# Combining phosphorus placement and water saving technologies enhances rice production in phosphorus-deficient lowlands.

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**Abstract**

Lowland rice production in sub-Saharan Africa (SSA) is often limited by water supply and low phosphorus (P) availability and efforts are needed towards more efficient management of both resources. Field and pot experiments were set up to evaluate combinations of water saving technologies and P placement methods with due attention to treatment effects on root architecture. A two-year field experiment was set up in a lowland rice field in Tanzania with factorial combinations of different levels of water supply (field capacity, alternating wetting drying, permanent flooding) and P application (no P; 3.45 and 6.90 kg $ha^{-1}$ placement versus 25 kg $ha^{-1}$ broadcast), thereby testing residual effects in year 2. A trial in large pots was additionally performed with equivalent treatments and allowing measurements of soil solution composition, fertilizer efficiency, and root density versus depth. Rice grain yields ranged 0-5 ton $ha^{-1}$ and mainly responded to P application. The P placement at the lowest P rate resulted in higher grain yield at field capacity (2.0-2.5 ton $ha^{-1}$) than in flooded rice (1.2-1.6 ton $ha^{-1}$), whereas these differences were absent at higher P rates. Lower water supply at field capacity enhanced root growth and rooting depth, decreased nodal root thickness and enhanced root P uptake efficiency compare to flooded condition. Modelling P diffusion outwards the granules showed more restricted P diffusion under reduced water supply and, therefore, less P immobilization in the soil under field capacity. These differences between water treatments were more pronounced at lower than at higher P supply. This study shows that root responses and P diffusion outwards granules explain how water and P resources can be saved with P placement in combination with water saving technologies. P placement forms a good option to intensify rice production while countering soil P decline in P deficient lowlands when resources are limited.

**Highlights:**

- Combinations of P and water management options were tested in P deficient lowlands
- Root development of rice can be modified by specific P- but mainly by water management
- Under P limitation, reduced irrigation enhances rice development, P uptake, and yield
- Micro-dose placements can reverse P depletion in deficient lowlands
- For small P placement rates, interactions with water management should be considered

**Key words:** Water Saving Technologies, Phosphorus Efficiency, P Micro-dosing, P Placement, Alternate Wetting and Drying, Aerobic Rice, Root Plasticity, Root Architecture

## Introduction

In large parts of sub-Saharan Africa (SSA), rice (*Oryza* spp.) serves as an important staple crop. Population growth and urbanization drastically increase rice consumption and demand. Rice production should concomitantly increase to reduce dependence on rice imports, which endangers food security in many African countries (Saito et al., 2015; van Oort et al., 2015). The total rice production in SSA has increased during the last decades, but this mainly resulted from area expansion rather than system intensification on existing farmland (FAOSTAT, 2018). There is a strong need for intensification on the existing rice growing areas in SSA and a more efficient use of the available resources such as water and nutrients is a prime requirement to achieve such sustainable intensification. (Saito et al., 2013; van Oort et al., 2015; Zenna et al., 2017)

Drought and low phosphorus (P) availability are two major yield limiting factors in both upland and lowland rice growing areas. As lowlands are among the most productive rice growing areas in SSA (Zenna et al., 2017), optimization of management practices in P deficient and/or drought prone lowland systems offers major opportunities for further improvement of resource use and rice production (Becker et al., 2003; Nhamo et al., 2014).

In view of declining P resources (Schachtman et al., 1998; Zapata et al., 2004), more efficient P application methods have been developed for several crops (Nziguheba et al., 2016), but none are widely adopted in rice systems of SSA. Current low P fertilizer recovery rates and persistently low purchasing power of many smallholder rice farmers preclude a drastic improvement of P use in rice based systems. As P is rather immobile in soils, localized P applications form an option towards sustainable P management (Malhi et al., 2001; Margenot et al., 2016; Nziguheba et al., 2016). A P micro-dose placement implies a very localized application of a small P dose to a small surface or sub-surface area, often combined with seeds into the planting hole (ICRISAT, 2009; Nkebiwe et al., 2016; Vandamme et al., 2018). This technique of P micro-dose placement is successfully tested and adopted for several cereal crops (Aune and Bationo, 2008; Bagayoko et al., 2011; Bielders and Gérard, 2015; Camara et al., 2013; van der Eijk, 2006). However, the technique of P micro-dose placement in direct seeded rice systems has only been studied and evaluated in a few cases (Bayan and Lourduraj, 2000; Garrity et al., 1990; Vandamme et al., 2018) and, to our knowledge, it is only adopted in upland rice growing areas of Madagascar (Andriamananjara et al., 2018; Raboin et al., 2014). The P micro-dose placement was observed to strongly benefit shoot growth and yield in direct seeded rice systems (Vandamme et al., 2018), but little is known about the effects on root performance and the interactions with water management in lowlands.

With an increasing prevalence of dry spells, it also becomes critical to optimize water use for rice production. Because of the huge water requirements of conventionally flooded rice, water saving technologies have been developed to help farmers cope with water scarcity and to increase water productivity in lowland rice systems (Bouman et al., 2007; de Vries et al., 2010). With alternate wetting and drying (AWD) the field is only irrigated up to flooding after the soil water table drops below a certain level beneath the soil surface (-30 cm for normal AWD and -15 cm for safe AWD) (Carrijo et al., 2017; LaHue et al., 2016), and hence the field is not continuously flooded. Another water saving approach aims to permanently maintain the soil close to field capacity, while never flooding the soil ('aerobic rice') (Bouman et al., 2005). Such promising water saving technologies are mainly developed and adopted in Asia, but are not yet widespread in lowlands of SSA.

Reduced water supply theoretically reduces P mobility in soils due to reduced effective diffusion (Kirk et al., 1990). However, reduced water availability largely influences root development and an improved root functioning may counteract a reduced P supply (De Bauw et al., 2019; Sandhu et al., 2017; Zhan et al., 2014). Similarly, several root characteristics may respond to a reduced P supply, hence the combination of P and water management techniques may lead to differences in root performance, rice development, and yield (Kirk et al., 1998). De Bauw *et al.* (2019) previously examined how rice roots respond to several combinations of P and water availability, and showed that water availability has a dominant modifying role on root architecture, in turn affecting P uptake efficiency. Understanding root plasticity under specific combinations of P and water management is thus important in efforts towards enhancing resilience to both stresses. There is an urgent need to evaluate water saving technologies and P placement methods with due attention to treatment effects on root architecture, before recommending these methods as sustainable intensification strategies.

This work aims to 1) evaluate rice establishment, shoot growth, and yield under combined P and water management options in P deficient lowlands; more particularly focusing on the technique of P micro-dose placement 2) examine rice root development, root architecture, and rooting patterns under such management techniques; 3) assess the residual effects of such intensification options on rice production in P deficient lowlands. To this end, a two-year field experiment was conducted in a lowland field in Tanzania with factorial combinations of water supplies (field capacity, alternating wetting drying, permanent flooding) and P application (control, placements, and broadcast) in year 1 (field experiment 1). This was repeated in year 2 (field experiment 2), thereby testing residual effects. A trial in large pots was additionally performed with equivalent treatments and allowing measurements of soil solution composition, fertilizer effectiveness, and root density versus depth. Finally, P diffusion modelling outwards of the fertilizer granules was performed to assist the interpretation of the field data.

## Materials and Methods

### *Field experiment 1*

A field trial was conducted at a lowland site in Morogoro (6°50'31.4"S, 37°38'36.5"E; Tanzania) between May and October 2017. Both irrigation and drainage was ensured. Site and soil information is presented in Table 1.

A split-plot design with three replicate blocks was set up with different levels of water supply in the main plots and different P management treatments in the sub plots within each main plot. The size of the sub plots was 3.6 x 2.0 m. Replicate blocks and main plots were separated at a distance of 2 m and a plastic sheet was dug into the soil down to 50 cm in order to prevent horizontal water flow between water treatments and replicate blocks. Within each main plot, sub plots were levelled and separated by bunds and furrows at a distance of 50 cm. Water management comprised three levels (field capacity (FC), alternate wetting and drying (AWD), permanent flooding (PF)) while P management included four levels (a control (NoP), placement at a rate of 3.45 kg P $ha^{-1}$ (MicroP1), placement at a rate of 6.90 kg P $ha^{-1}$ (MicroP2), and a basal broadcast of 25 kg P $ha^{-1}$ (PlusP)).

Two seeds of the typical lowland rice variety NERICA-L-19 were sown at a distance of 20 x 20 cm. NERICA-L-19 is an interspecific rice variety developed by the Africa Rice Center, using crosses between *Oryza sativa* (Asian rice) and *Oryza glaberrima* (African rice). Before Triple Super Phosphate (TSP) was placed in the planting hole, the TSP fertilizer was first sieved in order to homogenize granule size (1.5 mm radius). For the plots with P placement (MicroP1 and MicroP2), three or six TSP granules (respectively 3.45 kg P $ha^{-1}$ and 6.90 kg P $ha^{-1}$) were first placed into each planting hole (2.5 cm depth) and covered with soil before sowing (1 cm depth). In the plots with broadcast P (PlusP), TSP was broadcast at a conventional rate of 25 kg P $ha^{-1}$ at 17 days after sowing (DAS).

At 17 DAS, all plots were also amended with a first basal application of urea, muriate of potash (MOP), $MgSO_4$, $ZnSO_4$, and $H_3BO_3$ at rates of 34 kg N $ha^{-1}$, 17 kg K $ha^{-1}$, 21 kg Mg $ha^{-1}$, 27 kg S $ha^{-1}$, 3 kg Zn $ha^{-1}$, and 2 kg B $ha^{-1}$ in order to avoid any nutrient deficiency other than P. Two top dressings of urea (34 kg N $ha^{-1}$) and MOP (17 kg K $ha^{-1}$) were later applied at 34 and 50 DAS.

