

1 **Micro-dose Placement of Phosphorus Induces Deep Rooting of Upland Rice**

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20

21 **Abstract**

22 *Purpose*

23 Upland rice production is often constrained by phosphorus deficiency (P) and drought events. Methods are
24 needed to maximize P use efficiency, while promoting deep root development to mitigate drought. This
25 study evaluates micro-dose P placement as a technique to enhance drought resilience of upland rice, thereby
26 hypothesizing that P placement enhances deep root development, stimulated by the local P supply in the
27 planting hole, compared to broadcast P.

28 *Methods*

29 Two pot experiments were conducted using P deficient upland soil in Tanzania (Expt.1) and Madagascar
30 (Expt.2), with factorial combinations of P doses (control and two P levels), application method (placement
31 versus broadcast), rice varieties (DJ123 & NERICA4) and water regimes (field capacity and drying
32 periods).

33 *Results*

34 Micro-dose P placement strongly boosted the establishment of upland rice and enhanced P recovery rates
35 (4- to 5-fold) and fertilizer use efficiency (9- to 14-fold) compared to broadcast P. Micro-dose P placements
36 significantly enhanced the fraction of roots found at largest depth (>30 cm, Expt. 1; >15 cm, Expt. 2) by
37 22- to 33%. Surprisingly, shoot P concentrations were markedly lower under P placement than under
38 broadcast at equivalent P doses or equivalent biomass, indicating a Piper-Steenbjerg effect.

39 *Conclusion*

40 This study is first in showing the enhanced deep rooting after P placement, and suggests replication at field
41 scale where subsurface moisture may yield stronger benefits than in pots. The depleted shoot P
42 concentrations induced by vigorous plant establishment under P placement may, however, counteract
43 benefits at later growth stages and need further attention.

44 Introduction

45 One third of the rice (*Oryza* spp.) area in sub Saharan Africa (SSA) is cultivated by smallholder farmers in
46 low-input, rainfed (non-irrigated) upland systems. With a total production of only 4 M t upland rice
47 compared to the 30 M t of total rice production per year in SSA (Diagne et al. 2013b; FAOSTAT 2018),
48 upland rice is often cultivated in marginal environments with suboptimal management practices (Tanaka et
49 al. 2017; Niang et al. 2017; Senthilkumar et al. 2018). Exploitable yield gaps of rice are largest in upland
50 systems (Kwesiga et al. 2020), where drought events and phosphorus (P) deficiency form two major
51 challenges that are often co-occurring (Diagne et al. 2013; Mueller et al. 2012). There is a strong need for
52 sustainable intensification of the existing rice growing areas in SSA by a more efficient use of the available
53 resources such as water and nutrients (Saito et al. 2013; van Oort et al. 2015; Zenna et al. 2017).

54 Current low P fertilizer recovery rates and persistently low purchasing power of many smallholder rice
55 farmers preclude a drastic improvement of P use in rice-based systems. A more efficient P application
56 method has been developed for several crops, by localizing the P dose (Nziguheba et al. 2016). A micro-
57 dose P placement implies a localized application of a small P dose to a small surface or sub-surface area,
58 often combined with seeds into the planting hole (ICRISAT 2009; Nkebiwe et al. 2016; Vandamme et al.
59 2018). The P is rather immobile in soils and P sorption is reduced under small localized P placements due
60 to the local saturation of the binding sites (Fe and Al oxyhydroxides). Hence, such localized micro-dose P
61 applications form an option towards sustainable P management (Malhi et al. 2001; Margenot et al. 2016;
62 Nziguheba et al. 2016; Oo et al. 2020). This method of combining fertilizers with seeds in the planting hole
63 is also referred to as pop-up fertilization (Olsson et al. 2018).

