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REGULAR ARTICLE

Increased availability of phosphorus after drying and rewetting of a grassland soil: processes and plant use

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Abstract
Aims Drying and rewetting (DRW) often increases soil phosphorus (P) availability. Our aims were to elucidate underlying processes and assess potential plant uptake of released P.
Methods Using a grassland soil with low available and high microbial P as a model, we studied the contributions of microbial and physicochemical processes to P release by determining DRW effects on i) C:P ratios of nutrient pulses in fresh and sterilized soils, ii) aggregate stability and iii) P forms released upon soil dispersion. Use of the P pulse by maize was examined in a bioassay and a split-root experiment.
Results The strong P pulse after DRW was larger than that observed for C. Experiments with sterilized soil pointed to a non-microbial contribution to the pulse for P, but not for C. Aggregate disruption after DRW occurred due to slaking, and this released molybdate-reactive and -unreactive P. Maize benefitted from the P pulse only in the bioassay, i.e. when planted after the DRW cycle.
Conclusions The majority of C and P released upon DRW originated from the microbial biomass, but for P release, physicochemical processes were also important. In the field, the released P would only be available to drought-resistant plants.

Keywords Soil moisture fluctuation · Split-root experiment · Resin-extractable P · Microbial P · Soil sterilization · Aggregate stability

Abbreviations

DRW	Drying and rewetting
P	Phosphorus
C_{org}	Organic carbon
N_{tot}	Total nitrogen
GWC	Gravimetric water content
P_{resin}	Resin-extractable P
P_{hex}	Hexanol-labile P
C_{K2SO4}	Organic C extractable with 0.5 M K_2SO_4
C_{chl}	Chloroform-labile C
MRP	Molybdate-reactive P
MUP	Molybdate-unreactive P
MWD	Mean weight diameter

Introduction

With a globally changing climate, fluctuations in soil water contents are likely to become more extreme in

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many regions of the world. Drying and rewetting (DRW) of soils often induces not only a substantial pulse in soil respiration but also changes in soil phosphorus (P) pools. While pulses in carbon (C) after DRW may affect C sequestration in soils (Fierer and Schimel 2003), pulses in P availability are important with respect to P losses to water bodies (Blackwell et al. 2010). At the same time, they could be important for plant P nutrition, especially in soils with low P availability. Therefore, it is important to understand both the underlying processes and the potential plant uptake of P release after DRW.

Release of CO_2 upon DRW can be derived from the lysis of microbial cells due to an osmotic shock upon rapid rewetting or from the release of intracellular solutes (Halverson et al. 2000; Fierer and Schimel 2003; Kieft et al. 1987). Alternatively, physical changes in the soil may release organic matter that can then be mineralized (Adu and Oades 1978). In particular, disruption of aggregates upon DRW has been observed (Denef et al. 2001). However, the water stability of aggregates can decrease or increase with DRW cycles, depending on a range of factors such as soil type, management history and microbial activity (Utomo and Dexter 1982).

The release of P after DRW is often suggested to be derived from microbial cell lysis, e.g. by Sparling et al. (1985) who observed an increase in $NaHCO_3$-extractable inorganic P after air-drying of soils by 15–180 %. Likewise, Turner and Haygarth (2001) found a positive correlation between the increase in water-soluble organic P upon DRW and amounts of microbial P in grassland soils. However, the relationship suggested that only 1.8 % of microbial P was recovered in water-soluble organic P, and that in the absence of microbial P, water-soluble organic P would still increase upon DRW, implying a partial non-microbial origin. Two studies on sandy forest soils postulated a contribution by microbial cell lysis to P release upon DRW of 30–45 % and 62 %, respectively (Grierson et al. 1998; Achat et al. 2012). However, Butterly et al. (2009) found P pulses after DRW to be unrelated to changes in microbial P, although corresponding CO_2-pulses were related to changes in microbial C. Thus, the processes behind increased P availability after DRW may differ from those behind CO_2-pulses. For example, physical breakdown of soil after DRW may release inorganic as well as organic forms of P, and thus the contribution to the P pulse may be larger for P than for C.

Physical breakdown of soil can occur due to various mechanisms, resulting in different fragment sizes. The aggregate stability tests by Le Bissonnais (1996) were devised to distinguish between different breakdown mechanisms, namely slaking (breakdown of aggregates due to compression of air which is entrapped during wetting), microcracking due to differential swelling of clays, mechanical breakdown by raindrop impact, and for soils high in sodium also physico-chemical dispersion. Slaking and differential swelling result in the destruction of macro- to microaggregates, whereas mechanical breakdown and physico-chemical dispersion destroy the structure to yield primary particles (< 50 μm). The dominant breakdown mechanism after DRW will affect the forms of released P and its potential availability to plants.

The availability of P to plants is difficult to study since drying of soils affects the availability of a range of nutrients and puts the plant under substantial water stress. We can imagine two ways of conducting plant assays to assess changes in P availability after DRW: 1) seeds or seedlings are planted into soils with different moisture pretreatment, e.g. constantly moist vs. a DRW regime and 2) plants are grown in a split-root setup where they have permanent access to a nutrient solution that provides all nutrients except P and relieves the plants from water stress, while the only source of P is a soil compartment subjected to different moisture regimes.

The first approach (subsequently termed “bioassay”) was followed by Barrow and Shaw (1980) with no significant effect of previous drying on the growth of subterranean clover. In contrast, Chepkwony et al. (2001) and Butterly (2008) observed increased dry matter and P uptake of wheat planted into soils after DRW. Changes in the availability of other nutrients may have contributed to improved plant growth, especially in the second case, since resin-extractable P was not affected by moisture pretreatment (Butterly et al. 2011a). Besides the problem of nutrient interactions, the main disadvantages with the bioassay approach are that i) only the effects of preceding DRW cycles can be studied and ii) the transient nutrient pulses may have disappeared by the time the seed or seedling has rooted in the soil and starts to take up nutrients at a significant rate. These two problems may be overcome by the split-root setup of the second approach.

We used a soil under permanent grassland with low available and high microbial P as a model. Our objectives

were to 1) elucidate the underlying processes of P release after DRW and 2) investigate whether an increase in available P after DRW can be used by plants. For the first objective, we conducted several incubation experiments to examine a) the C:P ratios of microbial biomass and nutrient pulses as depending on the extent of drying before rewetting, b) the potential occurrence of P and C pulses after DRW in sterilized soil, c) the breakdown mechanism and resulting fragment size distribution after DRW and d) the release of different P forms after DRW and after dispersion to primary particles. For the second objective, we developed a split-root setup and compared it to the bioassay approach, with maize chosen as the test plant due to its suitability for split-root experiments.

Methods

Soil sampling and soil characteristics

Soil was sampled from 0 to 10 cm depth under permanent grassland in Regensdorf-Watt (canton Zurich, Switzerland) at two dates (Table 1). The soil is a Cambisol with 22 % clay and 34 % silt in the top 10 cm (Philipp et al. 2004). Soil cores were taken in the border strips of a fertilization experiment. In these, the soil has remained unfertilized since 1992, while the vegetation has been cut and removed as hay three times per year. Soil was sieved moist at 4 or 7 mm (Table 1), breaking soil clods by hand, made into one composite sample per sampling date and stored at 4 °C until the beginning of the experiments. A subsample was dried at 40 °C for measurement of pH and finely ground for determination of organic C (C_{org}) and total N (N_{tot}) contents by dry combustion (Flash EA, Thermo Electron Corporation). Soil pH was similar on both sampling dates while C_{org} and N_{tot} were lower at the second (Table 1).

