

Interactive effects of soil water content and phytin supply on phosphorus nutrition of different crops species

Christine Brandt*, Christiane Balko**, and Bettina Eichler-Löbermann*

Abstract

An eight week pot experiment was conducted under semi controlled conditions to investigate the interactive effects of organic P nutrition and drought stress on P utilisation of four different crop species.

Two P treatments were established: organic P supply with phytin (0.40 g P per pot) and a control without any additional P supply. The two water treatments were irrigated according to 60 % (well watered) and 30 % (drought stress) water holding capacity of the soil.

The P uptake, shoot biomass and proline content of sorghum (*Sorghum bicolor* x *Sorghum sudanense*), amaranth (*Amaranthus cruentus*), oilseed rape (*Brassica napus*) and rye (*Secale cereale*) were studied. Furthermore, in the soil we measured the pH value, soil P pools (soluble in water, double-lactate and oxalate) as well as the P sorption capacity, degree of P saturation and the activities of acid and alkaline phosphatases.

Drought stress reduced the P uptake of sorghum and rye, while P uptake of amaranth and oilseed rape was not affected by water supply. The application of organic P increased the plant P uptake and biomass production in both water treatments about 30 % but did not mitigate the effects of water stress. Drought resulted in higher proline contents in plant tissue; significantly elevated values were measured in oilseed rape and rye. The activity of acid phosphatase in soil was increased in the treatments with drought stress as well as after organic P supply. Soil P pools were affected by the balance of P supply and plant P uptake, but obviously not by the water treatments.

The results suggest crop specific reactions on water shortage and P deficiency, which should be taken into consideration for P fertilization recommendations.

Keywords: phosphorus, drought stress, organic fertilizer, phosphatase activity

Zusammenfassung

Wechselseitiger Einfluss von Wassergehalt des Bodens und Phytin-Zufuhr auf die Phosphor-Ernährung verschiedener Fruchtarten

In einem achtwöchigen Gefäßversuch wurden die wechselseitigen Effekte von organischer P-Zufuhr und Trockenstress auf die P-Versorgung vier verschiedener Fruchtarten untersucht. Dabei wurde Phytin als organische P-Quelle (0.40 g P pro Gefäß) genutzt. Zur Kontrolle wurde eine Variante ohne P-Zufuhr angelegt. Zwei Wasserstufen wurden entsprechend 60 % (optimale Versorgung) und 30 % (Trockenstressvariante) der maximalen Wasserhaltekapazität des Bodens eingestellt.

Die P-Aufnahme, der Biomassertrag sowie der Prolin-Gehalt der Fruchtarten Sorghum (*Sorghum bicolor* x *Sorghum sudanense*), Amaranth (*Amaranthus cruentus*), Raps (*Brassica napus*) und Roggen (*Secale cereale*) wurden untersucht. Im Boden wurden der pH Wert, ausgewählte P-Fractionen, sowie der Grad der P-Sättigung ermittelt. Zudem wurde die Aktivität der sauren und alkalischen Phosphatase bestimmt.

Trockenstress reduzierte die P-Aufnahme von Sorghum und Roggen, während Amaranth und Raps keinen Rückgang in der P-Aufnahme zeigten. Die Zufuhr von organischem P erhöhte die P-Aufnahme sowie die Biomasse aller Fruchtarten in beiden Wasserstufen um etwa 30 %. Die Wirkung des Trockenstress im Vergleich zur optimalen Wasserversorgung wurde allerdings durch eine P-Zufuhr nicht abgeschwächt. Unter Trockenstress wurden stark erhöhte Prolin-Gehalte bei Raps und Roggen gemessen. Die Aktivität der sauren Phosphatasen im Boden stieg ebenfalls unter Trockenstress sowie durch die Zufuhr von organischem P an. Die P-Pools im Boden wurden durch die Bilanz von P-Zufuhr und P-Aufnahme der Pflanzen beeinflusst, offensichtlich jedoch nicht durch die unterschiedliche Wasserversorgung.