**Table 1.** **Soil characteristics of soil from pot and field experiments.**

| Trials | Location | Coordinates | pH | $Al_{ox}$ | $Fe_{ox}$ | $Mn_{ox}$ | $P_{ox}$ | ----Texture---- | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | [mg kg$^{-1}$] | [mg kg$^{-1}$] | [mg kg$^{-1}$] | [mg kg$^{-1}$] | [%sand] | [%silt] | [%clay] |
| (a) Lowland field trials | Morogoro, Tanzania | 6°50'31.4"S 37°38'36.5"E | 6.6 ($CaCl_2$; S/W = 1:5) | 1193 | 2010 | 317 | 50 | 18 | 56 | 26 |
| (b) Soil for pot trial Jan. 2017 | Dakawa, Tanzania | 06°23'56.6''S 37°33'47.5''E | 6.7 ($CaCl_2$; S/W = 1:5) | 936 | 1848 | 532 | 22 | 9 | 62 | 29 |

Plots were watered daily up to field capacity until 22 DAS. Then contrasting water regimes were imposed. A water level of 5 cm was maintained in the PF treatment. For the AWD and FC treatments, perforated PVC tubes (10 cm diameter, 30 cm length) were installed in each plot to monitor the soil water table. Under AWD, plots were re-irrigated to flooding (water level at 5 cm) when the water table dropped below -15 cm. Under FC, it was ensured that the soil water table never rose above -20 cm. Water management was maintained daily until the end of the trial.

The dates of 85% and 100% maturity were noted. At 100 DAS, four adjacent rows were demarcated and four representative plants (based on the average tiller number and plant height) were selected for further shoot and root analysis. The shoots were cut, oven dried (60 °C), weighed, and manually ground by mortar. P concentrations in the shoot tissues ($Pc_{shoot}$) were then determined by ICP-OES (Thermo Scientific iCAP 7000 series) after digestion in $HNO_3$. Immediately after cutting the shoots, the root system of each selected plant was excavated by digging out a block of soil around the stem (20x20x20 cm). The root system was carefully washed out by gently shaking the block on a 2 mm net in water and subsequently placed in a dish with clean water. The number of nodal roots was counted and the average nodal root thickness was measured using a transparent ruler. Lateral root density and secondary branching degree were determined as described by De Bauw *et al.* (2019). Lateral root thickness (both at the root base and for deeper roots) was scored according to five classes described in Table S1 (**Supplementary Information**). After root analysis, the root system was oven dried and weighed. The P uptake in the shoot per unit root weight ($Pup_{root}$) and per nodal root ($Pup_{nodal}$) was calculated to provide estimators for P uptake efficiency.

At maturity, grain yield was determined in a net plot of 2.2 x 1.6 m (88 hills), excluding border rows and rows used for root analysis. Grain yield is reported at a moisture content of 14%. Agronomic P efficiency at harvest was calculated as $AEP_{grain}$ = *(grain yield with P – grain yield without P)/amount of P applied*. The P concentrations in the grains ($Pc_{grains}$) was determined by ICP-OES after digestion in $HNO_3$. The seasonal P balance per hectare was calculated as: $P_{balance}$ = *(P input by fertilizer – P export by grain harvest)*.

***Field experiment 2***

In order to assess residual P effects and the consistency of treatment effects, a second trial was conducted between May and October 2018. The same plots were used with the same P micro-dose rates as in the previous season (2017) and established exactly in the same way. Control plots from 2017 were kept as a control in 2018. In order to assess the residual P effects from a former broadcast, the plots amended with 25 kg $ha^{-1}$ in 2017 were split in 2018 and half of each plot was sown as a control without P application (P0) while the other half was amended with a placement of 6.90 kg $ha^{-1}$ (MicroP3). Water treatments were implemented in the same way as during the first season.

Plant establishment, grain yield, agronomic P efficiency, and P balances were monitored and calculated as described for the first season. Root data were not collected.

***Large pot experiment***

A pot trial with P deficient soil in large pots (10.5 L) was set up in the greenhouse with four levels of water supply and four P management treatments and five replicates of each combination (n=80). The water treatments included drying periods (DP), field capacity (FC), safe-alternate wetting and drying (AWD), and permanent flooding (PF); while P treatments included no application (NoP), a micro-dose P placement (MicroP), suboptimal basal application (SubP), and a non-limiting basal application (PlusP).

The trial was conducted in a greenhouse located at Sokoine University of Agriculture in Morogoro (6°50'53.9"S, 37°39'31.3"E; Tanzania). Average daily minimum and maximum temperatures during the experiment were respectively 21.9 and 33.4°C.

Initially, a P-deficient soil (P <0.01 mg $L^{-1}$ in solution) was collected from a lowland rice field in Dakawa, Tanzania (Table 1). After sampling, the bulk soil was shade dried, crushed to an aggregate size of 4 mm, and amended with salts of $NH_4NO_3$, $CaCl_2$, $MgSO_4$, $ZnSO_4$, $CuSO_4$, $H_3BO_3$ and $Na_2MoO_4$ at rates of 37 mg N $kg^{-1}$, 95 mg K $kg^{-1}$, 15 mg Mg $kg^{-1}$, 20 mg S $kg^{-1}$, 2.5 mg Zn $kg^{-1}$, 0.04 mg B $kg^{-1}$, 0.08 mg Cu $kg^{-1}$, and 0.034 mg Mo $Kg^{-1}$ soil, to avoid any nutrient deficiency other than P.

To mimic a P deficient subsoil, no P was initially added to this bulk soil. Eighty large pots (height: 52 cm, diameter: 16 cm) were first filled with 6.8 kg of this P deficient soil (28.5 cm in pot height). To avoid downwards P transport by wetting the whole pot at once, each pot with this layer of subsoil was first watered to field capacity (38% w/w) before adding the topsoil. Pots of flooded treatments (PF) were sealed at the bottom. The remainder of the soil was used to create three different topsoils by subjecting them to different P treatments. One fourth was amended with a non-limiting amount of ground TSP (63.1 mg P $\mathrm{kg}_{\mathrm{topsoil}}^{-1}$ or 280 mg P per pot) up to a theoretical P concentration of 0.4 mg P $L^{-1}$ in soil solution, representing a non-limiting basal broadcast (PlusP). Another quarter was amended with a sub-optimal amount of ground TSP (18.6 mg P $\mathrm{kg}_{\mathrm{topsoil}}^{-1}$ or 82 mg P per pot) up to a theoretical P concentration of 0.1 mg P $L^{-1}$ in soil solution, representing a sub-optimal basal broadcast (SubP). The remaining half was not amended with TSP and was later divided into two treatments (NoP and MicroP). The same amount of Ca was added in all treatments by using $CaCl_2$. Pots were subsequently filled with 4.4 kg of these topsoils and the whole pot was watered to field capacity.

A pre-germinated seed of NERICA-L-19 was sown in each pot. For the treatment with micro-dose P placement (MicroP), 0.12 g TSP (24 mg P $pot^{-1}$) was first applied in the planting hole of the non-amended topsoil before sowing. This placement rate corresponds with a micro-dose rate of 6 kg $ha^{-1}$ when plants are conventionally spaced at 20x20 cm. Two top dressings of $NH_4NO_3$ (in solution) were applied at a rate of 323 mg N per pot at 21 and 34 DAS. Additional top dressings of $ZnSO_4$, KCl, and MgSO4 were added at 21 DAS to each pot at rates of 0.37 g Zn, 1.4 g K, and 0.12 g Mg, to avoid deficiency of these nutrients.

Water treatments were initiated at 17 DAS and were maintained and monitored on a daily basis until the end of the trial. In the treatment with permanent flooding (PF), a water layer of 5 cm above soil level was maintained. For the safe-alternate wetting and drying treatment (AWD), the soil water level was monitored by perforated tubes with diameter of 1.5 cm, and pots were re-irrigated when the water table dropped below 15cm. Pots were watered daily up to field capacity for the treatment with field capacity (FC) while in the last treatment, pots were only re-watered up to field capacity with intervals of ca. six days to represent drying periods (DP) during erratic rainfall.

Plant development was monitored by measuring plant height and counting tillers and leaves twice a week. To monitor P concentration in the soil pore water, rhizon samplers (10 cm length, 2.5 mm diameter, 0.15 µm pore size) were installed in each pot at a distance of 4 cm from the seedling (and P placement). Soil pore water samples were taken at a frequency of seven days, during the whole experiment.

At 49 DAS, shoots were cut and analyzed as described for the field experiment. Immediately after removing the shoot, the soil cylinder was carefully taken out of the pot and precisely cut into three segments. One part comprised a segment from 0 to 15 cm depth which included the ‘basal roots’, another segment comprised soil from 15 to 30 cm depth including the ‘intermediate roots’, and the last segment between 30-52 cm incorporated the ‘deep roots’. The latter segment was defined according to most rice studies, where deep roots are defined as roots below 30 cm (Gowda et al., 2011; Kato et al., 2013, 2006). For each soil segment, roots were carefully washed out by using water and nets (2 mm size). After removing the soil, roots of each segment were placed in a dish with clean water and root architectural variables were determined as described for the field experiment.

The root segments were oven dried (60°C) and weighed to determine root distribution and biomass allocation. The P uptake efficiency parameters ($Pup_{root}$, $Pup_{nodal}$) were subsequently calculated. A provisional indicator of the agronomic efficiency of the P fertilizer at 49 DAS was calculated as $AEP_{49DAS}$ = *(straw mass with P – straw mass without P)/ amount of P applied*.

***Data analysis***

All statistics were computed in R version 3.4.1. (R Development Core Team 2012) and the level of significance to detect effects was set at p=0.05. Two-way ANOVAs were performed on the shoot and root variables with water and P treatments as fixed effects. Replicate pots or blocks were included as random effects. Means (μ) and standard errors of the mean ($\frac{\sigma}{\sqrt{n}}$, with σ = standard deviation and *n* = the number of observations) were calculated for all treatment combinations and significance between treatment means was determined by calculating the Least Significant Difference, after confirming normality of the residuals.

***Modeling P diffusion, adsorption and availability of placed P under different water regimes***

Given the strong interaction between soil moisture and P, this section aims to assess the physical and chemical influences through diffusion and sorption of contrasting water management on P availability under several placement rates. The P diffusion outwards P fertilizer granules was modelled to interpret the results. Locally placed P in soils generally moves away from the point of application through diffusion, while sorption and precipitation reactions may reduce P mobility (Degryse and McLaughlin, 2014). The diffusion from micro-dose P placements was modelled using the spherical diffusion model described by Degryse and McLaughlin (2014):

$$\frac{\delta c}{\delta t} + \frac{\rho\, \delta(k\, c^n)}{\theta\, \delta t} = f\frac{D}{r^2}\frac{\delta}{\delta r}(r^2\frac{\delta c}{\delta r})$$

With $c$ the P concentration in soil solution (mg $L^{-1}$), $\rho$ the bulk density (kg $L^{-1}$), θ the volumetric water content, $f$ the tortuosity factor, $D$ the diffusion coefficient in water ($cm^2$ $s^{-1}$), $r$ the radial distance (cm), and $t$ the time (s). The P sorption was accounted for by the Freundlich parameters ($k$ and $n$). Soil parameters ($k$, $n$, $\rho$) were determined for the P deficient lowland soil from the field trial**,** for which $\theta$ was altered between field capacity (pF = 2) and soil saturation (pF = 0).