For all experiments, initial gravimetric water content (GWC) was adjusted to 40 %, which is slightly lower than the GWC of 43 % found after 4 days of equilibration at a suction of −10 hPa. All experiments were conducted at a bulk density of 1 g cm^{-3} , and assuming a particle density of 2.65 g cm^{-3}, this resulted in a water-filled pore space of 64 %, at which soil respiration is usually at its maximum (Franzluebbers 1999).

Experiment 1: incubation experiment with varying degrees of drying

The aim of this experiment was to quantify P and C pulses after DRW as a function of water content (GWC of 2, 5, 10, 15, 20 or 40 %) before rewetting. To this end, portions of moist soil equivalent to 20 g dry soil were incubated for 1 week at 25 °C in the dark. Thereafter, drying was initiated by adding porous plastic bags filled with self-indicating silica. Silica bags were exchanged daily with dry ones until the desired water content was reached, i.e. up to 8 times. The actual water content was determined gravimetrically and soil rewet to 40 % GWC using deionized H_2O. Four rewetted soil cores per nominal water content were transferred immediately to separate jars for measurement of CO_2-release during 8 days, and four cores were extracted 1 h after rewetting for resin-extractable P (P_{resin}), hexanol-labile (microbial) P (P_{hex}), organic C extractable with 0.5 M (C_{K2SO4}) and chloroform-labile (microbial) C (C_{chl}).

Experiment 2: incubation experiment with sterilized soils

The aim of this experiment was to test if P and C pulses after DRW occur in sterile soil. The following treatments were imposed:

Table 1 Gravimetric water content, soil pH, and organic C and N contents at the two sampling dates

Sampling date	Used in experiment	Sieved at mm	GWC g H_2O g^{-1} soil	pH_{H2O}[a]	C_{org} gkg^{-1}	N_{tot}
12/5/2009	2, 5b	4	0.34	5.4	26.5	2.7
20/11/2009	1, 3, 4, 5a	7[b]	0.37	5.3	20.2	2.5
Significance level (p)				0.268	<0.001	0.001

[a] Measured in H_2O (soil:solution ratio 1:2.5)

[b] Larger sieve used to facilitate sieving of the larger amount of soil taken on this date

MS Constantly moist soil, sterile
MN Constantly moist soil, non-sterile
DS Drying to 3–4 % GWC, rewetting, sterile
DN Drying to 3–4 % GWC, rewetting, non-sterile

Since the form of sterilization can have distinct impacts on soil properties (Wolf et al. 1989), two sterilization treatments were tested in order to assure the general validity of the results. Portions of moist soil equivalent to 2 g dry soil were sterilized by either autoclaving (three times within 1 week) or gamma-irradiation (one dose of 50–53 kGy). Soils were remoistened to 40 % GWC either by addition of autoclaved H_2O under a laminar flow (MS, DS) or by addition of 0.4 ml inoculum solution (supernatant of a 1:5 soil:water suspension) and additional autoclaved H_2O if required (MN, DN). All tubes were then preincubated for 4 weeks at 25 °C in the dark at constant soil moisture.

For drying, the tubes were left open in a laminar flow to dry to 3–4 % GWC before rewetting to 40 % GWC with autoclaved H_2O. One hour after rewetting, P_{resin} and P_{hex} were extracted. To this end, the soil was suspended in sterile H_2O under the laminar flow. To check for sterility, 5 aliquots of 10 µl each were taken from the 1:15 soil:water suspensions and put onto agar plates (Difco Nutrient Agar) which were incubated for 7 days at 25 °C in the dark. Resin membranes were then added to the soil suspensions. Contamination of samples after 16 h of shaking with the non-sterile resins was negligible as checked by plate counts. Similarly, C_{K2SO4} was extracted 1 h after rewetting by addition of 0.5 M K_2SO_4 under non-sterile conditions, but given the extractant and the short duration, any microbial growth was unlikely.

Experiment 3: aggregate stability tests

The aim of this experiment was to identify the relevant disaggregation mechanism during DRW using aggregate stability tests (Le Bissonnais 1996). The 2–4 mm aggregate fraction was obtained from the soil by dry sieving of the moist soil in order to start with a controlled initial soil structure. The resulting aggregate fraction had a GWC of 33 %. Three different pretreatments were established:

MM Constantly moist aggregates, equilibrated for 1 h at 10 hPa
DD Aggregates dried down to a GWC of 2 %
DM Aggregates dried down to a GWC of 2 %, equilibrated for 1 h at 10 hPa

Drying to 2 % GWC in treatments DD and DM was done with silica bags. Before starting the stability tests, the aggregate fractions in MM and DM were equilibrated for 1 h on a 10 hPa tension table, while in DD the dried fraction was used directly. With the pretreatments MM and DD, we tested the disaggregation mechanism of moist vs. dry soils. Pretreatment DM was included to resemble the extraction of soils 1 h after rewetting and thus to test if slaking would occur under these conditions.

Three aggregate stability tests were performed in triplicates: fast wetting, slow wetting and mechanical breakdown after prewetting, followed by determination of fragment size distribution. For the first aggregate stability test (fast wetting), 5 g (dry weight equivalent) of the pretreated aggregate fraction were gently immersed in a 250 ml beaker filled with 50 ml deionized water. After 10 min, the water was removed and the soil material transferred to a 50 µm sieve immersed in ethanol. For the second aggregate stability test (slow wetting), 5 g of the fraction were saturated on a 30 hPa tension table for 30 min and transferred to a 50 µm sieve as above. For the third aggregate stability test (mechanical breakdown), 5 g of the fraction were immersed in a 250 ml beaker filled with 50 ml ethanol in order to remove any air from the aggregates. After 30 min, the ethanol was removed and the material transferred to a 250 ml flask with 50 ml deionized water which was then adjusted to 250 ml. The flask was closed and agitated 10 times end over end, followed by transfer to a 50 µm sieve as above.

For the determination of fragment size distribution in each of the three tests, the material on the 50 µm sieve was wet-sieved immersed in ethanol in circular motions to separate the <50 µm from the >50 µm fraction. The >50 µm fraction was dried at 105 °C for 48 h before sieving it by hand, moving the soil on the sieve forward and back ten times, through 6 stacked sieves to obtain the fractions with a diameter of 50–100, 100–200, 200–500, 500–1,000, 1,000–2,000, and 2,000–4,000 µm. The dry weight of each fraction was determined and the difference between the initial

soil weight and the sum of the six fractions taken as the weight of the <50 μm fraction. The mean weight diameter (MWD) was calculated as

$$MWD(mm) = (d1 * w1 + d \ldots * w \ldots + d7 * w7)/100\%$$

where d is the average diameter (in mm) and w the weight percent of each fraction. Large and small macroaggregates are defined as material in the size classes >2,000 and 1,000–2,000 μm, respectively, while primary particles constitute the <50 μm fraction and microaggregates are found in all size fractions between 50 and 1,000 μm.