Schlüsselwörter: Phosphor, Trockenstress, organische Düngung, Phosphatase-Aktivität

* University of Rostock, Faculty of Agriculture and Environmental Sciences, Agriculture by Tillage and Crop Husbandry, Justus-von-Liebig-Weg 6, 18051 Rostock, Germany,

** Julius Kühn-Institut, Federal Research Centre for Cultivated Plants, Institute for Resistance Research and Stress Tolerance, Rudolf-Schick-Platz 3, 18190 Groß Lüsewitz, Germany

Corresponding author: PD Dr. habil. Bettina Eichler-Löbermann, E-mail: bettina.eichler@uni-rostock.de

Introduction

Drought stress is one of the major abiotic factors that constrains crop productivity. Climate periods with drought will occur more frequently in the near future (Jacob et al., 2008). The growth and the physiological responses of crop plants and therewith the plant yield are highly sensitive to a reduction of water availability in soils (Bartels and Sunkar, 2005).

Plants develop different mechanism to adapt to drought stress. Drought tolerance may increase by stomatal regulation (Sing and Sing, 1995), maintained water uptake through changes in root characteristics like root length, thickness and rooting depth (Asch et al., 2005) and accumulation of osmolytes like soluble sugars, alcohols or proline (Stoddard et al., 2006). The positive effect of proline as a major osmoregulatory solute under drought stress was shown in different studies (Delauney et al., 1993; Somal et al., 1998; Kuznetsov and Shevyakova, 1999; Diaz et al., 2005).

Drought affects nutrient availability in soil. Generally, a decrease in soil moisture content limits the capacity of mass flow and nutrient diffusion. Especially the less mobile nutrients in soil, such as P, are affected by water deficit. Drought leads to formation of stabile P compounds in soil (Hu and Schmidhalter, 2005) and can result in a decreased P absorption by plants (Samarah et al., 2004).

On the other hand, several studies reported that the application of P can improve growth and P uptake of plants under drought conditions and therefore ameliorate negative effects of water stress. For instance P fertilization can increase drought tolerance by advanced root growth. Therewith a larger volume of soil can be explored leading to a higher water and nutrient uptake and higher biomass production (Rodriguez and Oyarzabal, 1996; Gutiérrez-Boem and Thomas, 1999). Furthermore, P supply can enhance chlorophyll content and therewith rate of photosynthesis (Garg et al., 2004). Increased P fertilization has also a beneficial influence on the leaf metabolism, the relative water content (Shubhra et al., 2004) as well as the water use efficiency (He et al., 2002).

In general, P efficiency of crops varies widely. Well adapted plant species develop strategies to enhance the acquisition of P from soil. E.g. they explore a greater volume of soil through modified root morphology like increased root hair density and roots length (Bates and Lynch, 2001; Ma et al., 2001; Abel et al., 2002,) and they increase the root to shoot ratio (Ramaekers et al., 2010). Furthermore, the availability of P compounds can be improved by crop species through rhizosphere modification like shifting pH and excretion of protons (Wittenmayer and Merbach, 2005), organic acids (Römer, 2006; Carvalhais, 2011) and phosphatases (Wang et al., 2008). Therefore, the cultivation of

different crops can result in very different contents of high soluble P in soil (Schiemenz & Eichler-Löbermann, 2010; Eichler-Löbermann et al., 2008).

Organic P compounds are important sources for plant P supply. The largest fraction of organic P appears in form of phytin and its derivatives (Dalal, 1978; Schilling, 2000).

Primarily the activity of phosphatases in soils plays an important role in P cycling transforming organic P in plant available forms (Nuruzzaman et al., 2006). Alkaline (AIP) and acid phosphatase (AcP) can be excreted by crops and microorganisms, whereas higher crops avoid excretion of AIP (Dick et al., 2000).