64 The technique of micro-dose P placement has been successfully tested and adopted for several cereals such
65 as maize, millet, and sorghum (van der Eijk et al. 2006; Aune and Bationo 2008; Bagayoko et al. 2011;
66 Camara et al. 2013; Biielders and Gérard 2015; Ibrahim et al. 2016a). However, micro-dose P placement in
67 direct seeded rice systems has only been studied and evaluated in a few cases in Tanzania and Benin (Bayan
68 and Lourduraj, 2000; De Bauw et al., 2019; Garrity et al., 1990; Vandamme et al., 2018) and, to our
69 knowledge, it is only adopted in upland rice growing areas of Madagascar (Raboin et al. 2014;
70 Andriamananjara et al. 2018). Phosphorus micro-dose placement strongly benefits shoot establishment and
71 grain yield in direct seeded rice systems (De Bauw et al. 2019; Vandamme et al. 2018), following a high
72 fertilizer efficiency and P recovery from the soil. In theory, P placements provide the P initially needed by
73 the seedlings (He et al. 2003; Sanusan et al. 2009), resulting in an increased early root growth, which gives
74 the plant a competitive advantage early on in the growth period. Through this early root development, it
75 was argued that plants can take up more of the water and other nutrients that are present in the soil (Ibrahim
76 et al. 2015a; Ibrahim et al. 2015b).

77 As the intensity and frequency of dry spells are expected to increase in many regions of SSA (Cook et al.
78 2014; Zhao et al. 2015), multiple studies have highlighted the importance of deep roots for drought
79 resistance and drought avoidance in future crops (Uga et al. 2011; Maeght et al. 2013; Lou et al. 2015).
80 Plants with deep roots are able to access water from deeper soil layers, which enables the plants to tolerate
81 droughts by drought avoidance (Fukai and Cooper 1995; Uga et al. 2013). Therefore, modifying the root
82 distribution of rice from shallow to deep rooting by genetic selection is a promising strategy for drought-
83 resistance breeding (Gowda et al. 2011; Uga et al. 2011). In addition, soil management practices can also
84 promote deeper rooting of crops in acid upland soils (Garrity et al. 1990; Haefele et al. 2016). To this end,
85 effects of P banding on deep root development have yet been observed in multiple crops (Singh et al. 2005;
86 Nkebiwe et al. 2016; Hansel et al. 2017), but implications of micro-dose P placements on root development
87 of upland rice were never assessed. In this regard, it has been hypothesized that an increase in root growth
88 after P placements can result in enhanced drought resistance (ICRISAT 2015). However, this was never
89 confirmed before. Additionally, it is also unclear how such P placements can influence water acquisition
90 and how this affects plant performance under drought.

91 This study was set up to evaluate micro-dose P placements as a method to counteract drought effects in rice
92 systems, thereby hypothesizing that P placement enhances deeper rooting stimulated by the local P supply
93 in the planting hole, compared to broadcast P. Pot experiments were set up by using P deficient upland soil
94 in large pots, and including factorial combinations of P doses, P application method (placement versus
95 broadcast), rice varieties, and water regimes (field capacity and dry periods). Shoot growth, root
96 distribution, fertilizer efficiency, and P content of the rice shoots was determined.

97

98 **Materials & Methods**

99

100 Two pot experiments were conducted in Tanzania and Madagascar, using P deficient upland soil (Table 1),
101 in a full factorial design of five P treatments (a zero P control (NoP), two rates of micro-dose P placement
102 (Micro1 & Micro2), a small dose of P broadcasting (SubP), and a high dose of P broadcasting (PlusP)), two
103 contrasting water regimes (permanent Field Capacity vs. Drying Periods) and two upland rice varieties
104 (DJ123 & NERICA4). A summary of the similarities and differences of the imposed treatments in both
105 experiments is presented in Table 1.