Experiment 4: P release upon DRW and soil dispersion

The aim of this experiment was to determine the quantities and forms of P released due to physical soil disruption after DRW and physico-chemical dispersion with sodium (Na), respectively. The hypothesis was that Na-facilitated dispersion of moist soils results in a larger increase in water-extractable P than physical soil disruption after DRW, because Na-facilitated dispersion leads to destruction down to primary particles (Bartoli et al. 1991; Feller et al. 1991), while DRW results only in a reduction of aggregate sizes. The combination of DRW and Na-facilitated dispersion should thus not release additional P.

To test this hypothesis, soils kept constantly moist (M) or dried to 2 % GWC (D) and rewetted as described in experiment 1 were extracted with water in the presence or absence of Na-saturated cation exchange resin membranes (BDH #551652U, 3 cm×2 cm per g of soil) by horizontal shaking at 150 rpm for 16 h. The supernatant after centrifugation (10 min at 3,000 rpm) was filtered through 0.2 μm and analyzed for dissolved molybdate-reactive (MRP) and molybdate-unreactive P (MUP). Water-extractable rather than resin-extractable P was investigated in order to assess the release of different forms of dissolved P, since resin membranes capture mainly MRP (Cheesman et al. 2010).

Experiments 5a and 5b: plant experiments

Experimental design

The aim of the plant experiments was to evaluate the net effect of P pulses after rewetting on plant P uptake. Two approaches to assure that the plant is well-supplied with water and nutrients other than P were tested: a) a bioassay in which pre-germinated maize seedlings were planted into the soil just after rewetting and grown in moist soil, with all nutrients except P added to the soil at planting, and b) a split-root experiment where part of the maize roots grew in a compartment with a P-free nutrient solution and the other part in soil that was kept constantly moist or subjected to two cycles of DRW. To test the sensitivity of both systems, P response curves with constantly moist soils that received P additions at the time of rewetting of dry soils were also established.

The treatments in the plant experiments were:

0P	Constantly moist soil, no P addition
5P	Constantly moist soil, 5 mg P kg^{-1} added at the time of rewetting in treatments D and V (see below)
10P	Constantly moist soil, 10 mg P kg^{-1} added at the time of rewetting in D and V
20P	Constantly moist soil, 20 mg P kg^{-1} added at the time of rewetting in D and V
D	"dry"; drying to 11 % (bioassay) or 16 % (split-root experiment) GWC, followed by rewetting
V	"very dry"; drying to 4 % (bioassay) or 12 % (split-root experiment) GWC, followed by rewetting

Both plant experiments were conducted with 8 replicates per treatment (48 pots).

Detailed procedure of experiment 5a (bioassay)

Opaque plastic pots (480 ml) were filled with moist soil equivalent to 460 g dry soil at a bulk density of 1 $g cm^{-3}$. Pots for treatments D and V were dried in an oven at 35–40 °C until reaching GWCs of 11 % and 4 %, respectively. To facilitate drying, a mesh-covered window of approximately 8 cm×5 cm was opened on one side of each pot. During the drying period, pots of treatments 0P, 5P, 10P and 20P were left at room temperature, covered with aluminum foil. One day before transplanting, the foil was removed and the soil air-dried to 32 % GWC.

Maize seeds (European Hybrid PR37Y15) weighing 0.33–0.36 g were surface-sterilized with 5 % $Ca(OCl)_2$, washed and germinated on moist filter paper at 30 °C for 4 days. Thereafter, each seed was wrapped in polyester wool, placed into a hole in a styrofoam plate floating on H_2O (treated by reverse osmosis, 6.5±1.2 μg P l^{-1}) and pregrown for 6 days.

One hour before transplanting, all pots were brought back to 40 % GWC. All treatments received part of the water addition as a blanket nutrient application, adding (in mg kg^{-1} soil) 90 N, 45 K, 15 Ca, 16 Mg, 24 S, and trace amounts (0.1–2) of Zn, Mo, Fe, B, Mn and Cu (Online resource 1). Treatments 5P, 10P and 20P also received a KH_2PO_4 solution (1 mg P ml^{-1}) which added 5, 10 and 20 mg P kg^{-1}, respectively.

One maize seedling was planted into each pot and the pots were placed in blocks into a climate chamber (15/9 h, 28/20 °C, 50 % humidity). Light intensity at the surface of the pots was 275 μmol s^{-1} m^{-2} (38 kLux). Pots were watered daily to replace water loss by weight. Plants were harvested 22 days after transplanting.

To quantify the P pulse and its duration in the bioassay, soil samples were taken in treatments 0P, D and V at three time points: 1 h after rewetting and after 11 and 22 days. About 10 g moist soil were taken from the top 4 cm of four pots per treatment and analyzed for P_{hex} and P_{resin}.

Detailed procedure of experiment 5b (split-root experiment)

The primary root of maize seeds pregerminated as above was cut to enhance nodal root growth (Buljovcic and Engels 2001) and the seedlings were pregrown on H_2O for 5 days. At transplanting, one seedling was placed near the edge of each pot and two nodal roots were led through an opening in the rim of the pot into a compartment with nutrient solution. The remaining 1–3 nodal roots were planted into the soil and a plastic support was placed around the seedling to keep it upright.

The climate chamber was set as above, except that humidity was lowered to 30 % in an attempt to increase drying intensity during dry periods. The roots from 6 pots (one per treatment) were hanging into the same compartment with 30 l of a modified P-free Hoagland solution at 25 % strength (Online resource 1), which was aerated and changed every 10 days. Daily watering by weight was done by placing the pot (including the roots that were otherwise hanging into the nutrient solution) carefully on a balance. Four unplanted pots each for treatments 0P, D and V were placed next to the planted pots to estimate plant effects on soil water content.

The first drying-rewetting cycle in treatments D and V was initiated 10 days after transplanting by ceasing the daily watering, opening the window in the pots and by additionally placing the pots of treatment V in front of a fan several times for a few hours. After 1 week, GWCs in treatments D and V were 17 and 13 %, respectively, while those in treatments 0P, 5P, 10P and 20P had oscillated between 35 % before and 40 % after the daily watering. Unplanted pots of treatments D and V had slightly higher GWCs (19 and 14 %, respectively) than planted ones, showing that a potential hydraulic lift via the roots in the nutrient solution to the soil was not important. All pots were brought back to 40 % GWC, with part of the water addition applied with a KH_2PO_4 solution (1 mg P ml^{-1}) for treatments 5P, 10P and 20P.

Subsequently, all pots were watered daily for 1 week. Another week of drying was then initiated, reaching GWCs of 15 and 12 % in treatments D and V, respectively, while corresponding values in unplanted plots were 19 and 16 %. All pots were rewetted as described above, including a second P addition to treatments 5P, 10P and 20P. Thus, the total amounts of P added in the split-root experiment were 10, 20 and 40 mg P kg^{-1} in 5P, 10P and 20P, respectively. All pots were kept moist for another week until the harvest 38 days after transplanting.

To monitor the P pulse in the split-root experiment, soil was taken 1 h after each rewetting event from the top 4 cm in four replicates of treatments 0P, D and V and analyzed for P_{resin} and P_{hex}.