The activity of phosphatases is influenced by crop species and even varieties. Investigations of Li et al. (2004) showed that chickpea roots were able to secrete greater amounts of AcP than maize and therewith increased hydrolyse of phytates. Cierieszko et al. (2011) found differences in two wheat varieties related to their ability to induce soil phosphatase activity.

The activity of phosphatases usually increases when the P nutrition status in soil decreases (Tarafdar and Claassen, 2005; Krey et al., 2011). Therefore, the activity of phosphatase may play a key role to enhance availability of organic P under dry conditions.

In the past mainly the effects of mineral P were investigated in the context of drought stress. However, information about the utilisation of organic P under water deficiency is rarely available. Therefore, in a pot experiment we cultivated 4 different crops on a soil differing in water and phytin supply.

The objective of this work was to (I) evaluate the ability of different crop species to utilize P under drought conditions, (II) explore the effect of organic P supply on plant and soil parameters in relation to the water supply.

Material and methods

Soil

The soil used for the pot experiment was collected from the A-horizon of a long-term field experiment of the University of Rostock in Northern Germany. The soil was classified as loamy sand. Initial plant-available soil P content of 40.6 mg kg⁻¹ (P_d) indicated a suboptimal P status of the used soil (Table 1). The soil reaction was medium acid (pH(H₂O) = 5.3, pH(CaCl₂) = 4.9).

Treatments and experimental design

An outdoor pot experiment was established in May, 2009 consisting of 4 plant species, 2 levels of irrigation, 2 fertilization treatments and 4 replicates.

Table 1:
Soil properties at the beginning of the pot experiment

| pH (CaCl ₂) | Pw (mg kg ⁻¹) | Pdl (mg kg ⁻¹) | Pox (mmol kg ⁻¹) | DPS (%) | PSC (mmol kg ⁻¹) | K dl (mg kg ⁻¹) | Mg dl (mg kg ⁻¹) |
|----------------------------|------------------------------|-------------------------------|---------------------------------|------------|---------------------------------|--------------------------------|---------------------------------|
| 4.91 | 6.15 | 40.6 | 16.9 | 49.3 | 26.2 | 64.9 | 140.0 |

Pw = water soluble P; Pdl, Kdl, Mgdl = double lactate P, K, Mg; Pox = oxalate soluble P; DPS = degree of P saturation; PSC = P sorption capacity

Mitscherlich pots were filled with 6 kg air dried and 2mm sieved soil. Before sowing, plant nutrients had been mixed thoroughly with the soil (per pot: 1.4 g NH₄NO₃, 1.4 g MgSO₄+7H₂O, 1.9 g KCl). Organic P supply (P1) was established with 0.4 g P per pot by supply of phytin (C₆H₁₆CaO₂₄P₆). A treatment without P supply (P0) was used as control.

The following crops (species and varieties) were cultivated: sorghum (*Sorghum bicolor* x *Sorghum sudanense*, Inka), amaranth (*Amaranthus cruentus*, Bärnkrafft), oil-seed rape (*Brassica napus*, Palma) and rye (*Secale cereal*, Arantes).

Until BBCH 13 irrigation was done according to crop demand with distilled water for all pots. Afterwards two levels of irrigation were established. The drought treatment was irrigated according to 30 % of the water holding capacity (WHC) of the soil. The well watered control treatment was irrigated according to 60 % WHC. The pots were weighed every second day and the consumed amount of water was replaced accordingly to the treatments. Pots were placed under natural weather conditions; a shelter excluded rainfall to avoid uncontrolled irrigation of the pot experiment.

All plants were harvested after eight weeks of growth. Leave samples were taken, ground in liquid nitrogen and stored at -21 °C until chemical analyses were performed. The remaining plant material was oven-dried at 60 °C until constancy of weight.

Six soil cores (3 cm diameter) were taken per pot, mixed and divided into two sub-samples. Soil samples for biochemical analyses were stored frozen. The other samples were air-dried and passed through a 2 mm sieve before determining chemical soil parameters.