The P sorption ($k$ and $n$) can theoretically change under altered water availability due to reduction/oxidation of iron oxides. However, when the molar P/Fe ratio (oxalate extracted) of a soil is low (<0.12; i.e. P deficiency), it has been shown that there is no additional P release under anaerobic conditions (Smolders et al., 2017), and this assumption is confirmed by the soil solution data (data not shown). Under P deficiency the Freundlich parameters ($k$ and $n$) thus remain constant under both soil saturation and field capacity. The k and n parameters were derived from a P adsorption experiment. Briefly, the topsoil of the field experiment was dried and sieved. Replicate samples of 3 g were suspended in 30 mL water and amended with $KH_2PO_4$ at various rates between 0-60 mg P $L^{-1}$. The soils were equilibrated end-over-end for 24h followed by centrifugation and filtration (0.45µm) and analyzed of P by Inductively Coupled Plasma Mass Spectrometry (ICP-MS, Agilent7700X). The value of k was 180 $mg^{0.3}$ $L^{0.7}$ $kg^{-1}$ and n was 0.7.

The fertilizer was described as a sphere of 2.18 mm radius containing 12 mg P or 2.74 mm containing 24 mg P, corresponding with application rates of 3 and 6 kg $ha^{-1}$ respectively. In this model, P uptake by plants during diffusion was not incorporated as this section focuses on the P availability through soil processes and management only. For P deficient soils, the initial P concentration in soil solution was assumed to be 0 mg $L^{-1}$, as the measured concentration in the control soil was <0.03 mg $L^{-1}$. The P diffusion over time was spherically modeled for the two placement rates and two water levels (field capacity and saturation) and the diffusion equation was numerically solved in Microsoft Excel using the initial and boundary conditions as described in Degryse and McLaughlin (2014).

## Results

### ***Field experiment 1***

*Shoot development and grain yield*

Without P application, plant development (height and number of tillers) was very slow, but it was enhanced by maintaining the soil at FC compared to AWD and PF (Figure S1, **Supplementary Information**). There was a significant interaction effect between water and P on shoot development. Shoot mass at 100 DAS strongly increased with P application. Shoot mass was similar for both micro-dose rates under FC but for MicroP1, shoot growth (and also P uptake) was lower under AWD and PF compared to FC, while this reduction was not significant for MicroP2. FC enhanced shoot biomass production compared to PF only at NoP and MicroP1 (Table 2). The same trends were confirmed at harvest, i.e. grain yield was consistently highest under FC for MicroP1 and NoP compared to other water treatments while these differences due to water were absent at higher P applications (Micro P2 and PlusP) (Figure 1). P broadcast and micro-dosing increased grain yields 7-fold and 3-fold respectively.

P application reduced the time needed to reach 85% maturity, with an average of 143, 134, 133, and 131 days respective to the applied P rates (increasing order). Water management did not affect the duration of the phenological stages. (Table 4)

**Table 2: Shoot and root mass, shoot P uptake (Pup), and P uptake efficiency parameters (shoot P uptake per unit of root mass: $Pup_{root}$; shoot P uptake per nodal root: $Pup_{nodal}$) of rice at 100 DAS in Field Experiment 1. Rice plants were grown on a P deficient lowland field that was subjected to combinations of water management options (field capacity (FC), safe alternate wetting and drying (AWD), and permanent flooding (PF)) and P management options (No P application (NoP), two rates of micro-dose placement (MicroP1 and MicroP2, respectively 3.45 and 6.90 kg P $ha^{-1}$), and a conventional broadcast of 25 kg P $ha^{-1}$ (PlusP)). Data are presented as means with (standard errors of the mean).**

| *Field experiment 1* | | | | | | |
|---|---|---|---|---|---|---|
| **P** | **Water** | **Shoot mass** | **Root mass** | **Pup** | **$Pup_{root}$** | **$Pup_{nodal}$** |
| | | **[g $plant^{-1}$]** | **[g $plant^{-1}$]** | **[mg $plant^{-1}$]** | **[mg $g^{-1}$]** | **[µg $nodal^{-1}$]** |
| **NoP** | **FC** | 4.4 (0.6) | 2.1 (0.2) | 3.1 (0.6) | 1.43 (0.16) | 23 (3) |
| | **AWD** | 2.7 (0.6) | 1.2 (0.2) | 1.2 (0.3) | 1.11 (0.10) | 13 (2) |
| | **PF** | 2.1 (0.6) | 1.2 (0.3) | 0.9 (0.2) | 0.80 (0.09) | 9 (1) |
| **MicroP1** | **FC** | 16.7 (1.1) | 6.2 (0.5) | 8.3 (0.6) | 1.47 (0.14) | 37 (2) |
| | **AWD** | 8.6 (0.8) | 4.9 (0.6) | 4.1 (0.5) | 0.95 (0.17) | 22 (2) |
| | **PF** | 9.2 (0.5) | 4.8 (0.4) | 4.4 (0.5) | 0.92 (0.06) | 20 (1) |
| **MicroP2** | **FC** | 15.5 (1.1) | 6.1 (0.4) | 7.6 (0.6) | 1.32 (0.15) | 33 (2) |
| | **AWD** | 14.6 (1.4) | 6.9 (0.6) | 7.0 (0.7) | 1.04 (0.10) | 30 (2) |
| | **PF** | 12.9 (0.9) | 7.2 (0.6) | 6.4 (0.6) | 0.91 (0.07) | 26 (2) |
| **PlusP** | **FC** | 35.6 (2.5) | 10.9 (0.8) | 25.8 (2.8) | 2.42 (0.25) | 83 (7) |
| | **AWD** | 33.6 (3.4) | 10.6 (1.2) | 19.9 (2.0) | 1.94 (0.16) | 61 (3) |
| | **PF** | 39.1 (2.4) | 12.5 (0.7) | 26.2 (2.3) | 2.11 (0.17) | 68 (3) |
| | **water** | ns | ns | ns | * | ** |
| | **P** | *** | *** | *** | *** | *** |
| | **water×P** | * | ns | (0.057) | ns | ns |

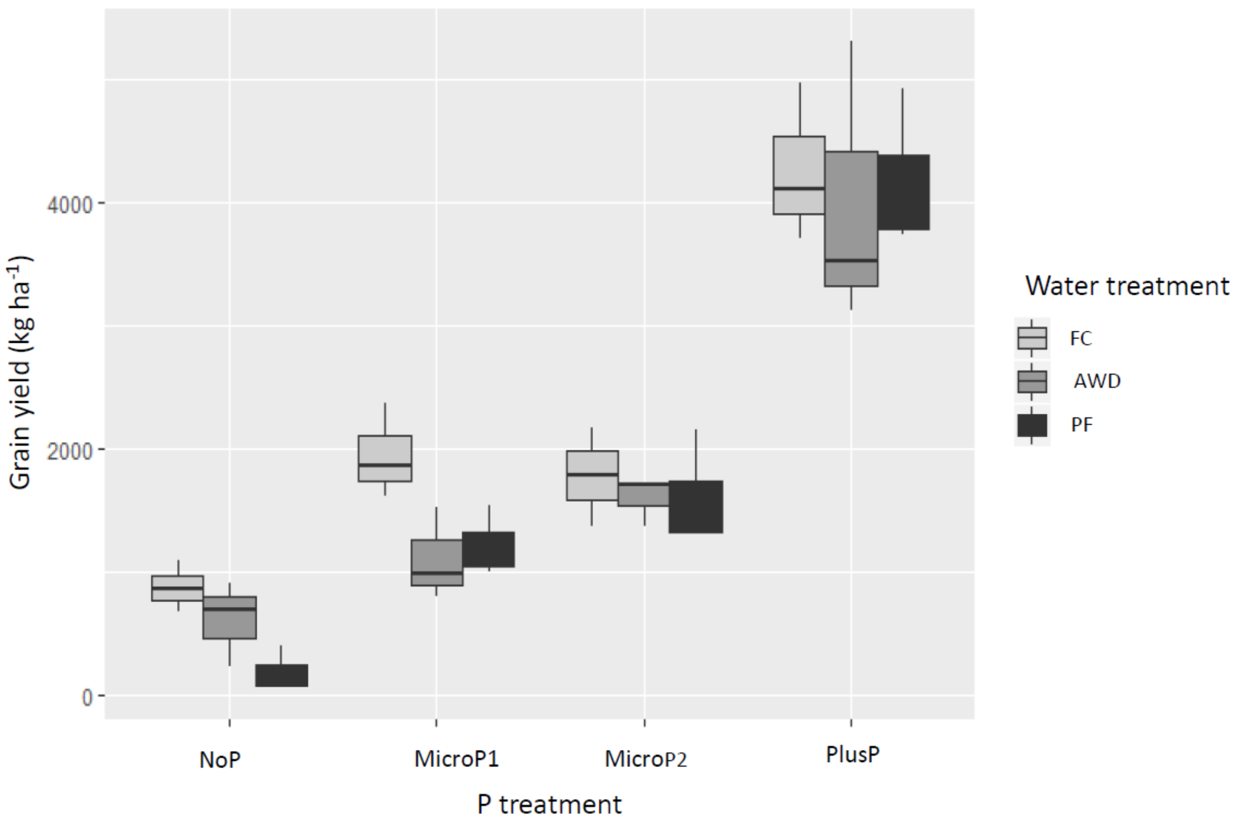


**Figure 1: Grain yield of field grown lowland rice (field experiment 1; 2017) subjected to combinations of water management techniques (field capacity (FC), alternate wetting and drying (AWD), and permanent flooding (PF)) and P management options (No P application (NoP), two rates (3.45 and 6.90 kg P ha$^{-1}$) of micro-dose placement (MicroP1 and MicroP2), and a conventional broadcast of 25 kg P ha$^{-1}$ (Plus P).**

*Root development, architecture and distribution*

At 100 DAS, the nodal root thickness increased according to P application (NoP < MicroP1 and MicroP2 < PlusP), and there was no significant difference between the two placement rates. Within each P application method, nodal root thickness reduced under FC, but it showed an opposite trend without P amendment (Table 3).