Analytical methods

Hexanol-labile and resin-extractable P

Hexanol-labile P (P_{hex}) was determined by simultaneous liquid fumigation and extraction with anion-exchange resin membranes (BDH #55164) in bicarbonate form (soil:water ratio 1:15, 1 resin of 2×6 cm with 2 g soil) for 16 h as described by Kouno et al. (1995), but using hexanol as the fumigant instead of chloroform and eluting the resins with 0.1 *M* NaCl/HCl. The concentration of P in the eluate was determined colorimetrically with malachite green at 610 nm (Ohno and Zibilske 1991).

The amount of P extracted from non-fumigated subsamples corresponds to resin-extractable P (P_{resin}), while P_{hex} is reported as the difference between fumigated and non-fumigated subsamples. The recovery of P spikes added to non-fumigated samples in experiments 1 and 2 ranged between 85 and 90 %, regardless of the moisture treatment. Therefore, P_{hex}

was not corrected for sorption, and no conversion factor was applied.

Molybdate reactive and unreactive P in water extracts

In the dispersion experiment, MRP was analyzed colorimetrically (Ohno and Zibilske 1991) in fresh filtrates. Total dissolved P was determined in digested (2 ml filtrate autoclaved with 1 ml digestion mix (3.3 g ammonium persulfate in 100 ml of a 0.9*M* H_2SO_4 solution)) and neutralized aliquots. Dissolved MUP was calculated by difference.

Soil respiration, chloroform-labile and K_2SO_4-extractable organic C

The CO_2 released from soil was trapped in 1*M* NaOH solution, precipitated with $BaCl_2$ and determined by back-titration with 1*M* HCl (Alef 1995). Chloroform-labile C (C_{chl}) and C extractable with 0.5*M* K_2SO_4 (C_{K2SO4}) were determined by fumigation-extraction according to Vance et al. (1987) and determination of organic C in the extracts (Formacs TOC/TN analyzer, Skalar). No conversion factor (kEC) was used.

Plant analysis

At harvest, the shoots - and in the split-root experiment also the roots in the nutrient solution - were cut, and the roots in the soil were washed out over a 1 mm sieve before drying at 60 °C. The remainder of the maize seed was not included in any plant part. A subsample of root and shoot material was ashed at 550 °C for 3 h, dissolved in concentrated HNO_3 and the P concentration was measured colorimetrically after filtration (Whatman 40). Shoot N concentrations were determined by dry combustion (Flash EA, Thermo Electron Corporation).

Statistical analysis

All statistical analyses were done with SPSS 16.0 (SPSS Inc., Chicago, Illinois 60606). One- or two-factorial ANOVA was used, either with treatments or with the experimental factors (e.g. moisture, sterility, presence of the plant), followed by pairwise comparisons using LSD tests.

Results

Experiment 1: incubation experiment with varying degrees of drying

Significant increases in P_{resin} were observed in soils that had been dried to GWCs of 10 % or lower, with P_{resin} reaching 7.6±0.5 mg P kg^{-1} for soils with a water content of 2–5 % before rewetting (Fig. 1). For GWCs of 15–40 %, P_{resin} remained unchanged at 0.7±0.3 mg P kg^{-1}. Similar to the pulse in P_{resin}, soil respiration began to increase at GWCs before rewetting of about 10 %. For soils with a water content of 2–5 %, CO_2-release during 8 days after rewetting averaged 595±153 mg C kg^{-1}, compared to 115±31 mg C kg^{-1} in constantly moist soil. Changes in C_{K2SO4} were less pronounced than those in CO_2-release and P_{resin}, and they became significant only when soils had been dried to GWCs of 5 % or lower. Since the relative increase in P_{resin} was greater than that in CO_2-release, the C:P ratio of the pulse after DRW (approx. 80) was smaller than the ratio in constantly moist soil (approx. 240).

Significant reductions in P_{hex} occurred in soils that had been dried to water contents of 10 % or lower (Fig. 2). For soils dried to 2 % GWC, P_{hex} after rewetting was only 31 % of P_{hex} in constantly moist soil. A negative linear correlation between P_{hex} and P_{resin} was observed ($P_{hex}=-2.6*P_{resin}+30.2$, $R^2=0.98$, $p<0.001$). Thus, only 38 % of the decrease in P_{hex} were recovered in P_{resin}. Similar to the smaller pulse in C_{K2SO4} than in P_{resin}, also C_{chl} was less sensitive to DRW events than P_{hex}, reaching a minimum of 61 %

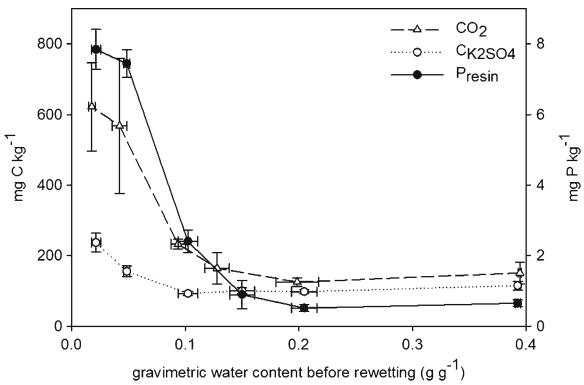

Fig. 1 Soil respiration (CO_2) during 8 days after rewetting, and extractable C (C_{K2SO4}) and resin-extractable P (P_{resin}) 1 h after rewetting, as a function of the water content before rewetting (means and standard deviations of four replicates). Points in a series are connected to assist visualization of trends

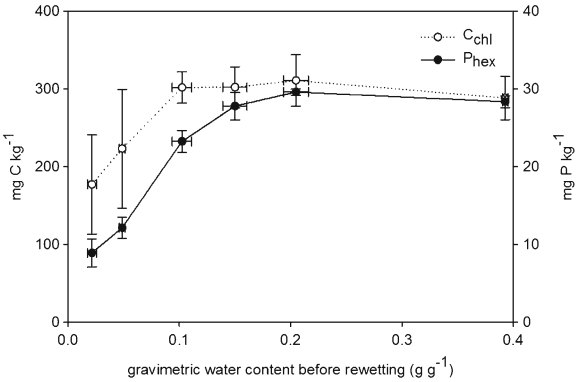

Fig. 2 Chloroform-labile C (C_{chl}) and hexanol-labile P (P_{hex}) 1 h after rewetting in relation to the water content before rewetting (means and standard deviations of four replicates). Points in a series are connected to assist visualization of trends

of C_{chl} in constantly moist soil when soils were dried to 2 % GWC. In addition, C_{chl} was recovered completely in C_{K2SO4} (C_{chl}=−1*C_{K2SO4}+400, R^2=0.67, p<0.001). Due to the larger reductions in P_{hex} than in C_{chl}, the C:P ratio in the microbial biomass increased from 10±1 in constantly moist soils to 20±4 in soils that had been dried to 2 % GWC.