Plant and soil analyses

The shoot P concentration was measured after dry ashing and digestion in 20 % HCl. For P determination the vanadate-molybdate method by Page et al. (1982) was used. The P uptake was calculated from dry matter yield and P content.

Proline analyses were performed from the plant samples as described previously by Bates et al. (1973). Absorbance was measured at 520 nm using a spectrophotometer.

Content of double lactate soluble P (Pdl) as well as soil pH (CaCl₂) were measured according to Blume et al. (2000). Water-extractable P (Pw) in soil was determined as described by Van der Paauw et al. (1971). The P concentration was measured with the phosphomolybdate blue method via flow-injection analysis. The oxalate soluble content of P, aluminium (Al), and iron (Fe) in soil (Pox, Alox, Feox) were analysed by shaking 2 g of soil in acid oxalate solution (100 ml) for 1 h in the dark in accordance to Schwertmann (1964). With these data the P sorption capacity (PSC = [Alox + Feox]/ 2 (mmol kg⁻¹)) and the degree of P saturation (DPS [%] = Pox / PSC x 100) were calculated according to Lookman et al. (1995) and Schoumans (2000). Concentration in the filtrate of the elements was determined by inductively coupled plasma (ICP) spectrometry.

Acid and alkaline phosphatase (AcP and AlP) activities were determined using the method of Tabatabai and Bremner (1969). The enzyme activity was measured in µmol p-nitrophenol released from p-nitrophenylphosphate solution in 1 g soil within 1 hour (µmol p-nitrophenol g⁻¹ h⁻¹).

Statistics

Soil and plant data of 4 replicates were subjected to an analysis of variance (General linear model, GLM).

To compare means of soil and plant parameters the Duncan multiple range test was used. Significance was determined at p < 0.05, and significantly different means were indicated using different letters.

Results

Effects of water and P supply on plant biomass, P uptake and proline accumulation in leaves

On average, **shoot biomass** increased significantly with organic P and higher water supply. The effect of organic P supply on shoot biomass in this study was found to be higher than the effect of drought stress (Eta² 0.822 vs. 0.587). P supply resulted in 30 % biomass increase (average of all crops), whereas higher water supply resulted in about 10 % higher biomass weights. Shoot biomass of rye and oilseed rape were highest in both water levels. Low shoot biomass was found for sorghum.

The impact of drought stress, as well as the effect of organic P supply on shoot biomass was found to be different in relation to the cultivated crop species. In our experiment sorghum and rye, but not amaranth and oilseed rape showed a significant reduction of shoot biomass under drought stress compared to well watered conditions (Table 2).

The positive effects of P supply on shoot biomass was comparable in the 60 % WHC and 30 % WHC treatments for amaranth (30.7 % to 33.3 %) and oilseed rape (16.8 % to 16.6 %). For sorghum (73.1 % to 38.7 %) and rye (40.7 % to 19.5 %) the effect of P supply was higher in well watered treatment compared to drought treatment.

In general, the **P uptake** differed between crop species and was influenced by the P supply. A low P uptake was found for sorghum, which was related to the low biomass of sorghum.

The P uptake for amaranth and oilseed rape was not decreased under drought stress, whereas drought stress reduced the P uptake of sorghum and rye in comparison to well watered conditions (Table 2).

Compared to treatments without P supply the organic P application significantly increased the P uptake for amaranth, oilseed rape and rye and in tendency for sorghum in both water treatments.

The **proline** content is a common metabolic response of higher plants to osmotic stresses like water deficits. Huge differences of the proline concentrations were found between crops. Highest values of proline were measured in C3 plants oilseed rape ($46.7 \mu\text{mol g}^{-1} \text{TM}$) followed by rye ($7.38 \mu\text{mol g}^{-1} \text{TM}$), whereas much lower contents were determined in the C4 plants sorghum ($1.30 \mu\text{mol g}^{-1} \text{TM}$) and amaranth ($1.97 \mu\text{mol g}^{-1} \text{TM}$) (Table 2).