106 **Pot Experiment 1**

107 *Soil preparation, P treatments, and pot filling*

108 The pot trial was conducted in a greenhouse located at Sokoine University of Agriculture in Morogoro
109 (6°50'53.9"S, 37°39'31.3"E; Tanzania). Average daily minimum and maximum temperatures during the
110 experiment were 21.9 and 33.4 °C, respectively. A P-deficient soil (0.035 mg P L⁻¹ in soil solution,
111 measured by Inductively Coupled Plasma Mass Spectrometry (ICP-MS, Agilent7700X) after a water
112 extraction; 1:10 solid:liquid ratio; 24 hours equilibration; 30 minutes centrifugation at 2000 g; and 0.45 µm
113 membrane filtration) was collected from an upland rice field in Matombo (Tanzania), on which P deficiency
114 was previously ascertained. Characteristics of the soil are presented in Table 2. After sampling the P
115 deficient rice field (0–30 cm), the bulk soil was shade dried, crushed to an aggregate size of 4 mm, and
116 amended with salts of NH₄NO₃, KCl, CaCl₂, MgSO₄, ZnSO₄, CuSO₄, H₃BO₃ and Na₂MoO₄ at rates of 37
117 mg N kg⁻¹, 95 mg K kg⁻¹, 16 mg Mg kg⁻¹, 21 mg S kg⁻¹, 3.5 mg Zn kg⁻¹, 0.04 mg B kg⁻¹, 0.08 mg Cu kg⁻¹,
118 and 0.03 mg Mo kg⁻¹ soil, to avoid any nutrient deficiency other than P.

119 As P generally accumulates in the topsoil, no P was initially added to the bulk soil in order to mimic a P
120 deficient subsoil at the bottom layer of the pots across treatments. Large pots of 10.5 L (height: 55 cm,
121 diameter: 16 cm) were first filled with 7.3 kg of the P deficient soil. To avoid downwards P transport by
122 wetting the whole pot at once, this bottom layer of mimicked subsoil was first watered to field capacity
123 (38% w/w, based on the water retention curve of this soil) before adding the treated top layers of soil. To
124 this end, the remaining of the bulk soil was subjected to different P amendments to obtain five different P
125 treatments.

126 The top soil layer of 16 pots was amended with a large amount of ground Triple Super Phosphate (TSP)
127 (70.8 mg P kg⁻¹_{topsoil} or 354 mg P per pot) up to a P concentration of 0.5 mg P L⁻¹ in soil solution (PlusP),
128 which was based on a previously determined P adsorption isotherm. Briefly, the soil was dried and sieved.
129 Replicate samples of 3 g were suspended in 30 mL water and amended with KH₂PO₄ at various rates
130 between 0–60 mg L⁻¹. The soils were equilibrated with an end-over-end shaker for 24 h followed by
131 centrifugation and filtration (0.45 µm) and analyzed for P by ICP-MS. The top soil layer of 16 other pots
132 was amended with a lower amount of ground TSP (25.0 mg P kg⁻¹_{topsoil} or 125 mg P per pot) up to a P
133 concentration of 0.1 mg P L⁻¹ in soil solution (SubP). The top soil layer of the remaining pots (i.e. 48 pots)
134 was not amended with TSP as this upper soil layer was later used for a control without P amendments and
135 two rates of micro-dose placements. Salt of CaCl₂ was broadcasted to equalize the amended Ca in all
136 treatments. Pots were filled with 5 kg of treated topsoil, affixed on top of each subsoil. The thickness of the
137 layer of the subsoil was 30 cm and that of the topsoil was 20 cm. Pots were then irrigated to bring the whole
138 pot to field capacity (38% w/w). For the two rates of micro-dose P placement (i.e. Micro1 & Micro2), 0.06
139 g and 0.12 g of recompressed TSP powder were locally applied together with the seeds in the planting hole
140 of the non-amended topsoil. These micro-dose placement rates correspond with amendments of 12 mg P

141 pot⁻¹ and 24 mg P pot⁻¹, respectively, and they are equivalent to an application rate of 3 and 6 kg P ha⁻¹,
142 when plants are conventionally spaced at 20 x 20 cm.