Lateral root density at the nodal base was significantly highest for P placements and lowest under PlusP. Reduced water use significantly reduced the basal lateral root density (FC<AWD<PF). (Table 3)

The lateral thickness at the nodal base as also in deepest layers increased with reduced water use. Lateral roots in deepest layers were thinner without P application. (Table 3)

Secondary branching degree at the nodal base was smallest without P application, and a similar trend was observed for secondary branching in deepest layers. For these deep roots, secondary branching consistently increased with reduced water application, but this trend was not observed for MicroP2. (Table 3)

*P uptake & acquisition efficiency at 100 DAS*

The $Pc_{shoot}$ was consistently highest for PlusP and there was no difference in $Pc_{shoot}$ between MicroP1 and MicroP2. Without P application, $Pc_{shoot}$ significantly increased with reduced water use. P application increased total P uptake, and without P application this P uptake increased with reduced water application. The shoot P uptake under placement was similar for both rates under FC, however the P uptake under FC was larger than under AWD and PF at the MicroP1 while it was unaffected by water treatment at MicroP2. (Table S2, **Supplementary Information**)

**Table 3: Architectural root variables of field grown rice at 100 DAS. The field was subjected to combinations of water management techniques (field capacity (FC), safe alternate wetting and drying (AWD), and permanent flooding (PF)) and P management strategies (No P application (NoP), two rates of micro-dose placement (MicroP1 and MicroP2, respectively 3.45 and 6.90 kg P ha$^{-1}$), and a conventional broadcast of 25 kg P ha$^{-1}$ (PlusP)). Lateral root thickness and secondary branching were determined for the nodal root base, but also for the deepest roots. Data are presented as means with (standard errors of the mean).**

| *Field experiment 1* | | | | | | | |
|---|---|---|---|---|---|---|---|
| **P** | **Water** | **Nodal thickness** | **Lateral root density** | **Lateral root thickness** | **Secondary branching** | **Lateral root thickness** | **Secondary branching** |
| | | ---------------------------***Basal Roots***--------------------------- | | | | --------***Deep Roots***-------- | |
| | | **[mm]** | **[score]** | **[score]** | **[score]** | **[score]** | **[score]** |
| **NoP** | **FC** | 0.80 (0.03) | 5.2 (0.16) | 1.88 (0.15) | 2.5 (0.3) | 3.2 (0.2) | 3.4 (0.2) |
| | **AWD** | 0.70 (0.05) | 6.1 (0.15) | 1.29 (0.12) | 2.0 (0.2) | 2.1 (0.3) | 2.3 (0.2) |
| | **PF** | 0.64 (0.06) | 6.8 (0.22) | 1.08 (0.06) | 2.3 (0.3) | 1.7 (0.3) | 1.8 (0.2) |
| **MicroP1** | **FC** | 0.92 (0.03) | 5.3 (0.18) | 1.92 (0.14) | 3.0 (0.2) | 3.6 (0.2) | 4.2 (0.2) |
| | **AWD** | 1.08 (0.05) | 6.8 (0.23) | 1.21 (0.13) | 3.4 (0.3) | 2.7 (0.2) | 3.8 (0.1) |
| | **PF** | 1.08 (0.05) | 7.0 (0.20) | 1.00 (0.00) | 3.0 (0.3) | 2.1 (0.1) | 3.2 (0.2) |
| **MicroP2** | **FC** | 0.96 (0.03) | 5.4 (0.18) | 1.96 (0.07) | 2.7 (0.2) | 3.7 (0.1) | 3.8 (0.2) |
| | **AWD** | 1.22 (0.04) | 6.3 (0.40) | 1.33 (0.11) | 3.2 (0.3) | 2.6 (0.2) | 3.8 (0.1) |
| | **PF** | 1.17 (0.06) | 6.8 (0.20) | 1.04 (0.04) | 3.1 (0.2) | 2.0 (0.2) | 3.6 (0.3) |
| **PlusP** | **FC** | 1.07 (0.03) | 5.1 (0.22) | 2.00 (0.15) | 3.4 (0.3) | 3.5 (0.1) | 4.4 (0.1) |
| | **AWD** | 1.30 (0.03) | 5.7 (0.24) | 1.54 (0.16) | 2.7 (0.3) | 2.7 (0.2) | 3.4 (0.2) |
| | **PF** | 1.35 (0.03) | 6.2 (0.25) | 1.17 (0.09) | 3.1 (0.2) | 2.1 (0.3) | 3.3 (0.2) |
| | **water** | ** | *** | *** | ns | *** | ns |
| | **P** | *** | *** | ns | *** | ** | *** |
| | **water×P** | *** | ns | ns | ns | ns | *** |

**Table 4:** **Time (in days) needed to reach 85% maturity and the agronomic efficiency of the P fertilizer (AEP) based on grain yield for both field experiment 1 and 2. Data are presented as means with (standard errors). A two-year field experiment was conducted in a lowland field in Tanzania with factorial combinations of water supplies (field capacity (FC), alternating wetting drying (AWD), permanent flooding (PF)) and P application (control (NoP, two rates of micro-dose placement (MicroP1 and MicroP2, respectively 3.45 and 6.90 kg P ha$^{-1}$), and a broadcast (PlusP)) in year 1 (field experiment 1). This was repeated in year 2 (field experiment 2), thereby testing residual effects of a broadcast.**

| | | *----Field experiment 1----* | | *----Field experiment 2----* | |
|---|---|---|---|---|---|
| **P** | **Water** | **Time to 85% maturity** | **AEP** *At harvest* | **Time to 85% maturity** | **AEP** *At harvest* |
| | | **[days]** | **[kg kg$^{-1}$]** | **[days]** | **[kg kg$^{-1}$]** |
| **NoP** | **FC** | 139 (3.4) | - | 145 (2.0) | - |
| | **AWD** | 145 (1.2) | - | 149 (0.0) | - |
| | **PF** | 145 (2.6) | - | 156 (14.5) | - |
| **MicroP1** | **FC** | 134 (0.7) | 310 (45) | 138 (0.7) | 395 (48) |
| | **AWD** | 136 (1.2) | 144 (28) | 138 (0.6) | 489 (68) |
| | **PF** | 133 (0.6) | 297 (69) | 136 (1.2) | 396 (43) |
| **MicroP2** | **FC** | 133 (0.7) | 130 (44) | 137 (0.0) | 178 (26) |
| | **AWD** | 132 (0.9) | 143 (37) | 135 (1.0) | 320 (59) |
| | **PF** | 133 (0.7) | 205 (51) | 136 (1.2) | 305 (53) |
| **PlusP** | **FC** | 132 (0.9) | 136 (10) | - | - |
| | **AWD** | 131 (0.6) | 135 (23) | - | - |
| | **PF** | 130 (0.3) | 159 (18) | - | - |
| **MicroP3** | **FC** | - | - | 137 (0.3) | 210 (41) |
| **Placement 2** | **AWD** | - | - | 138 (0.3) | 239 (58) |
| **after PlusP in 2017** | **PF** | - | - | 138 (0.3) | 201 (42) |
| **P0** | **FC** | - | - | 144 (1.0) | - |
| **No P** | **AWD** | - | - | 143 (1.5) | - |
| **after PlusP in 2017** | **PF** | - | - | 146 (0.3) | - |
| | **water** | ns | * | ns | ns |
| | **P** | *** | ** | *** | *** |
| | **water×P** | ns | (0.068) | ns | ns |

The $Pup_{root}$ was largest under PlusP. The $Pup_{nodal}$ showed a similar trend according to P application and was smaller in the control than for both placement rates. Water management similarly affected both efficiency parameters and P uptake efficiency was consistently largest under FC compared to that at larger water supply. (Table 2)

*Agronomic efficiency and P balance*

The $AEP_{grain}$ of PlusP was similar as that for MicroP2. The $AEP_{grain}$ was largest for MicroP1, only under FC and PF (not for AWD). (Table 4)

The seasonal P balance was significantly affected only by the P treatments. Without fertilizer application, the P balance was obviously negative (ca. -0.6 kg P $ha^{-1}$), while for PlusP the balance was strongly positive (ca. 20.3 kg $ha^{-1}$). For MicroP1, the P balance was relatively close to zero (ca. 2.1 kg $ha^{-1}$), while the balance for MicroP2 was fairly positive (ca. 5.2 kg $ha^{-1}$). (Figure 2)

***Field experiment 2***

Plant development was similar for all placements. Without P application, growth was enhanced in the plots that were broadcasted in 2017 and benefits were observed from reduced irrigation (Figure S1, **Supplementary Information**).

P application reduced the time needed to reach 85% maturity similarly for all placement rates compared to both controls (Table 4). Without P application, a residual P effect from the former basal application facilitated plant development.