Experiment 2: incubation experiment with sterilized soils

Drying and rewetting of autoclaved or of gamma-irradiated soils led to significant increases in P_{resin} by 1–4 mg P kg^{-1}, regardless of whether the soils had been kept sterile or re-inoculated (Table 2). In re-inoculated samples P_{hex} had reached 6–7 mg P kg^{-1} after 4 weeks of incubation, and a reduction by 1–3 mg P kg^{-1} was observed upon DRW. In sterile samples, P_{hex} was non-detectable in autoclaved soils. In gamma-irradiated soils, P_{hex} showed very low amounts (<1 mg P kg^{-1}), which were not altered by DRW. However, plate counts did not reveal any bacterial or fungal contamination of samples kept sterile, whereas extensive growth of hyphal structures and cellular colonies was observed for re-inoculated samples (data not shown).

Interestingly, a significant increase in C_{K2SO4} after DRW was observed in re-inoculated soils but not in soils that were kept sterile. Re-inoculation reduced P_{resin} in gamma-irradiated soils but increased it in autoclaved soils, while it decreased C_{K2SO4} in both sterilization treatments.

Experiment 3: aggregate stability tests

Physical disruption of dry soil was observed in the fast wetting treatment, with the MWD of aggregates being significantly lower in dry (DD) than in constantly moist (MM) soil, while dry soil allowed to rewet for 1 h (DM) was intermediate (Fig. 3). The distribution of the aggregate size classes showed a transfer of material in large macroaggregates (>2,000 μm) to the small macroaggregate fraction (1,000–2,000 μm) in treatments DD and DM, with DD showing an additional accumulation of

Table 2 Hexanol-labile P, resin-extractable P and C extractable with 0.5 M K_2SO_4 after drying and rewetting of sterilized soils (means of 4 replicates; analysis 1 h after rewetting)

Treatment	Autoclaved soils			Gamma-irradiated soils		
	P_{hex} mg P kg^{-1}	P_{resin}	C_{K2SO4} mg C kg^{-1}	P_{hex} mg P kg^{-1}	P_{resin}	C_{K2SO4} mg C kg^{-1}
MN	7.4a[a]	11.2b	420c	6.3a	13.4c	245c
DN	4.7b	15.0a	601b	5.2b	14.7b	384b
MS	n.d.	7.5c	2681a	0.5c	15.7b	1232a
DS	n.d.	10.8b	2717a	0.7c	17.5a	1265a
Significance level (p)						
Moisture (M, D)	<0.001	<0.001	0.016	0.119	<0.001	0.043
Sterility (N, S)	N/A	<0.001	<0.001	<0.001	<0.001	<0.001
Moisture * Sterility	N/A	0.336	0.081	0.032	0.361	0.193

M=constantly moist, D=drying to 3–4 % GWC; N=non-sterile (re-inoculated), S=sterile

n.d. not detected, *N/A* not applicable

[a] Within columns, means followed by different letters are significantly different according to the LSD test (p<0.05)

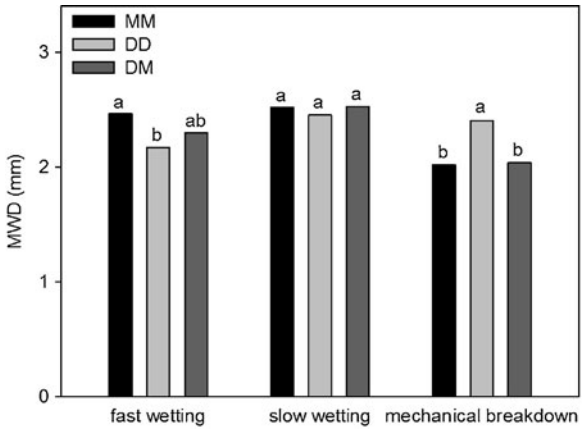

Fig. 3 Mean weight diameter (MWD) of aggregates in the three aggregate stability tests (fast wetting, slow wetting, mechanical breakdown) after Le Bissonnais (1996) as affected by sample pretreatment (MM constantly moist, DD dried to 2 % GWC, DM dried to 2 % GWC and rewetted for 1 h). Within each test, letters indicate significant differences according to the LSD test ($p<0.05$). Means of three replicates

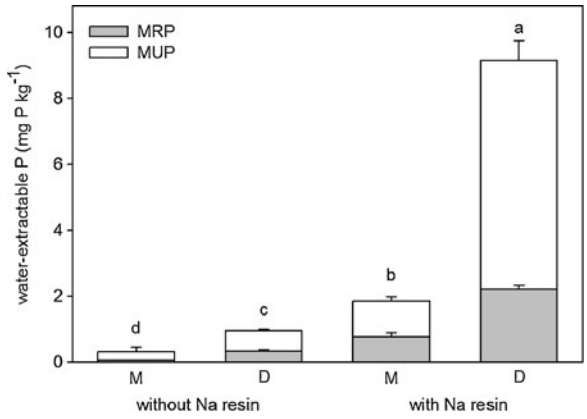

Fig. 4 Water-extractable P (molybdate-reactive (MRP) and molybdate-unreactive (MUP)) in constantly moist soils (M) or soils dried to 2 % GWC (D) extracted 1 h after rewetting in the presence or absence of Na-saturated resin membranes. Means and standard deviations of four replicates; letters indicate significant differences in total water-extractable P according to the LSD test ($p<0.05$)

material in the microaggregate fractions between 100 and 1,000 μm (data not shown).

Aggregate stability under slow wetting was not affected by the soil moisture regime, but the dry soil was less susceptible to mechanical breakdown than the two treatments using moist soil (Fig. 3). In treatments MM and DM, less material than in DD was recovered in the >2,000 μm fraction and more in all fractions <1,000 μm (data not shown).

Experiment 4: P release upon DRW and soil dispersion

Both DRW and Na-facilitated dispersion of moist soil increased water-extractable MRP compared to constantly moist soils extracted with water only (Fig. 4). In fact, the dispersion treatment increased water-extractable MRP twice as much as the DRW treatment without Na resins. However, by far the greatest increase in water-extractable MRP was observed for the combination of DRW and dispersion with Na resins. Similar observations were made for water-extractable MUP which was up to four times greater than MRP, depending on the treatment.

Experiments 5a and 5b: plant experiments

Significant increases in P availability after DRW were observed in both plant experiments (Table 3). One hour after DRW, P_{resin} had increased from 0.5 to 0.8 mg P kg^{-1} in 0P to 4–8 mg P kg^{-1} in treatments D and V. In the DRW treatments of the bioassay, P_{resin} decreased over time but remained more than twice as high as in treatment 0P until the harvest after 22 days.

One hour after rewetting, P_{hex} in DRW treatments had decreased to between 30 and 60 % of the values in the constantly moist soil. The slow recovery in P_{hex} observed during the bioassay was not yet complete after 22 days, reaching about 55 % of P_{hex} in the constantly moist soil.

In both experiments, total plant dry matter increased significantly with P addition (Fig. 5). Total plant dry matter in the non-P-fertilized control (0P) was similar in the split-root experiment (1.4±0.5 g $plant^{-1}$) and the bioassay (1.1±0.2 g $plant^{-1}$), and the increase in dry matter with the various P additions was also similar. The roots in the nutrient solution contributed only 15–27 % to the total root biomass in the split-root experiment, without significant differences between treatments. Shoot and root P concentrations were low, ranging from 0.7 to 1.0 mg P g^{-1}, with a significant response to P additions observed only in the split-root experiment (data not shown).