143

144 *Sowing, maintenance, and water treatments*

145 One pre-germinated seed of each variety was sown into the pots (1 cm depth) at the center of the surface.
146 The two upland varieties used in the trial were NERICA4 and DJ123, because of their contrasting
147 performance under P deficiency. NERICA4 is an upland rice variety developed by the Africa Rice Center
148 (AfricaRice) using interspecific crosses between *Oryza sativa* (Asian rice) and *Oryza glaberrima* (African
149 rice). NERICA4 is known for its robust performance under droughts, but it is relatively susceptible to low
150 P availability (De Bauw et al., 2019b, 2019a; Koide et al., 2013). The root system of the latter variety was
151 previously characterized as having relatively limited number of nodal roots, able to penetrate to deep layers
152 (De Bauw et al. 2020). DJ123 is an upland rice variety from the *aus* group, originating from Bangladesh.
153 This variety was previously found to perform well under P deficient soils and it was suggested to have a
154 high phosphorus acquisition efficiency (PAE) (Saito et al. 2015; Nestler and Wissuwa 2016; Vandamme et
155 al. 2016b; Mori et al. 2016), in this work defined and assessed by the amount of P taken up per unit of root
156 mass. DJ123 was previously observed to have a large number of nodal roots and longer root hairs (Nestler
157 et al. 2016).

158 Two top dressings of NH₄NO₃ (in solution) were applied at a rate of 349 mg N per pot at 21 and 34 days
159 after sowing (DAS). An additional top dressing of ZnSO₄, ZnCl₂, KCl, and MgSO₄ were added to each pot
160 at rates of 0.27 g Zn, 0.58 g K, 0.16 g S, and 0.11 g Mg at 21 and 34 DAS.

161 Pots were daily irrigated to field capacity (based on pot weight, 38% w/w) until 25 DAS, and two
162 contrasting water treatments were then initiated and maintained until the end of the trial. Half of the pots
163 were daily irrigated to field capacity (FC), while the other half was subjected to drying periods (DP) to
164 mimic drying cycles during erratic rainfall. To do so, pots were watered up to field capacity after a period
165 of ca. six days of drying, and drying spells were repeated 5-fold until harvest. Each treatment combination
166 was replicated four times.

167 Plant development was monitored by measuring plant height and counting tillers and leaves twice a week.
168 At 52 DAS, shoots were cut, oven dried (60 °C), weighed, and manually ground by mortar. The P
169 concentrations in the shoot tissues were then determined by Inductively Coupled Plasma Optical Emission
170 Spectrometry analysis (Thermo Scientific iCAP 7000 series) after digestion in hot (120°C) HNO₃ and total
171 P content of the shoot was calculated. Immediately after removing the shoot, the soil cylinder was carefully
172 taken out of the pot and precisely cut into three segments. One part comprised a segment (A) from 0 to 15

173 cm depth which included the '*shallow roots*'; another segment (B) comprised soil from 15 to 30 cm depth
174 including the '*intermediate roots*'; and the last segment incorporated the '*deep roots*' below a depth of 30
175 cm. The latter segment (C) was defined according to most rice studies, where deep roots are defined as
176 roots below 30 cm (Kato et al. 2006, 2013; Gowda et al. 2011). For each soil segment, roots were carefully
177 washed out by gently shaking the soil segments on a 2 mm net in water. After removing the soil from the
178 roots, the roots from each segment were oven dried (60°C) and weighed to determine root distribution and
179 biomass allocation.