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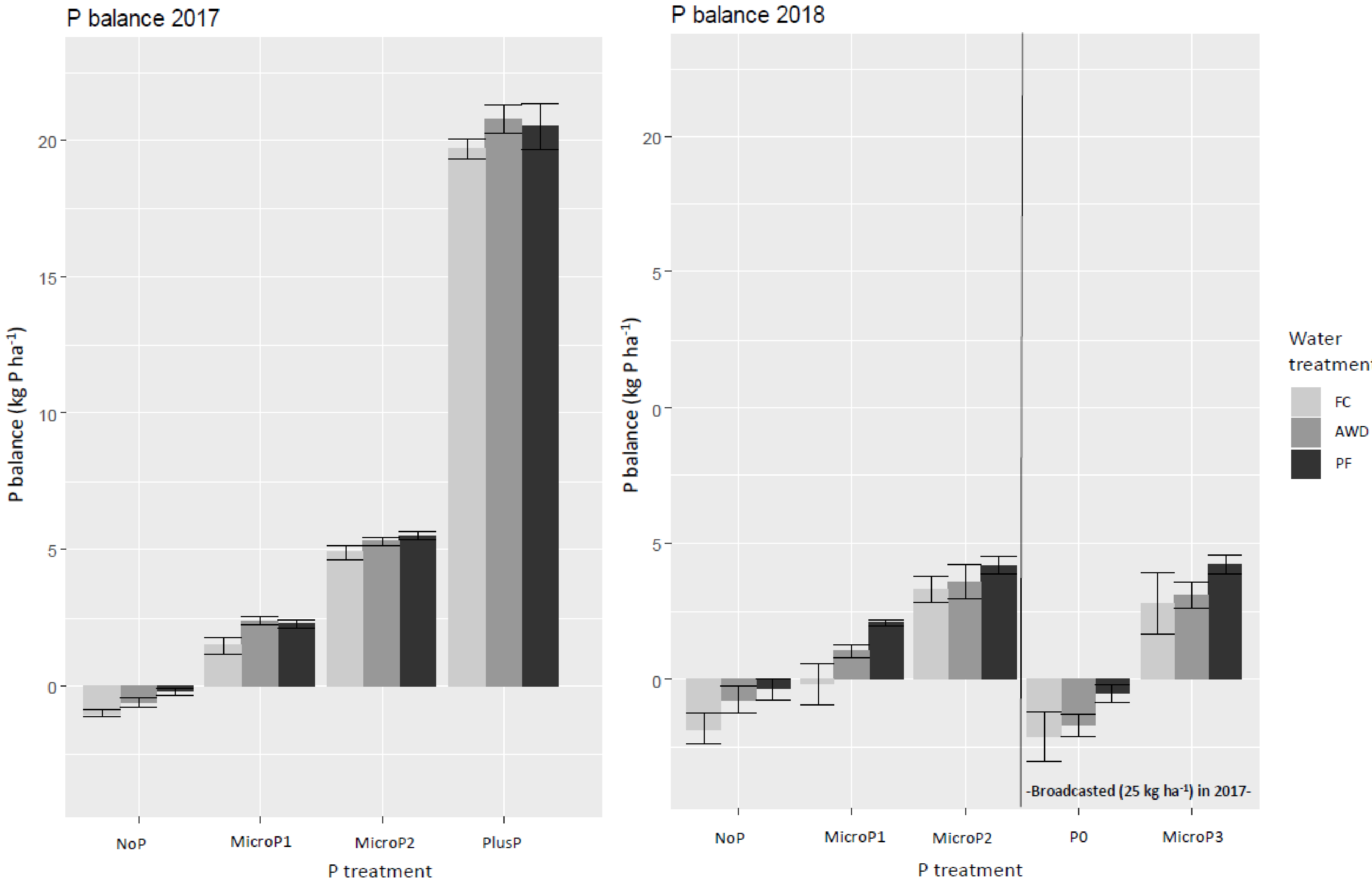


**Figure 2: The seasonal P balance (kg P ha$^{-1}$) for field experiment 1 (left panel) and 2 (right panel). Plots broadcasted (PlusP) in 2017 were split in 2018 and half of these plots were sown as a control without P fertilizer (P0) while the other half was amended with a P placement rate of 6.9 kg P ha$^{-1}$.**

Grain yield (Figure 3) was consistently lower than the potential yield observed in the previous experiment. The yield was significantly affected by both P and water management. There was a positive effect of the residual P, but the effect was only significant without P application (P0>NoP). PF consistently reduced yield compared to AWD and FC, and this negative effect was strongest for MicroP1 confirming results from the year 1 experiment. (Figure 3)

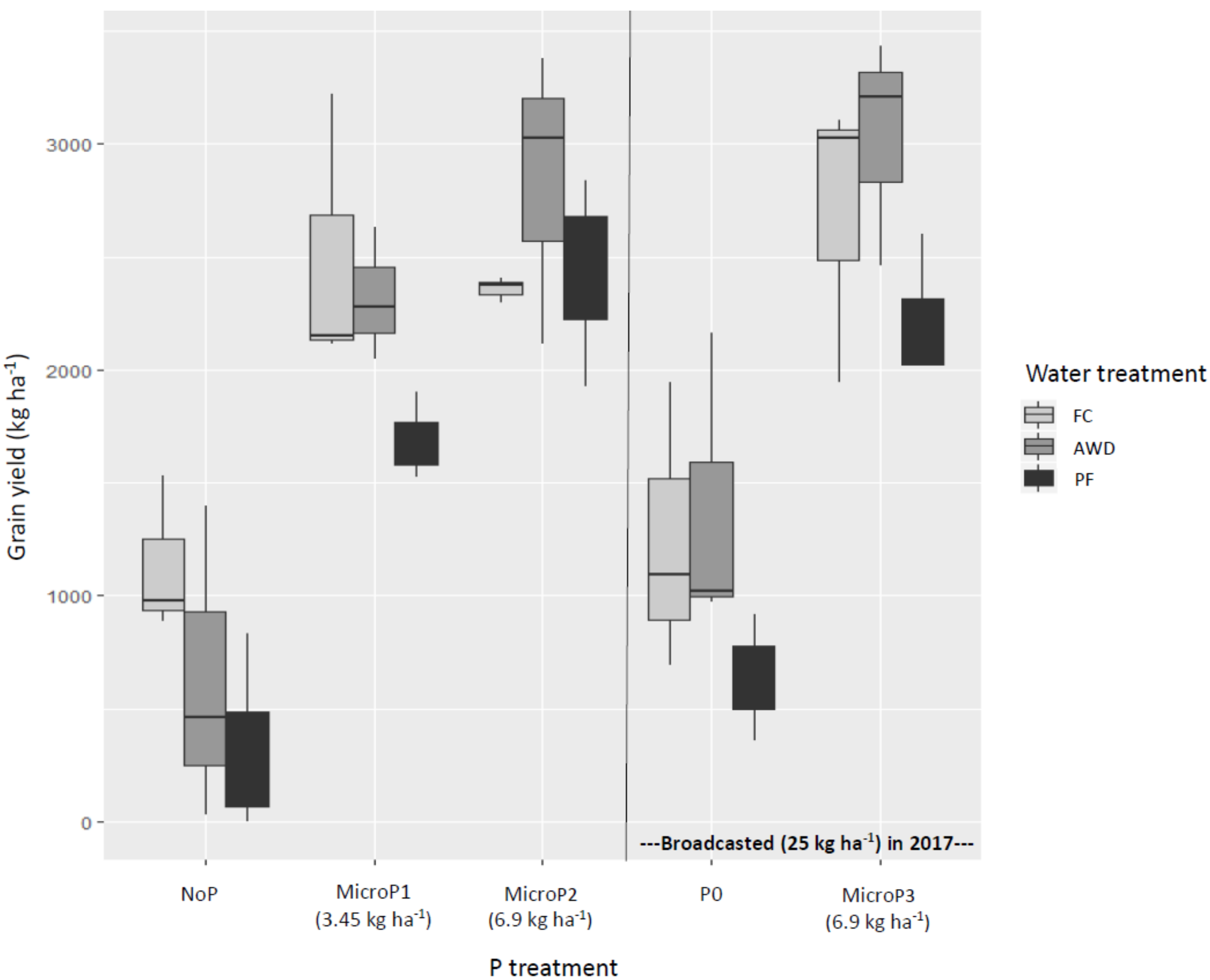


**Figure 3: Grain yield of field grown lowland rice (field experiment 2; 2018) subjected to combinations of water management techniques (field capacity (FC), alternate wetting and drying (AWD), and permanent flooding (PF)) and P management options (No P fertilization (No P), two rates (3.45 and 6.90 kg P ha$^{-1}$) of micro-dose placement (MicroP1 and MicroP2); Plots broadcasted with 25 kg P ha$^{-1}$ in 2017 were split and half of each plot was kept as a control (P0) while the other half was amended with a micro-dose placement of 6.9 kg P ha$^{-1}$ (MicroP3)).**

The $AEP_{grain}$ was largest for MicroP1 and no residual P effect was observed for the highest placement rate (MicroP2=MicroP3) (Table 4). Water treatment did not affect the $AEP_{grain}$ in year 2 in contrasts to that in year 1.

The P balance (Figure 2) was significantly affected by both P and water management. Reduced irrigation consistently decreased the P balance. Without P application (NoP = P0) the P balance was smallest and negative, while the balance was largest and moderately positive (ca. 3.6 kg $ha^{-1}$) for MicroP2 and MicroP3.

***Pot experiment***

*Shoot development*

All P application methods enhanced the plant development at early stage of the crop compared to the control, but an extra benefit from optimal broadcasting became clear around 28 DAS in tiller number. With MicroP, plants developed relatively similar as for SubP, however, the P rate in the latter treatment was much larger (ca. 4 fold). (Figure 4)

For shoot mass, three similar clusters were observed coinciding with the P treatments. MicroP yielded similar biomass than obtained under SubP, despite larger soil P dose in the latter than in the placement, both being significantly larger than NoP and smaller than PlusP. DP significantly reduced biomass under MicroP and PlusP, while it enhanced biomass production under SubP. (Table 5)