In both experiments, plant P uptake increased with P addition (Fig. 6). Linear regressions of P uptake (in mg $plant^{-1}$) as depending on added P (in mg kg^{-1} soil) could be established for the bioassay ($y=0.10*x+0.72$, $R^2=0.92$, $p<0.001$) as well as for the split-root experiment ($y=0.04*x+1.00$, $R^2=0.76$, $p<0.001$). Total P uptake

Table 3 Resin-extractable and hexanol-labile P sampled 1 h, 11 and 22 days after drying and rewetting (DRW) in the plant experiments (means of 4 replicates)

Measurement	Treatment	Bioassay			Split-root experiment	
		1 h	11 d	22 d	1 h (DRW1)	1 h (DRW2)
P_{resin} (mg P kg^{-1})	Moist (0P)	0.5b[a]	0.6b	1.1b	0.8b	0.5c
	Dry (D)	4.2a	2.4a	2.3a	6.2a	6.1b
	Very dry (V)	3.9a	2.0a	2.6a	6.7a	7.8a
P_{hex} (mg P kg^{-1})	Moist (0P)	22.3a	19.8a	21.1a	40.7a	42.1a
	Dry (D)	7.8b	9.0b	11.9b	22.3b	25.7b
	Very dry (V)	6.4b	9.9b	11.4b	21.6b	21.0c

0P=constantly moist pots without P addition;

D=drying to 11 % GWC in the bioassay and 16 % in the split-root experiment; V=drying to 4 % in the bioassay and 12 % in the split-root experiment

[a] within columns and measurements, means followed by different letters are significantly different according to the LSD test ($p<0.05$)

was similar between the two plant experiments for all P treatments except 5P. However, the bioassay received only one P addition instead of two and had a shorter duration (22 days) than the split-root experiment (38 days). Therefore, the increase in P uptake per mg P added was smaller for the split-root experiment.

In contrast to the similar P response curves, the two plant experiments differed with respect to plant growth and P uptake in the DRW treatments. In the bioassay, DRW treatments had significantly higher dry matter (Fig. 5), shoot P concentrations (data not shown) and P uptake (Fig. 6) than the constantly moist, non-P-fertilized treatment 0P. Based on the regression derived from the P response curve, P uptake in treatments D and V corresponded to P additions of 13.1±4.4 and 14.5±4.7 mg P kg^{-1} soil, respectively. In the split-root experiment, however, dry matter, P concentrations and P uptake in DRW treatments were similar to those in treatment 0P. Therefore, calculating with the regression above did not render a net P addition.

Shoot N concentrations and uptake were lower in the split-root experiment than in the bioassay (Table 4). In both experiments, shoot N concentrations decreased with increasing P fertilization, while they were similar in DRW treatments and 0P. Shoot N uptake in the DRW treatments of the bioassay was even greater than in treatment 20P, whereas in the split-root experiment it was similar to 0P.

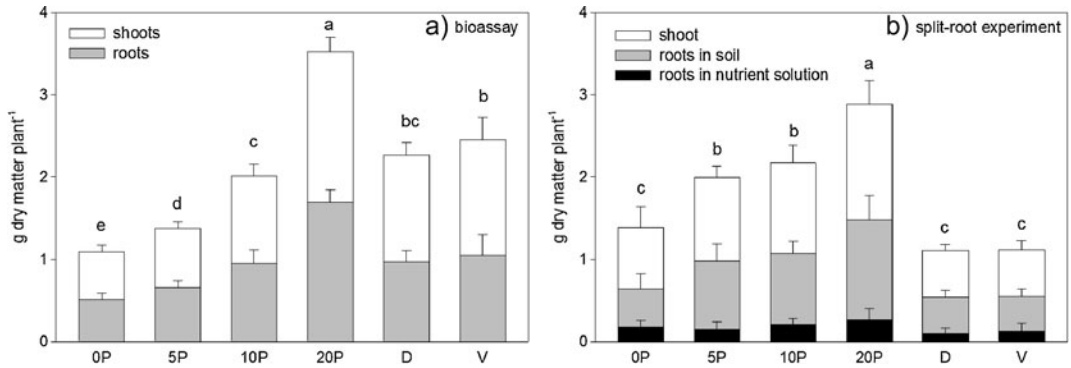

Fig. 5 Dry matter of roots and shoots in a) the bioassay and b) the split-root experiment (means and standard deviations of eight replicates shown for each plant part). 0P, 5P, 10P, 20P=constantly moist soil with P additions from 0 to 20 mg P kg^{-1} at each rewetting; D=drying to 11 % GWC in the bioassay and 16 % in the split-root experiment; V=drying to 4 % in the bioassay and 12 % in the split-root experiment. Letters indicate significant differences within each experiment in total dry matter according to the LSD test ($p<0.05$)

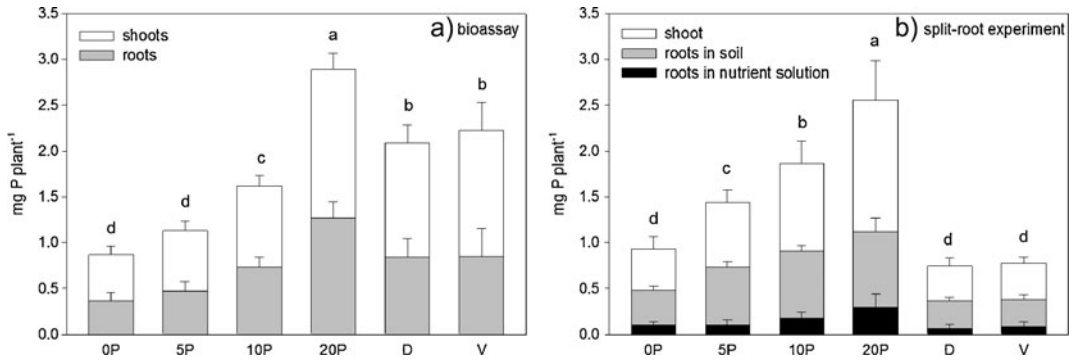

Fig. 6 P uptake of roots and shoots in a) the bioassay and b) the split-root experiment (means and standard deviations of eight replicates shown for each plant part). 0P, 5P, 10P, 20P=constantly moist soil with P additions from 0 to 20 mg P kg^{-1} at each rewetting; D=drying to 11 % GWC in the bioassay and 16 % in the split-root experiment; V=drying to 4 % in the bioassay and 12 % in the split-root experiment. Letters indicate significant differences within each experiment in total P uptake according to the LSD test ($p<0.05$)

Discussion

The grassland soil chosen for this study had very low P availability as shown by the strong response of maize dry matter and P uptake to P additions (Figs. 5 and 6). In non-P-fertilized soil from the same site, also microorganisms were shown to experience P limitation as indicated by extremely fast P immobilization, presumably due to expression of high affinity P transporters (Bünemann et al. 2012).