180

181 Pot Experiment 2

182 A second pot trial was conducted in a greenhouse located at the Laboratoire des Radio Isotopes
183 (19°12'37''S; 47°29'13''E; Madagascar). Average daily minimum and maximum temperatures during the
184 experiment were 15 and 26 °C, respectively. A P-deficient soil (0.006 mg P L⁻¹ in soil solution, measured
185 by ICP-MS after a 1 mM CaCl₂ extraction; 1:10 solid:liquid ratio; 5 days equilibration; 30 minutes
186 centrifugation at 2000 g; and 0.45 µm membrane filtration) was collected from the top 20 cm of an upland
187 rice field in Behenji (Madagascar). Characteristics of the soil are presented in Table 2. The bulk soil was
188 shade dried, crushed to an aggregate size of 4 mm and limed with Ca(OH)₂ from a pH of 4.2 to 5.4, in
189 order to avoid toxicity of Al and Mn. After liming, the bulk soil was amended with salts of NH₄NO₃, KCl,
190 MgSO₄, ZnCl₂, CuSO₄, H₃BO₃ and (NH₄)₆Mo₇O₂₄ at rates of 33 mg N kg⁻¹, 95 mg K kg⁻¹, 15 mg Mg kg⁻¹,
191 20 mg S kg⁻¹, 2.5 mg Zn kg⁻¹, 0.04 mg B kg⁻¹, 0.08 mg Cu kg⁻¹, and 0.03 mg Mo kg⁻¹ soil, to avoid any
192 nutrient deficiency other than P. Application of ammonium nitrate was later split in two additional doses of
193 33 mg kg⁻¹ soil at 22 DAS and one 34 DAS.

194 Pots of 5.5 L (height: 30cm, diameter: 16cm) were then filled with 2.5 kg of the P deficient soil, mimicking
195 a subsoil layer from 15-30 cm. Later, 2.5 kg of topsoil was added to the pots (i.e. 0-15 cm) after establishing
196 the different P treatments by mixing powdered TSP into this topsoil. For the NoP, Micro1, and Micro2
197 treatments no P fertilizer was initially added to the topsoil. For the suboptimal broadcast, 10 mg P kg⁻¹ soil
198 (corresponding to 25 mg P pot⁻¹) was mixed in the soil, corresponding to a P concentration of 0.01 mg L⁻¹
199 in a 1:10 1 mM CaCl₂ extract (SubP). For the large rate of P broadcasting, 100 mg of P kg⁻¹ soil
200 (corresponding to 250 mg P pot⁻¹) was mixed into the soil, up to a P concentration of 0.02 mg L⁻¹ (PlusP).
201 The same two varieties as used in Expt. 1 (i.e. NERICA4 & DJ123) were then planted, and the same two
202 micro-dose placements were established at similar application rates (i.e. 12 and 24 mg P per pot).

203 Half of the pots were daily maintained at Field Capacity (FC; 43% w/w) while the other half was subjected
204 to the local precipitation pattern during the growing season (DP). The weather data was retrieved from

205 New_LocClim (longitude 47.483°, latitude -19.2°, altitude 1480 masl), using the single point mode and the
206 nearest neighbor method (LocalClimateEstimator (FAO 2001)). To simulate the temporal precipitation
207 distribution and drying periods, water was added according to the amount of rainy days per month. Doing
208 so, pots were watered to field capacity at an interval of four days between 1 and 12 DAS, and at an interval
209 of two days between 12 and 49 DAS. Each treatment combination was replicated four times.

210 At 49 DAS, plants were harvested to measure shoot growth, P concentration, and P content of the shoots
211 with identical methods as in Expt. 1. For this experiment, roots were collected from two segments over
212 depth: the ‘*shallow roots*’ (0-15 cm) and the combination of intermediate and deep roots (>15 cm), in this
213 experiment referred to as ‘*deeper roots*’.

214

215 Data analysis

216 A provisional indicator of the agronomic efficiency of the P fertilizer at 52 DAS was calculated as $AEP =$
217 $(\text{biomass with } P - \text{biomass without } P) / \text{amount of } P \text{ applied}$, expressed in $[\text{g g}^{-1}]$. The apparent P recovery
218 from the fertilizer was calculated as $P_{rec} = (\text{Shoot } P \text{ content with } P - \text{Shoot } P \text{ content without } P) / \text{amount of}$
219 $P \text{ applied}$, expressed in percentage. The partial soil P balance was assessed as $P_{\text{balance}} = \text{Shoot } P \text{ content} /$
220 $\text{amount of } P \text{ applied}$, expressed in percentage (Fixen et al. 2015). The shoot P uptake per unit root mass
221 was calculated as a measure of phosphorus acquisition efficiency (PAE).

