycles. Biol Fertil Soils 52:685–696

Yuste J, Peñuelas J, Estijarte M, Garcia-Mas J, Mattana S, Ogaya R, Pujol M, Sardans J (2011) Drought-resistant fungi control soil organic matter decomposition and its response to temperature. Glob Chang Biol 17:1475–1486

Zhang H, Shi L, Wen D, Yu K (2016) Soil potential labile but not occluded phosphorus forms increase with forest succession. Biol Fertil Soils 52:41–51