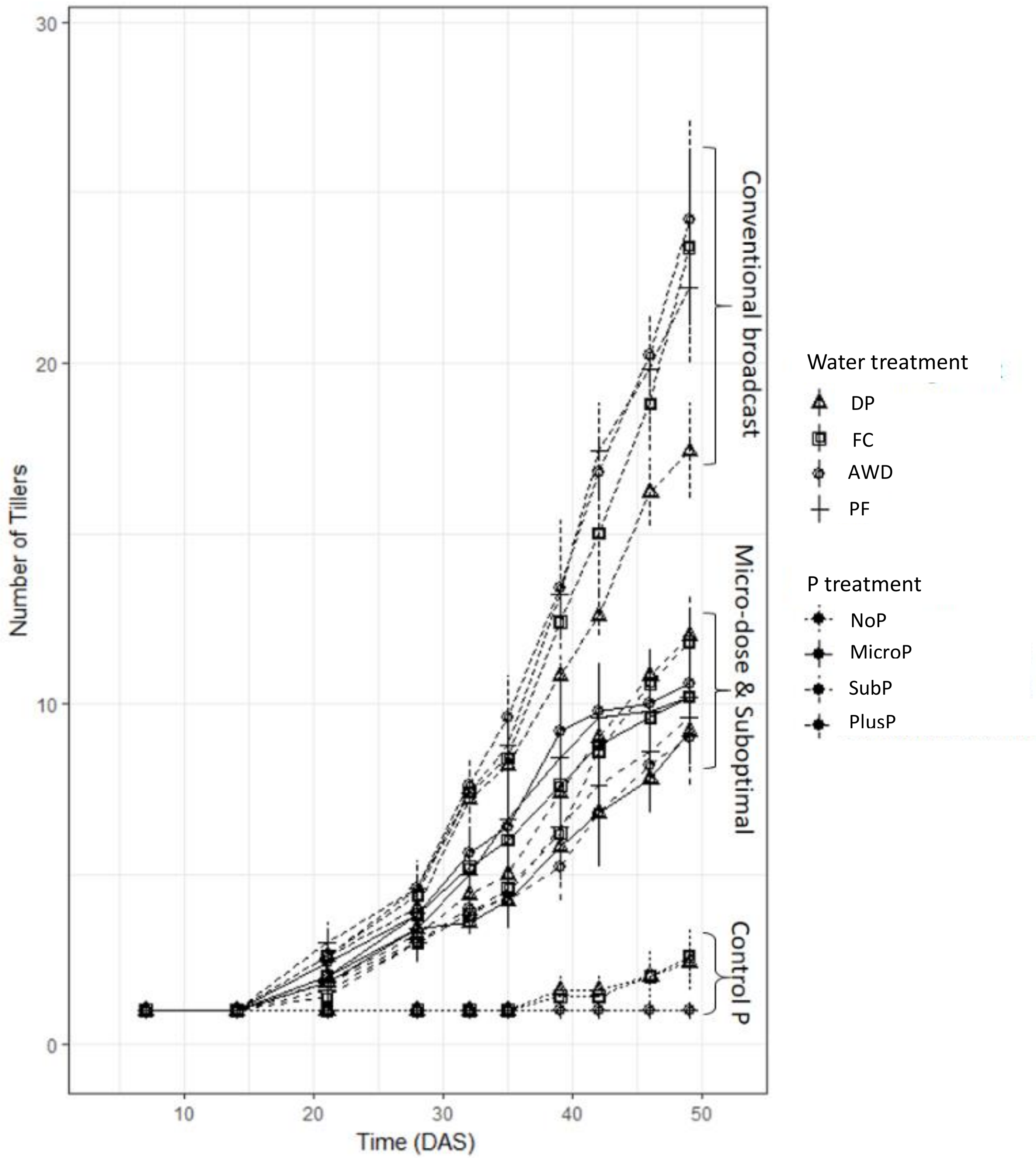


**Figure 4: Plant development (tillers) of lowland rice grown in pots with P deficient lowland soil treated with combinations of water management techniques (Drying periods (DP), field capacity (FC), alternate wetting and drying (AWD), and Permanent Flooding (PF)) and P management options (No P application (NoP), micro-dose placement (MicroP), suboptimal broadcasting (SubP), and conventional broadcasting (PlusP)). For both the number of leaves and tillers at 49 DAS, the interaction between P and water management was significant ($P<0.001$) in the ANOVA**

**Table 5: Results from a large pot trial: shoot and root mass distribution, P uptake efficiency, and nodal root and tip thickness of lowland rice at 49 DAS. Root mass A, B, and C correspond to the absolute root mass grown in the basal segment (0-15 cm), the intermediate segment (15-30 cm), and the deep segment (>30 cm) respectively. Plants were grown in pots subjected to combinations of four water management options (drying periods (DP), field capacity (FC), safe alternate wetting and drying (AWD), and permanent flooding (PF)) and four P management options (No P application (NoP), micro-dose placement (MicroP), suboptimal broadcasting (SubP), and optimal broadcasting (PlusP). Data are presented as means with (standard errors).**

| P | Water | Shoot mass | Root mass A | Root mass B | Root mass C | $Pup_{root}$ | $Pup_{nodal}$ | Nodal thickness |
|---|---|---|---|---|---|---|---|---|
| | | [g] | [g] | [g] | [mg] | [mg $g^{-1}$] | [µg $nodal^{-1}$] | [mm] |
| NoP | DP | 0.95 (0.12) | 0.12 (0.05) | 0.05 (0.02) | 38 (14) | 5.2 (0.6) | 113 (21) | 0.64 (0.18) |
| | FC | 0.85 (0.13) | 0.21 (0.03) | 0.06 (0.01) | 20 (2) | 3.2 (0.2) | 31 (3) | 0.93 (0.01) |
| | AWD | 0.28 (0.02) | 0.07 (0.01) | 0.04 (0.01) | 4 (2) | 1.6 (0.2) | 7 (1) | 0.60 (0.03) |
| | PF | 0.32 (0.05) | 0.12 (0.02) | 0.04 (0.01) | 6 (4) | 1.1 (0.1) | 8 (1) | 0.56 (0.05) |
| MicroP | DP | 6.90 (0.75) | 1.50 (0.28) | 0.64 (0.10) | 440 (160) | 2.5 (0.2) | 68 (5) | 1.29 (0.04) |
| | FC | 8.98 (0.68) | 2.15 (0.15) | 0.71 (0.07) | 284 (66) | 2.2 (0.2) | 44 (4) | 1.30 (0.02) |
| | AWD | 9.97 (1.39) | 3.09 (0.30) | 0.58 (0.05) | 135 (20) | 1.9 (0.3) | 34 (5) | 1.59 (0.10) |
| | PF | 9.57 (1.28) | 2.76 (0.38) | 0.49 (0.16) | 82 (38) | 1.9 (0.2) | 28 (2) | 1.42 (0.05) |
| SubP | DP | 9.34 (0.47) | 1.75 (0.19) | 0.76 (0.08) | 497 (23) | 3.6 (0.4) | 124 (9) | 1.08 (0.09) |
| | FC | 9.22 (0.65) | 2.18 (0.10) | 0.57 (0.08) | 196 (23) | 3.1 (0.2) | 65 (3) | 1.18 (0.12) |
| | AWD | 7.45 (0.73) | 2.27 (0.11) | 0.31 (0.05) | 56 (12) | 2.7 (0.4) | 43 (4) | 1.68 (0.06) |
| | PF | 7.82 (0.47) | 2.15 (0.20) | 0.33 (0.06) | 55 (21) | 2.6 (0.4) | 38 (3) | 1.56 (0.05) |
| PlusP | DP | 15.38 (0.54) | 2.57 (0.18) | 0.78 (0.07) | 366 (83) | 4.6 (0.3) | 140 (7) | 1.22 (0.11) |
| | FC | 20.40 (1.00) | 4.86 (0.28) | 0.98 (0.07) | 220 (29) | 3.8 (0.5) | 104 (11) | 1.48 (0.06) |
| | AWD | 21.98 (1.42) | 4.93 (0.37) | 1.33 (0.18) | 260 (67) | 3.6 (0.3) | 80 (8) | 1.72 (0.04) |
| | PF | 21.67 (0.99) | 4.62 (0.36) | 0.63 (0.10) | 84 (21) | 3.4 (0.1) | 75 (3) | 1.86 (0.05) |
| | Water | ** | *** | ** | *** | *** | *** | *** |
| | P | *** | *** | *** | *** | *** | *** | *** |
| | Water×P | *** | *** | *** | ** | *** | *** | *** |

*Root development, architecture and distribution*

Three similar clusters as for shoot biomass were observed for total root mass, this was significantly reduced with DP only for PlusP (Table S4, **Supplementary Information**). The absolute root biomass found in each layer is presented in Table 5. The root biomass in the deepest layer (> 30cm) strongly increased with reduced water availability (DP > FC > AWD > PF). Under soil submergence there were no significant differences between the P treatments, while deep root biomass under AWD increased for PlusP. Within DP and FC, deep root biomass was decreased without P application.

Figure 5 shows how the relative root biomass increases towards deeper layers when less water is applied. The mass fraction consistently decreased in the basal part while it increased in deepest layers. The response was relatively similar for each P treatment and strongest allocation shifts were observed under DP followed by FC.

Nodal thickness generally increased with P application. Without P application, nodal thickness was largest under FC, while this decreased with decreasing water application (FC and DP) when P was applied. (Table 5)

Lateral root density at the nodal root base was consistently highest under PF, and lowest under DP (Figure S2, **Supplementary Information**). In contrast, the lateral root density for the deepest roots consistently increased under FC and DP. P application did not affect the lateral root density at the root base, and the deep roots, but an inconsistent P × water interaction was observed for the intermediate roots. (Figure S2)

Lateral root thickness at the root base generally increased with decreased water application (DP and FC) but a difference between AWD and FC was only observed for NoP and MicroP. Lateral root thickness was significantly largest under DP with MicroP. The lateral root thickness in the intermediate and deep roots increased with decreased water application and this lateral root thickness similarly increased with any method of P application compared to the control. (Figure S2)