222 All statistics were computed in R version 4.0.2 (R Development Core Team, 2012). Three-way ANOVAs
223 (Type III, using ‘aov’ from the {stats} package) were performed on the shoot and root variables with water
224 regime, P treatment, and variety as fixed factors and each combination included four replicates. Means and
225 standard errors of the mean ($\frac{\sigma}{\sqrt{n}}$, with σ = standard deviation and n = the number of observations) were
226 calculated for every treatment combination and significance between treatment means was determined by
227 calculating the Least Significant Difference (LSD). Plots of shoot mass, relative root mass distribution, and
228 tissue P concentration were created using ‘ggplot’ from the { ggplot2 } package.

229

230 Results

231

232 *Rice establishment and shoot growth*

233 Shoot weights were lower in Expt. 2 compared to Expt. 1, which might be related to the different growth
234 conditions but also to the soil P supply (Figure 1). The most P deficient soil was that of Expt. 2, suggested

235 by the much lower P concentrations in soil solution (Table 1). In both experiments, all P application
236 methods enhanced rice development at early stages compared to the control (NoP), which was most
237 pronounced in the most P deficient soil (i.e. Expt. 2). The highest broadcast rates (PlusP) consistently
238 yielded largest shoot mass production.

239 Shoot weight under Micro2 was equal to that under Micro1 for Expt. 1, while this was largest for Micro2
240 in Expt. 2. The shoot weight with SubP broadcast (125 mg P) did not significantly differ from that under
241 micro-dose placements in Expt. 1, despite the much higher P dose in this broadcast application. In contrast,
242 the shoot weight of SubP in Expt. 2 (25 mg P) was consistently lower than that under both placement rates,
243 where the highest placement rate was equal as in the broadcast P (SubP). (Figure 1)

244 Drying periods slightly reduced biomass production compared to permanent field capacity in both
245 experiments. Largest effects of soil water were found when shoot biomass under field capacity were largest,
246 i.e. at high P supply and more with higher yielding DJ123 than with NERICA4. In contrast, only the shoot
247 growth under SubP in Expt. 2 increased under drying period compared to field capacity (Figure 1).

248 During the first weeks of plant establishment, a fast initial shoot development was indeed observed for both
249 placement rates. Increments of tiller and leaf number under both placement rates were similar to that with
250 PlusP, however, these growth curves of rice plants receiving P placements started to level off from the
251 growth curves of the rice that received the highest broadcast rates after ca. 40 DAS in Expt. 1 and 30 DAS
252 in Expt. 2 (Figure S1 & S2, Supplementary Information).

253 *Phosphorus uptake and tissue concentration of the rice shoots*

254 Similar to shoot weight, total P content was consistently lowest without P application (NoP) and largest
255 under PlusP (Table 3 & Table 4). In Expt. 1, the P content under SubP was higher than the P content under
256 Micro1 and Micro2 for DJ123, while this was not the case for NERICA4 (Table 3). In Expt. 2, shoot P
257 content under both P placement rates was similar to SubP. However, the significance of these differences
258 depended on both variety and water treatment (Table 4), as DP increased the P content under SubP only
259 and DJ123 acquired more P under Micro2 which was not the case for NERICA4.

260 The P concentration in the shoot tissue observed in Expt. 1 was consistently lowest under both rates of
261 micro-dose placement compared to that under broadcast and this contrasts the opposite trends for the effects
262 of placement on shoot yield (Figure 2 & Figure S3, Supplementary Information). The P concentration was
263 higher in NERICA4 than in DJ123 (Table 3). For Expt. 2, P concentrations in the shoot tissue were also
264 very low for the P placements (below values of SubP and PlusP), and these concentrations were similar to

265 the control values of NERICA4 (NoP), but slightly higher than the control value of DJ123 (NoP) (Table 4,
266 Figure 2 & Figure S2, Supplementary Information).