In our experiment oilseed rape and rye had a considerably higher proline concentration under drought conditions than in the treatment with 60 % WHC. In contrast, sorghum and amaranth did not show any differences in proline concentration in dependency of water supply.

P supply lead to a significant decrease of proline content in sorghum leaves under both irrigation regimes. The same tendency was shown for amaranth. In contrast, the proline values of rye were about 4 times higher after P supply in combination with drought stress.

Effects of water and P supply on chemical soil characteristics in relation to crop species

Generally, the organic P supply as well as the crop species but not the water supply had significant effects on pH value and on soil P pools.

Table 2: Shoot biomass, P uptake and proline accumulation as affected by water treatment, P supply and crop species

| P supply | WHC % | Sorghum | Amaranth | Oilseed rape | Rye |
|--|-------|---------------|---------------|---------------|---------------|
| Shoot biomass (g pot ⁻¹) | | | | | |
| PO | 60 | 6.70 ab | 12.7 a | 17.3 ab | 23.6 b |
| | 30 | 6.20 a | 12.9 a | 15.7 a | 20.0 a |
| P1 | 60 | 11.6 c | 16.6 b | 20.2 c | 33.2 c |
| | 30 | 8.60 b | 17.2 b | 18.3 bc | 23.9 b |
| Mean | | 8.30 A | 14.9 B | 17.9 C | 25.2 D |
| P-uptake of the shoots (mg pot ⁻¹) | | | | | |
| PO | 60 | 18.6 bc | 35.9 a | 38.1 a | 37.7 b |
| | 30 | 12.1 a | 43.6 b | 42.0 a | 32.7 a |
| P1 | 60 | 20.3 c | 56.4 c | 47.9 b | 53.9 d |
| | 30 | 14.1 ab | 61.5 c | 52.6 b | 42.0 c |
| Mean | | 16.3 A | 49.4 D | 45.2 C | 41.6 B |
| Proline content ($\mu\text{mol/g TM}$) | | | | | |
| PO | 60 | 1.61 b | 2.11 a | 3.80 a | 0.84 a |
| | 30 | 1.51 b | 2.24 a | 78.4 b | 4.75 a |
| P1 | 60 | 0.90 a | 1.50 a | 18.6 a | 0.68 a |
| | 30 | 1.13 a | 1.93 a | 75.2 b | 23.2 b |
| Mean | | 1.30 A | 1.97 A | 46.7 B | 7.38 B |

different letters indicate significant different means at $p \leq 0.05$ between the water and the fertilizer treatments, different capital letters indicate significant differences at $p \leq 0.05$ between crop species

Table 3:

Chemical properties in soil (pH, Pw, Pdl, Pox, DPS and PSC) as affected by water treatment, P supply and crop species