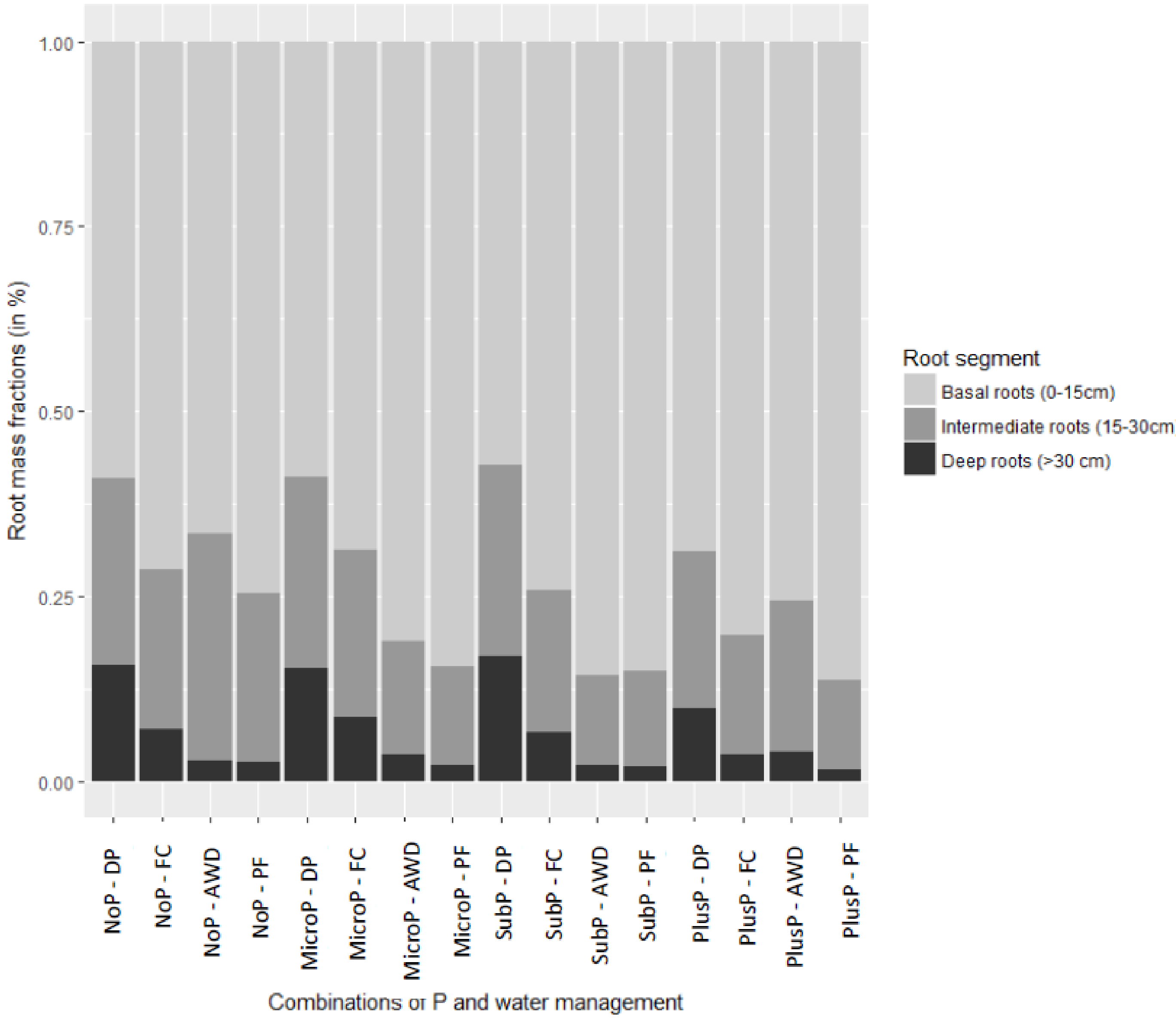


**Figure 5: The root mass distribution of rice in the soil. Fractions of the total root mass are presented for each segment of soil depth (basal roots (0-15 cm), intermediate roots (15-30 cm), deep roots (>30 cm)). Plants were grown in pots with P deficient lowland soil subjected to combinations of water management techniques (Drying periods (DP), field capacity (FC), alternate wetting and drying (AWD), and soil submergence (PF)) and P management options (No P application (NoP), micro-dose placement (MicroP), suboptimal broadcasting (SubP), and conventional broadcasting (PlusP)).**

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Secondary branching degree at the nodal root base and at the intermediate segment generally increased with decreasing water application, but this trend was not observed without P application. For the deepest roots, this secondary branching degree showed a similar increasing trend with decreased water application. Under DP and FC, secondary branching degree at the nodal root base decreased under MicroP compared to SubP and PlusP. In contrast, this secondary branching degree at the deepest roots increased under MicroP compared to SubP under FC. (Figure S2)

*Soil P concentrations*

The P concentration in the soil solution ranged <0.03 (detection limit) – 0.39 mg P $L^{-1}$ and was significantly affected by the P treatments, not by water management. The SubP and PlusP consistently and significantly increased the P concentrations in the soil solution, while corresponding concentrations for the control and the P placement were both below detection limit (data not shown).

*P uptake,  acquisition efficiency, and fertilizer use efficiency*

Total P uptake at 49 DAS can be grouped into three clusters ( NoP < MicroP ~ SubP < PlusP), and reduced water use under SubP significantly increased total P uptake (DP>FC>AWD>PF), while DP reduced P uptake under PlusP. (Table S4, **Supplementary Information**)

The $Pup_{root}$ was consistently smaller for MicroP compared to PlusP, with the SubP treatment in between. An increasing trend of $Pup_{root}$ was observed when less water was applied, but differences between AWD and PF were never significant. The difference between FC and AWD (& PF) was only significant without P application (Table 5).

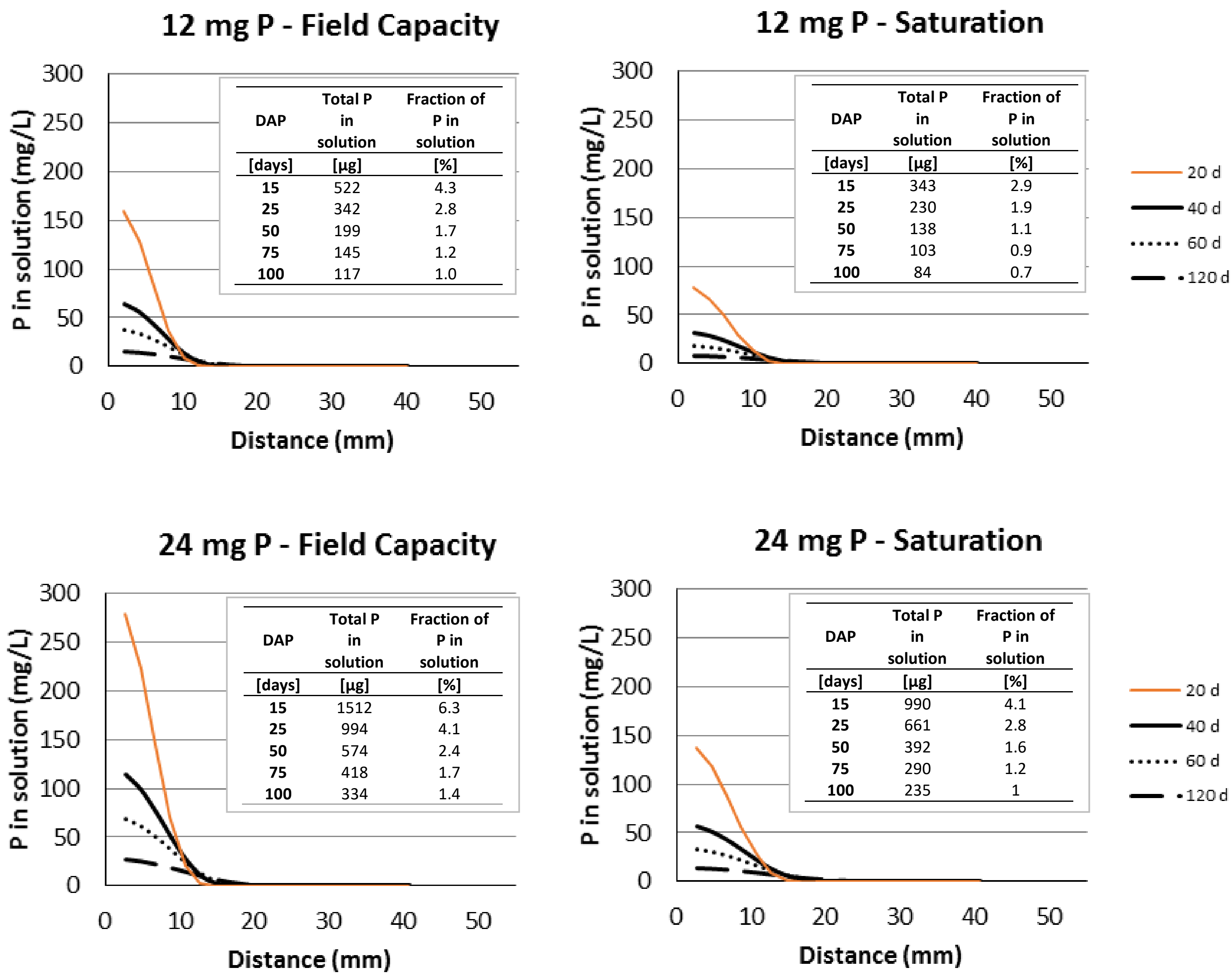
The P uptake in the shoot per unit nodal roots ($Pup_{nodal}$) increased at decreasing water supply and was larger under FC than at higher water supply, a trend repeating the field observation. (Table 5)

The $AEP_{49DAS}$ was consistently largest for MicroP, exceeding the other treatments with a factor of ca. 4. For MicroP, the $AEP_{49DAS}$ decreased by DP, while water management had no such significant effects under SubP and PlusP. With reduced irrigation (i.e. FC and DP), the $AEP_{49DAS}$ was larger under SubP compared to PlusP. (Table S4, **Supplementary Information**)

***Modeling P diffusion, adsorption and plant availability of placed P under different water regimes***

The modelled diffusion from the placed P fertilizer over time is given in Figure 6. Increased water content of the soil, increases the P diffusion, thereby leading to smaller P concentrations in solution because more sorption sites are reached and, consequently, contributing to a larger amount of P that is finally adsorbed (Figure 6).

With larger placements rates, smaller fractions of P (in %) will be adsorbed because a larger proportion of the binding sites are saturated. Soil saturation at the lowest dose of P yields highest immobilization of added P (Figure 6).




**12 mg P - Field Capacity**

| DAP [days] | Total P in solution [µg] | Fraction of P in solution [%] |
|---|---|---|
| **15** | 522 | 4.3 |
| **25** | 342 | 2.8 |
| **50** | 199 | 1.7 |
| **75** | 145 | 1.2 |
| **100** | 117 | 1.0 |

**12 mg P - Saturation**

| DAP [days] | Total P in solution [µg] | Fraction of P in solution [%] |
|---|---|---|
| **15** | 343 | 2.9 |
| **25** | 230 | 1.9 |
| **50** | 138 | 1.1 |
| **75** | 103 | 0.9 |
| **100** | 84 | 0.7 |

**24 mg P - Field Capacity**

| DAP [days] | Total P in solution [µg] | Fraction of P in solution [%] |
|---|---|---|
| **15** | 1512 | 6.3 |
| **25** | 994 | 4.1 |
| **50** | 574 | 2.4 |
| **75** | 418 | 1.7 |
| **100** | 334 | 1.4 |

**24 mg P - Saturation**

| DAP [days] | Total P in solution [µg] | Fraction of P in solution [%] |
|---|---|---|
| **15** | 990 | 4.1 |
| **25** | 661 | 2.8 |
| **50** | 392 | 1.6 |
| **75** | 290 | 1.2 |
| **100** | 235 | 1 |

**Figure 6: The modeled P concentration in soil solution (mg $L^{-1}$) over the distance from the application point (mm) at 20, 40, 60, and 120 days after placement (DAP). Calculations were done for two placement rates (12 vs. 24 mg P) and two water regimes (field capacity (pF = 2) and soil submergence (pF = 0)). Modeled total available P in solution (µg) integrated over the distance to the application point at 15, 25, 50, 75, and 100 days after placement (DAP) and the adsorbed fraction from the placed P (%) are presented in the tables. These variables can be used as estimators for the plant available P from P placements under contrasting water management.**

## Discussion

### ***Combined effects of phosphorus and water supply on rice development, P uptake, and grain yield***

This study confirmed that P management has a major effect on rice establishment and grain yield in P deficient lowlands. While in our study effects of water management were subordinate to P effects, interactions between P and water management should definitely be considered. Contrasting responses to reduced irrigation (i.e. field capacity and alternate wetting and drying) versus permanently flooded conditions on rice yields have previously been reported in literature (Yang *et al.*, 2007; Chu *et al.*, 2015; Dodd *et al.*, 2015), but it remains important to understand the mechanisms explaining why yields and yield attributing characteristics of FC, AWD, and PF vary under different conditions.