At the same time, large C and P pulses upon DRW could be expected in this soil. In a study of 32 soils with clay contents from 0 to 27 %, the pulse in soil respiration was related positively to clay content (Butterly et al. 2010). Thus, we anticipated a relatively large C pulse in our soil with its clay content of 22 %. Sparling et al. (1985) postulated that P extracted from air-dried soils would contain a significant proportion of P released from microorganisms if the soils had more than 20 g organic C kg^{-1}, low available P, and originated from a climate zone in which extreme moisture deficits do not occur. Indeed, our soil fulfilled all these criteria, since the lowest GWC measured in the top 5 cm during the growing season of 2009 was 15 % (Liebisch 2011).

Table 4 Shoot N concentrations and shoot N uptake in the plant experiments (means of eight replicates)

Treatment	Bioassay gN kg^{-1}	Split-root exp.	Bioassay mgN $shoot^{-1}$	Split-root exp.
0P	40.0ab[a]	18.5a	23.1f	14.9b
5P	37.5b	13.0b	27.2e	13.0b
10P	33.3c	13.6b	34.8d	14.7b
20P	24.5d	14.2b	44.5c	20.3a
D	39.8ab	20.2a	51.0b	11.5b
V	40.6a	20.5a	55.7a	12.7b

0P, 5P, 10P, 20P=constantly moist soil with P additions from 0 to 20 mg P kg^{-1} at each rewetting; D=drying to 11 % GWC in the bioassay and 16 % in the split-root experiment; V=drying to 4 % in the bioassay and 12 % in the split-root experiment

[a] within columns, means followed by different letters are significantly different according to the LSD test ($p<0.05$)

The low P availability and expected large C and P pulses upon DRW made our model soil suitable for studying the processes behind increased P availability after DRW and associated use of released P by growing plants. An additional advantage was that P sorption as assessed by a known P addition during the determination of microbial P, i.e. during extraction with resin membranes, was not significantly altered by DRW. This is in contrast to other studies which found increased P sorption after drying (Barrow and Shaw 1980; Olsen and Court 1982) and simplifies our interpretation of results.

Extent and relationship of C and P pulses after DRW

The maximum extent of C and P pulses in the incubation experiment with non-sterilized soil was observed for the lowest soil water content before rewetting, inducing relative increases in C_{K2SO4}, CO_2 release and P_{resin} by factors of 2, 4 and 12, respectively, compared to soils kept at 40 % GWC (Fig. 1). Studies on Australian pasture soil did not see this divergence in C and P

pulses, with C_{K2SO4}, CO_2 release and P_{resin} all changing by a factor of 2–3 after DRW (Butterly et al. 2009, 2011b). Nevertheless, the large P pulse observed in our study is not unique: studies on temperate grassland soils recorded large increases in water-extractable P by up to a factor of 19 (Turner and Haygarth 2001), with drying-induced relative increases being particularly large in soils with low initial water-extractable P (Styles and Coxon 2006). In our soil, the observed reduction in P_{hex} (Fig. 2) would be more than sufficient to explain the increase in P_{resin}, suggesting partial sorption of microbial P released by DRW.

The observed narrowing of the C:P ratio of the pulse, i.e. of CO_2-release or C_{K2SO4} in relation to P_{resin}, with decreasing water contents before rewetting could point to different mechanisms behind C and P pulses. However, also maximum reductions in P_{hex} (by 70 %) were stronger than those in C_{chl} (by 40 %). A larger relative decrease in P_{hex} than C_{chl} is in accordance with other studies (Butterly et al. 2009; Aponte et al. 2010) and may point to preferential lysis of P-rich microbial cells. These could be actively growing cells with high P concentrations (Makino et al. 2003) and/or bacterial cells with typically higher P concentrations than fungi (Bünemann et al. 2008). A lower susceptibility of fungi to DRW events is in accordance with Cosentino et al. (2006), while other studies found the opposite (Butterly et al. 2009; Gordon et al. 2008). Such contrasting results may partly be explained by interactions with soil structure, i.e. whether physical protection of bacterial populations in aggregates is altered during DRW events (Denef et al. 2001).

Since the experiment with different degrees of drying gave no clear indication of the role of physicochemical processes in C and P release after DRW, we conducted a DRW experiment with sterilized soils. The main finding was that for both methods of sterilization, DRW of soils kept sterile induced a significant increase in P_{resin} but not in C_{K2SO4} (Table 2), pointing to a non-microbial contribution to the P but not to the C pulse, in accordance with Butterly et al. (2009). However, these findings have to be viewed against changes in the soil induced by sterilization and partial re-inoculation.

In our study, the main difference between the two sterilization treatments was the larger increase in P_{resin} after gamma-irradiation (Table 2) which can be explained by the fact that phosphatases remain active after gamma-irradiation and thus continue to hydrolyze organic P compounds, especially those from microorganisms killed during sterilization. This could also explain the increase in P_{resin} after re-inoculation of autoclaved soils, since the growing microorganisms would not only immobilize P but also produce phosphatase enzymes. Indeed, potential phosphatase activity measured at pH6.1 was diminished by 50 % 1 h after rewetting of non-sterilized soils dried to 2 % GWC (data not shown), suggesting that a large proportion is associated with microbial cells.

Other changes in soil organic matter related properties may occur during sterilization, and the larger increase in C_{K2SO4} after autoclaving than after gamma-irradiation is in agreement with Powlson and Jenkinson (1976). In both sterilization treatments, C_{K2SO4} decreased strongly after re-inoculation (Table 2), suggesting its use as a C source for a growing microbial biomass. This biomass was then reduced again by DRW in treatment DN, causing a C pulse detected as an increase in C_{K2SO4} and confirming the microbial origin of the C pulse.

While the experiment with sterilized soil provides evidence for a non-microbial contribution to the P pulse after DRW, the changes in several soil properties after sterilization and the incomplete recovery of microbial biomass after re-inoculation make it impossible to derive the relative contribution of microbial cell lysis and physicochemical P release to the P pulse after DRW in non-sterilized soil. Therefore, we conducted additional experiments to further elucidate the physicochemical processes of P release after DRW.

Physicochemical processes of P release

Irrespective of the moisture pretreatment, very stable aggregates were indicated by the MWD of >2 mm in each of the three aggregate stability tests (Le Bissonnais 1996). Nevertheless, differences between moisture treatments in the fast wetting test pointed to the role of slaking, especially in treatment DD, but also in DM (Fig. 3). Apparently, rewetting on a tension plate for 1 h in treatment DM was not sufficient to remove all entrapped air from the soil before immersion in water. However, in DM all material lost from the >2 mm macroaggregates was recovered in the small macroaggregates (1–2 mm), whereas the stronger destruction in DD increased all fractions down to 100 μm. In accordance with Denef et al. (2001), slaking did not disrupt microaggregates and thus did not increase primary particles (<50 μm). The other two aggregate stability tests showed that differential swelling of clays was not

important, and that mechanical breakdown was similar in treatments MM and DM, while soil in treatment DD was more stable because there was no water in the soil to break down the aggregates. Thus, the aggregate stability tests according to Le Bissonnais (1996) identified slaking as the most important mechanism to physically disrupt soil structure and potentially release P.

Both DRW and Na-facilitated dispersion of moist soil released water-extractable P in the form of MRP and MUP (Fig. 4). The presence of physically protected inorganic P, probably within water-stable aggregates, has been shown before (Sinaj et al. 1997). Physical protection of MUP is less documented, with stabilization of soil organic P thought to occur mainly through adsorption to minerals, complexation, precipitation with polyvalent cations and incorporation into humic substances (Celi and Barberis 2005). However, MUP can also include small mineral colloids (Sinaj et al. 1998). Our results show that physical protection is important for inorganic as well as other forms of P.