| P supply | WHC % | Sorghum | Amaranth | Oilseed rape | Rye |
|------------------------------|-------|---------------|---------------|----------------|----------------|
| pH (CaCl ₂) | | | | | |
| PO | 60 | 4.62 a | 4.35 a | 4.76 a | 4.73 a |
| | 30 | 4.66 a | 4.43 a | 4.69 a | 4.79 a |
| P1 | 60 | 4.69 a | 4.44 a | 4.76 a | 4.84 a |
| | 30 | 4.68 a | 4.41 a | 4.81 a | 4.88 a |
| Mean | | 4.66 B | 4.41 A | 4.75 C | 4.80 D |
| Pw (mg kg ⁻¹) | | | | | |
| PO | 60 | 4.99 a | 5.37 a | 5.38 a | 4.72 a |
| | 30 | 4.53 a | 5.68 b | 4.85 a | 5.23 a |
| P1 | 60 | 6.50 b | 6.53 bc | 5.77 a | 6.24 b |
| | 30 | 6.99 b | 6.88 c | 5.40 a | 6.30 b |
| Mean | | 5.75 B | 6.14 C | 5.38 A | 5.62 AB |
| Pdl (mg kg ⁻¹) | | | | | |
| PO | 60 | 35.8 a | 32.0 a | 31.5 a | 29.9 ab |
| | 30 | 37.2 a | 30.4 a | 31.0 a | 29.1 a |
| P1 | 60 | 39.9 b | 31.7 a | 32.9 a | 31.3 bc |
| | 30 | 42.7 c | 31.5 a | 31.2 a | 32.9 c |
| Mean | | 38.9 B | 31.4 A | 31.7 A | 30.8 A |
| Pox (mmol kg ⁻¹) | | | | | |
| PO | 60 | 14.3 a | 11.0 a | 13.0 a | 12.5 a |
| | 30 | 13.8 a | 9.78 a | 13.5 a | 12.1 a |
| P1 | 60 | 16.5 b | 13.0 b | 16.3 b | 14.4 a |
| | 30 | 16.7 b | 13.8 b | 16.8 b | 14.4 a |
| Mean | | 15.3 C | 11.9 A | 14.9 C | 13.3 B |
| DPS (%) | | | | | |
| PO | 60 | 46.4 a | 36.6 a | 45.7 a | 42.8 a |
| | 30 | 46.0 a | 33.8 a | 44.9 a | 42.1 a |
| P1 | 60 | 53.4 b | 43.8 b | 54.9 b | 48.8 a |
| | 30 | 54.2 b | 44.2 b | 55.2 b | 50.3 a |
| Mean | | 50.0 C | 39.6 A | 50.18 C | 46.0 B |
| PSC (mmol/kg ⁻¹) | | | | | |
| PO | 60 | 30.8 a | 30.1 a | 28.6 a | 29.2 a |
| | 30 | 30.1 a | 28.8 a | 30.0 a | 28.7 a |
| P1 | 60 | 30.9 a | 29.7 a | 29.8 a | 29.4 a |
| | 30 | 31.0 a | 31.3 a | 30.5 a | 28.6 a |
| Mean | | 30.7 A | 30.0 A | 29.7 A | 29.0 A |

different letters indicate significant different means at $p \leq 0.05$ between the water and the fertilizer treatments,
different capital letters indicate significant differences at $p \leq 0.05$ between crop species

In our experiment, the **pH values** were mainly influenced by the cultivation of different crop species, which all resulted in a further decrease of the initially low values. Mainly after amaranth cultivation extremely low values of pH 4.41 were found (Table 3),

The organic P supply had a positive effect on plant available P pools in soil, in both water treatments. In particular the **Pw** values increased with organic P application. Despite the high P uptake of amaranth, highest Pw concentration in soil were found after cultivation of this crop (Table 3).

P supply also increased the **Pdl** values in combination with sorghum and rye significantly compared to control without P addition. Pw and Pdl values tended to be higher under water deficiency, which can be explained by lower plant P uptake rates (Table 3). Negative correlation between P uptake and Pw ($r = -0.714^{**}$) and P uptake and Pdl ($r = -0.711^{**}$) were found.

The supply of organic P increased **Pox and DPS** significantly for sorghum, amaranth and oilseed rape and in tendency for rye in both water treatments. In contrast to the Pw content lowest Pox values were measured after amaranth cultivation ($11.9 \text{ mmol kg}^{-1}$) (Table 3).

Neither water and P supply, nor crop species affected the PSC in this experiment (Table 3).

Effects of water and P supply on enzyme activity of different crops

The activity of phosphatases was strongly influenced by water availability, P supply and crop species. The highest AcP values were measured for oilseed rape and rye with 210 and 223 $\mu\text{g p-nitrophenol/g/h}$.

Water shortage yielded a higher activity of AcP in soil in comparison to sufficiently watered treatments. Significantly higher values due to drought stress were found for oilseed rape (42.9 %), amaranth (25.1 %) and rye (9.54 %) in treatments without P supply, and for sorghum (15.4 %), amaranth (13.3 %) and rye (10.6 %) in treatments with P application. Generally, the activity of AcP was found to increase after organic P supply (Table 4).