In this study, drying periods reduced growth when P was sufficiently available, while it enhanced growth under P limitations. In addition, a beneficial effect of FC (compared to flooding) was generally observed when P limited growth, while no such water effect occurred when larger doses of P were applied. These observations are in contrast with the general assumption that P is released under anaerobic conditions (Kirk et al., 1990). After an initial P release upon flooding, P availability may indeed drop again in P deficient soils due to resorption of P on clays/metal oxyhydroxydes or due to precipitation of Fe(II)-P compounds (Amery and Smolders, 2012; Smolders et al., 2017). Enhanced growth and yield in response to reduced water application under P limitations, would follow from multiple co-occurring processes. Firstly, the presence of toxic compounds ($Fe^{2+}$, $H_2S$) in the soil under anaerobic conditions can inhibit root respiration and therefore affect growth (Ramasamy et al., 1997). Due to the interaction of P and Fe in soils, it is suggested that effects of Fe toxicity would be more severe when P is deficient as the alleviating capacity of roots is reduced when P is limiting (Becker and Asch, 2005; Das et al., 2017; Sahrawat, 2005). Secondly, beneficial interactions with mycorrhizae would be inhibited under soil submergence, but not under field capacity (Chen et al., 2017). Thirdly, rooting patterns (in terms of structure and distribution) can be affected under different water treatments and this would influence growth and nutrient acquisition (De Bauw et al., 2019; Yang et al., 2012; Zhang et al., 2009), as assessed in the following section. Finally, as shown by the diffusion model used in this study (Figure 6), reduced P diffusion and reduced P sorption of small localized P placements additionally enhance the P uptake and rice growth under field capacity in comparison with alternate wetting and drying or soil submergence.

Micro-dose placement enhanced rice development and grain yield and there were no differences between rates of 3.45 and 6.90 kg P $ha^{-1}$ under field capacity, which was also observed by Vandamme *et al.* (2018). The likelihood for P precipitation increases at a higher application rate and could explain why there are no growth differences between the different rates, while P is still deficient (Sánchez, 2019). Under saturation, it was shown that enhanced P diffusion increases P sorption, which thus reduces the final P availability of a P micro-dose placement for rice production.

P application strongly reduces the time to maturity, which was also observed for micro-dose placements by Vandamme *et al.* (2018). Placing such small doses of P fertilizers can thus reduce the length of the cropping season which not only reduces risk of pests and diseases, but it can also be used as a technique to escape terminal droughts (Fukai et al., 1998; Price et al., 2002).

### *Root development, root architecture and relations with stress resilience*

The promotion of root development in response to various soil conditions can be considered as a type of phenotypic plasticity, in which a plant alters its phenotype in response to changing environmental conditions (Gowda et al., 2011; Huang, 2006; Kano et al., 2011). Previously, Barison and Uphoff (2011) have shown a superior rice root functioning and an enhanced nutrient uptake under reduced irrigation. Under P deficiency, beneficial effects of root modifications due to reduced water availability were observed for rice by De Bauw *et al.* (2019) and it was hypothesized that such plastic root traits could successfully be exploited to enhance P uptake by altering soil and water management rather than targeting such plastic root traits in breeding only.

This work clearly confirms that the root development of lowland rice can indeed be manipulated by altering water management through modifying root architecture and biomass allocation and, to a minor extent, also by P management by enhancing root biomass production. For lowland rice, typically around 60 to 80% of the root biomass is located in the upper 15 cm of the soil, which entails a strong drought sensitivity (Kano-Nakata et al., 2013). Rice roots under flooding and AWD have previously been observed to reach depths of 49 and 78 cm, respectively, but only 7 to 15 % of the roots exist at depths below 30 cm (Kato et al., 2013; Wade et al., 1998; Yoshida, 1981). Reduced irrigation (DP and FC) strongly increased the fractions of root biomass (in %) in the deepest layer. While the fractions of root biomass in each layer were relatively similar for each P treatment, the differences in absolute root mass in each layer were huge, depending on P application. Root mass in deep layers can thus be enhanced by P application, but to what extent the maximum depth, the deep root fraction, or the absolute biomass in deep layers is important for drought avoidance has to be further examined and this probably depends on the root morphology and the distribution and fluctuations of the available water (Gowda et al., 2011).

The general structure of the rice root system is illustrated in Figure S2, which was also described by Kono *et al.* (1972); Yamauchi *et al.* (1987); and Nestler *et al.* (2016). The nodal root base is characterized by highly dense S-type roots (i.e. thin unbranched roots), and lateral root density gradually reduces when going to deeper layers. With increasing depth, thicker laterals with higher order branches (M- and L-type roots) are formed. It is now shown that lateral root density and secondary branching in the deeper layers increase with reduced water application, even when there is no water deficit. Several studies have demonstrated increased root length density at depth to be associated with greater water extraction from deep soil (Henry, 2013; Lilley and Fukai, 1994; Okada et al., 2002; Wade et al., 1999) and the stronger developed vascular system in deep M- and L-type laterals highlight their important role for drought tolerance (Bañoc et al., 2000; Kono et al., 1972). A stimulation of deep rooting and increased root density at deeper layers by reduced irrigation, while not imposing a deficit, thus contributes to drought avoidance and enhanced resilience under potential drought events during later stages of the growth cycle (Fukai and Cooper, 1995; Gowda et al., 2011).

In this study, lateral root density at the nodal base (S-type roots) decreased with reduced water application, while such a response was not observed by De Bauw *et al.* (2019). However, such a reduced basal lateral root density was previously observed to increase the drought tolerance in maize (Zhan et al., 2015), and for rice this was observed in response to aerobic conditions by Kato *et al.* (2013). Interestingly, the observed responses of the basal lateral root density to water management are much smaller than the genotypic variations observed by De Bauw *et al.* (2019), and when this basal lateral density is desired to be modified (in order to enhance drought tolerance or P uptake efficiency), thoughtful genotype selection would still be more effective than altering water management only.

P uptake efficiency consistently increased with reduced irrigation, especially when P was limiting. As P availability in the rhizosphere solution was not altered by the water treatments and P diffusion generally reduces with reduced water availability (Drew and Nye, 1970), it is indeed suggested that root modifications (i.e. reduced nodal thickness and increased secondary root branching) must be responsible for such an enhanced P uptake efficiency under reduced water application, as also observed by De Bauw *et al.* (2019). Such beneficial effects of root responses would be strongest when a suboptimal P concentration is more homogeneously distributed through the soil, but when P is placed in less deficient soils, both processes (diffusion & sorption, and root modifications) will contribute to enhanced P uptake under field capacity.

Contrary to our expectations, we did not observe strong effects of the type of P application on the root morphology of rice (i.e. root proliferation or cluster roots). Dense rooting “patches” in response to localized P application were however previously observed by He *et al.* (2003); and Hodge (2004) and it should be further examined under which conditions such micro-dose placements affect the root architecture of rice.

***Long term assessment and recommendations of combined P and water management options in P deficient lowlands***

Our results indicate the opportunity in strategic combinations of P and water management, depending on site characteristics and resources of the farmer. Obviously, broadcasting a large amount of P fertilizer remains advisable when P is strongly deficient, but in reality resource limitations often preclude such large P applications (Nziguheba et al., 2016). Yield gaps between conventional broadcasts and micro-dose placements are however expected to become smaller when P stress is less severe. The agronomic fertilizer use efficiencies obtained with micro-dosing were substantially larger than those under conventional broadcasting and much larger than commonly observed values below 120 $kg_{grain}$ $kg^{-1}$ P for rice (Dobermann et al., 1998; Fageria et al., 2011). Micro-dose placements therefore lead to a much better return on investment, especially when applying small rates. Given the prevalence of P deficiency in many lowlands of SSA (Margenot et al., 2016), placing micro-doses of P fertilizer may thus be an economically viable strategy for resource-poor farmers to increase rice yields (Vandamme et al., 2018).

Importantly, small P placement rates (i.e. 3.45 kg $ha^{-1}$) resulted in a slightly positive P-balance close to zero, and care should be taken to not further deplete the soil P reserves when this balance of the soil turns negative. In contrast, a placement rate of 6.9 kg $ha^{-1}$ resulted in a fairly positive balance, which highlights the potential of this method for resource poor farmers to reverse the declining P-trends in deficient soils. Additionally, placements can reduce the risk of runoff and nutrient losses (Kapoor et al., 2008), especially under flooding (Zhan et al., 2014). Therefore, we suggest that P micro-dose placements combined with additive, supportive broadcasts adjusted to the requirements can form a sustainable method to maintain the P balance in equilibrium (after overcoming P deficiency), while enhancing fertilizer efficiency and recovery rates. The application of micro-dose placements generally requires more labor when manually done (Aune et al., 2007), but opportunities for further mechanization towards precision agriculture do exist (Bautista *et al.* 2001).

In lowlands with P limitations, maintaining the field at field capacity benefits P uptake and yield versus permanent flooding. Negative effects of field capacity versus permanent flooding on P uptake were only observed in soils with a coarse texture (Kato et al., 2016; Seng et al., 1998) and attention should thus be paid in such situations. Without P application or when placing P at small rates, farmers should reduce irrigation to increase outputs in P-deficient lowlands, while the choice of water management would become less important when applying larger rates of P fertilizer.

Besides enhancing root morphology and root resilience, reduced irrigation implies a more sustainable and efficient water use (Bouman et al., 2005; de Vries et al., 2010; Matsuo and Mochizuki, 2009; Shaibu et al., 2015). While keeping the field at field capacity weed management requires more attention (Akobundu 1987; Zhao *et al.* 2007; de Vries *et al.* 2010). With this perspective, further research should examine to what extent normal AWD (or safe AWD under fast drying conditions) can also improve root functioning (Kano-Nakata et al., 2013; Kato et al., 2013), P uptake, and yield under P limitations (as observed for field capacity compared to soil submergence), while maintaining the advantage of suppressing weeds.

## **Conclusions**

We demonstrate that root development of rice largely responds to water management. Under P deficiency and at small placed P doses, reduced irrigation enhances rice development, P uptake, and yield. We argue that P micro-dose placements in combination with a moderate water supply could be an efficient entry point to intensify rice production and to reverse the declining trend in P reserves in deficient lowlands.

## Conflict of interest

The authors have no conflict of interest.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