The lower proportion of MRP (42 %) than MUP (58 %) released by DRW in the absence of soil dispersion is in agreement with observed changes in water-extractable dissolved P in air-dried compared to moist samples (Turner and Haygarth 2001; Styles and Coxon 2006). Likewise, dissolved P in leachate from soils after DRW was dominated by MUP (Blackwell et al. 2009). The large proportion of MUP in water-extractable P after DRW is another explanation (besides sorption) why the observed reduction in P_{hex} after DRW was 2.6 times greater than the concomitant increase in P_{resin} (Figs. 1 and 2), since the procedure using anion exchange resin membranes followed by mild acid elution has been shown to capture only negligible amounts of molybdate-unreactive P from soils (Cheesman et al. 2010).

The fact that dispersion of moist soil released more water-extractable P than extraction of previously dry soil without Na-facilitated dispersion (Fig. 4) agrees with the findings from the aggregate stability tests that slaking disrupts large macroaggregates but does not destroy soil structure down to primary particles, as occurs with Na-facilitated dispersion (Feller et al. 1991; Bartoli et al. 1991). However, when extracting previously dry soils, not only physically protected P but also microbial P is a potential source of water-extractable P. Thus, the proportion of physically protected P that is released by slaking cannot be derived from the comparison of these two treatments.

The large additional release of both MRP and MUP for the combination of DRW and Na-facilitated dispersion suggests that P released from microorganisms during DRW is trapped inside microaggregates and becomes water-extractable only in combination with soil dispersion. This is supported by the fact that microbial cells are often attached to soil particles (Mills 2003), with the microbial biomass being mostly concentrated in the clay and silt fraction (Kandeler et al. 2001).

Plant use of P pulses after drying and rewetting

The comparison of the two plant experiments could potentially be hampered by different soil organic matter (Table 1) and P_{hex} (Table 3) contents. We think this was an effect of sieving done by different operators rather than a seasonal effect. Support for this comes from a study of seasonal dynamics in the same field experiment (Liebisch 2011), where P_{hex} was similar at the two sampling times. Importantly, P_{resin} in constantly moist soil of the two batches was not affected (Table 3), and plant response to P additions was similar (Figs. 5 and 6), suggesting a similar sensitivity of both experimental systems. However, a positive response of plants to increased availability of P after DRW was observed only in the bioassay.

In the split-root experiment, soil had to be dried in the climate chamber under conditions that did not harm the plants. Therefore, average GWCs reached in the split-root assay in treatments D (16 %) and especially V (12 %) were not as low as those in the bioassay where pots were dried in an oven prior to planting, reaching average GWCs of 11 % for D and 4 % for V. In addition, for planted pots dried in the climate chamber to an average of 14 % GWC we found a moisture gradient from 4 % GWC in the top 2 cm to 17 % GWC at the bottom (data not shown). To some degree, such a gradient may also have occurred in the bioassay, which would explain the fact that the two DRW treatments were similar with respect to P_{resin} pulse, dry matter and P uptake (Table 3, Figs. 5 and 6). Reaching homogenous water contents is an important challenge in pot experiments with soils (Passioura 2006), and future DRW studies would benefit from using a better controlled system, e.g. with planted soil cylinders held on tension plates connected to a hanging water column (Hugueneni-Elie et al. 2002). Since the soil for analysis of P_{resin} and P_{hex} was taken at the top of the pots, the values shown in

Table 3 do not represent average P_{resin} and P_{hex} of the pot but serve only to roughly indicate the occurrence and duration of P pulses. Most importantly, they show that the missing plant response in the DRW treatments of the split-root experiment was not due to the lack of a P pulse.

In the bioassay, all nutrients except P were added to the soil, while in the split-root experiment, they were provided via the nutrient solution compartment. Shoot P concentrations increased with P additions in the split-root experiment but not in the bioassay (data not shown), suggesting an accumulation of P in the former due to a limitation by another nutrient, even though dry matter production in the P-fertilized treatments was similar in both plant experiments (Fig. 5). Therefore, we analyzed shoot N concentrations and uptake (Table 4). Indeed, they were significantly lower in the split-root experiment than in the bioassay and indicated N deficiency, especially in the P fertilized treatments of the split-root experiment. The reason for this is unclear, since the nutrient solution was changed 3 times during the experiment, potentially providing a total of 1 gN per plant. Most probably, the removal of the primary root and splitting of the root system stressed the plants in general. The fact that plant P uptake in 0P was similar between the two experiments (Fig. 6) may indicate that the majority of plant P in this treatment was still derived from the seeds. However, plant uptake of P from the soil is indicated by the fact that total P content of maize seeds averaged 0.73±0.03 mg (Preuß, personal communication), compared to plant P uptake in 0P of about 0.90 mg.

The other important finding with respect to N nutrition is the fact that shoot N uptake in the DRW treatments of the bioassay was greater than in treatment 20P (Table 4), although for P uptake the opposite order was observed (Fig. 6). Increased N availability after DRW has been observed before (e.g. Birch 1958; Appel 1998) and was apparently used by the plants in the bioassay in addition to the N supplied with the nutrient solution. In contrast, in the split-root experiment neither N nor P uptake were increased in the DRW treatments compared to 0P, suggesting that the dry period reduced the nutrient uptake capacity of the roots in the soil. Nitrate uptake ability of maize roots can recover within 3 days after DRW (Buljovcic and Engels 2001), but this may differ between varieties. In addition, translocation of nutrients into the shoot may recover more slowly than root uptake (Jupp and Newman 1987).

Despite the significant extent and duration of the P pulse after DRW, only the bioassay showed that maize may indeed benefit from it. Potential improvements of the split-root approach include i) not cutting the primary root ii) using different plant species or varieties which are more resistant to drought periods and iii) increasing the duration of the intermittent moist periods to allow recovery of root nutrient uptake and translocation to the shoots.

Conclusions

Using a grassland soil with low available and high microbial P, very stable soil structure and a lack of adaptation of microorganisms to dry periods as a model, we showed that destruction of large macroaggregates due to slaking as well as microbial cell lysis upon DRW released P in inorganic and organic form. In contrast, the C pulse appeared to be mostly of microbial origin. Our different experimental approaches to study the underlying processes of P pulses (examination of C:P ratios over a gradient of soil moisture before rewetting, DRW experiments with sterilized soil, and especially aggregate stability tests and soil dispersion experiments with determination of released P forms) should be used on a wider range of soils to further elucidate the processes of C and P release after DRW.

Enhanced plant uptake of P after DRW could be demonstrated in a bioassay with different preceding moisture regimes and uniform soil moisture during plant growth, while the split-root approach failed to show a benefit of moisture fluctuations during plant growth. For the situation in the field, our results suggest that increasingly severe droughts with climate change will result in pulses of P availability, but that these can be used by plants only if their root nutrient uptake capacity is not damaged or can recover before the P pulse has disappeared due to sorption, microbial immobilization and/or leaching.

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