The activity of AIP was about 10 % of the AcP activity. Highest AIP values were measured after sorghum and rye cultivation. The effects of drought stress on AIP depended on the P supply. In treatments without P supply drought stress significantly decreased AIP activity for sorghum and amaranth. In contrast, in the phytin treatments drought stress increased the activity of AIP in combination with amaranth, sorghum and rye cultivation (Table 4).

Discussion

Effect of water supply on P uptake of different crop species

Shoot biomass and P uptake of crop species are usually reduced under dry soil conditions (e. g. Pinkerton and Simpson, 1986). The results of our experiment showed a reduced biomass and P uptake only for sorghum and rye, while the P uptake of amaranth and oilseed rape was not affected by drought stress.

Oilseed rape is described to have a high P efficiency when cultivated on P poor soil, which can be explained by root exudates modifying the biochemical conditions in the rhizosphere (Zhang et al., 1997; Bertrand et al., 1999). This crop is also adapted to P starvation by developing an extensive root system to explore a higher soil volume (Hendriks et al., 1981; Wang et al., 2007). Advanced root growth may also enhance the uptake of water and other nutrients under drought conditions and therewith elevate plant growth. In addition, in our experiment oilseed rape showed by far the highest proline contents in leaves which

Table 4:

Enzyme activities in soil (AcP and AIP) as affected by water treatment, P supply and crop species

| P supply | WHC % | Sorghum | Amaranth | Oilseed rape | Rye |
|--|-------|----------------|----------------|----------------|----------------|
| AcP ($\mu\text{g p-nitrophenol/g TS/h}$) | | | | | |
| PO | 60 | 178.0 a | 148.7 a | 160.8 a | 206.6 a |
| | 30 | 180.7 a | 185.9 b | 229.9 b | 226.3 b |
| P1 | 60 | 190.2 a | 195.6 c | 221.2 b | 218.8 b |
| | 30 | 219.4 b | 221.6 d | 231.3 b | 242.0 c |
| Mean | | 192.1 A | 188.0 A | 210.8 B | 223.4 C |
| AIP ($\mu\text{g p-nitrophenol/g TS/h}$) | | | | | |
| PO | 60 | 12.4 b | 9.42 b | 11.6 a | 12.4 a |
| | 30 | 8.12 a | 7.80 a | 11.5 a | 12.3 a |
| P1 | 60 | 13.3 b | 10.8 c | 11.3 a | 12.6 a |
| | 30 | 17.3 c | 14.7 d | 11.4 a | 13.5 b |
| Mean | | 12.8 C | 10.7 A | 11.4 B | 12.7 C |

different letters indicate significant different means at $p \leq 0.05$ between the water and the fertilizer treatments,
different capital letters indicate significant differences at $p \leq 0.05$ between crop species

were further increased under drought stress. This seems to indicate an adaptation mechanism of oilseed rape to drought stress. Müller et al. (2010) found that oilseed rape plants react to drought stress with osmotic adjustment to keep up tissue metabolic activity and enable re-growth upon re-wetting. Maintenance of physiological plant parameters may also sustain the P uptake of the roots under water deficiency.

Besides oilseed rape **amaranth** was found to maintain P uptake also under drought conditions. The further decrease of pH values in soil after amaranth cultivation might have affected the P availability, although an improved availability due to a further decrease of soil pH can be hardly expected when considering the low initial pH values of the soil. In contrast to its high P uptake amaranth cultivation also resulted in highest values of plant available P_w in soil.

Our results confirmed findings in other studies, showing the overall high nutrient uptake of amaranth (Escudero et al., 1999), the high P uptake efficiency (Ojo et al., 2010) as well as a relatively good adaptation to drought stress (Hura et al., 2007). These authors demonstrated that amaranth maintained the leaf water potential under water deficiency which resulted in less water stress especially at an early stage of growth. Liu and Stützel (2004) found a decreased leaf area per root dry mass for amaranth under drought affecting the balance between water-losing and water-gaining organs.

In our experiment the shoot biomass and the water use efficiency (data not shown) of **rye** were highest of all crops in both water treatments. However, drought resulted in a decrease of shoot biomass and P uptake. Water deficiency was also found to reduce these characteristics for **sorghum**. Generally, rye and sorghum are considered to be adapted to marginal land and to be efficient in water and nutrient uptake (Baon et al., 1994; Berenji and Dahlberg, 2004). It might be speculated that the drought effects on sorghum had been lower under field conditions due to the fast growing root system of sorghum that can explore large soil volumes. Other relevant aspects are the intensity of drought and the growth stage (Al-Karaki et al., 1995; Khalili et al., 2008). Schittenhelm (2010) found that sorghum achieved its maximum biomass yield already at medium water supply with 40 to 50 % of plant available soil water, but reduced biomass considerably when water supply was lower. For rye, negative effect of drought stress on plant growth was also shown by Hlavinka et al. (2009).

The general low shoot biomass formation of sorghum in our investigation was most probably caused by the low temperatures at the beginning of our outdoor pot experiment. Sorghum is known for its cold stress sensitivity (Anda et al., 1994). Acid soil reaction was also shown to reduce the growth of varieties of *Sorghum bicolor* (Duncan, 1991).

Effect of P supply on P uptake of different crop species

In the present study the organic P supply was found to have a greater impact on plant growth than the water supply. P addition increased the P uptake and shoot biomass of the crops in both water treatments. Though, the increasing effect of P supply was usually higher in well watered treatments, which point to the growth limiting effect of water.

From the other point of view, the reduction of shoot biomass for sorghum and rye due to drought was more pronounced in treatments with P than in treatments without P supply. This can be explained by increased plant growth after P supply, which resulted in higher water consumption and the following negative effect through increasing drought stress, as also described by Hu and Schmidhalter (2005). Rye reacted with a significant increased proline accumulation in leaves when P was supplied, which was also an indicator for higher water stress in the fertilized treatment.

In general, the results showed a positive effect of organic P supply on plant parameters. However, the findings did not indicate an increased drought tolerance of the tested crop species as a consequence of the organic P supply.

Effect of water and P supply on chemical soil characteristics

The soil P pools in our study were affected by crop species and P supply. Generally plant available P pools in soil increased when phytin was applied, even the water soluble P content. Thus it may be assumed that organically bound P was mineralized rapidly into highly soluble mineral P forms, irrespective of the water supply.

Drought stress did not lower the plant available P pools in soil in the presented pot experiment. In contrast, increased values were found which were in accordance to lower rates of P uptake. Probably, permanent drought stress under field conditions could reduce plant available P by forming more insoluble compounds in soil, as was shown in other studies, e.g. by Garcia et al. (2008).

The cultivation of the different crop species strongly influenced P_d content in soil. A negative, significant correlation between P uptake and P_d was found ($r = 0,711^{**}$). Therewith P_d content decreased with increasing P demand.

Effect of water and P supply on enzyme activity

The supply of organic P as phytin increased the activities of AcP and AlP compared to treatments without P. Usually, the activity of phosphatases in soil increases with organic P application, catalyzing the transformation of organic P like phytin into plant-available P forms (Yadav and Tarafdar,

2001). In contrast, inorganic P sources did not cause an increase of phosphatase activity in soil (Yadav and Tarafdar, 2001; Wang et al., 2008).

The results of the present research also demonstrate that AcP activity increased under water deficiency. This may contribute to P supply of plants from organic sources under drought conditions.

Conclusions

The results of this study indicate that an application of organic P as phytin can improve the P availability in soil and increase shoot biomass and P uptake under drought conditions. On the other hand, increased plant growth by P supply causes a higher water demand and may enforce negative effects of drought stress. As a consequence, we suggest moderate P fertilizer rates on deficient soils in relation to the water availability of the site. Further studies under field conditions need to be carried out to quantify the interactive role of drought stress and organic P forms in relation to crop species on plant productivity.

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