267 The PAE was consistently lowest for DJ123, in Expt. 1 (Table S1, Supplementary Information), while this
268 was only the case for NoP and SubP in Expt. 2. In Expt. 2, the PAE of DJ123 was larger than NERICA4
269 under PlusP only (Table S2, Supplementary Information).

270 *Fertilizer efficiency, apparent P recovery, and P balances*

271 In both experiments (Table 3 & Table 4), a very large fertilizer efficiency (AEP) and apparent P recovery
272 (P_{rec}) have been observed for both micro-dose placements. However, both parameters were consistently
273 largest with Micro1 (12 mg P) compared to Micro2 (24 mg P).

274 The partial soil P balance ($P_{balance}$) of the P application methods was consistently highest under Micro1,
275 followed by Micro2. These (Micro1 & Micro2) were consistently larger compared to the partial P balance
276 under SubP and PlusP (Table 3 & Table 4). For Expt. 1, the partial P balance at 52 DAS consistently
277 exceeded the value of 100% under Micro1, while this only occurred under Micro2 in DJ123 grown under
278 Field Capacity (Table 3). The partial P balance never exceeded 100% in Expt. 2 (Table 4).

279 *Root distribution*

280 The root mass distribution of the upland rice in both experiments was affected by water, variety, and P
281 management. In Expt. 1, drying periods (DP) decreased the fraction of the shallow roots while it increased
282 the fraction of deep roots compared to field capacity (FC) (Figure S5, Supplementary Information). In Expt.
283 1, DJ123 had a smaller fraction of shallow roots and a larger fraction of deep roots compared to NERICA
284 4 (Figure S5, Supplementary Information). In Expt. 2, a similar effect of drying periods (DP) on deep
285 rooting was only found for NERICA4 (Figure S6, Supplementary Information), and it was not consistently
286 significant for all P treatments (Figure 5).

287 Interestingly, both rates of micro-dose P placements in Expt. 1 (Micro1 & Micro2) decreased the fraction
288 of the shallow roots, while it strongly increased the fraction of the deep roots, compared to all other P
289 treatments (i.e. NoP, SubP, and PlusP) by on average 22% (Figure 3). For Expt. 2, a similar trend was
290 observed under field capacity (FC), as both rates of micro-dose placements indeed displayed the lowest
291 fractions of shallow roots and highest fractions of deeper roots (here all roots deeper than 15 cm) (Figure
292 4). However, the effect of drying periods (DP) in Expt. 2 overruled the effect of placements, and hence the
293 difference of shallow root fractions under Micro2 compared to SubP and PlusP was not significant under
294 DP while it was indeed significant under FC (Figure 4).

295 Accordingly, the absolute root mass in the deepest layer was consistently largest under both placement rates
296 (Micro1 and Micro2) in Expt. 1 (Table 3). Similar for Expt. 2, largest values of absolute root mass in the
297 deeper layers (>15cm) were observed for both placement rates (Table 4), and the specific treatment ranking
298 depended on the water treatment.

299

300 **Discussion**

301

302 *Effects of micro-dose P placement on P deficiency and deep rooting of upland rice*

303 This work corroborates earlier findings that micro-dose P placements boost the initial establishment of
304 upland rice on P deficient soils (Vandamme et al. 2018). Such initial benefits of micro-dose P placements
305 were previously also observed for lowland rice (De Bauw et al. 2019), maize (Richards et al. 1985), pearl
306 millet (Muehlig-Versen et al. 2003), sorghum (Aune and Ousman 2011) and other crops like groundnut,
307 sesame and cowpea (Ousman and Aune 2011). Indeed, micro-dose P placements result in a high P recovery
308 and a high agronomic efficiency of P fertilizers, and the P content in the rice shoot often exceeds the amount
309 of P applied (Vandamme et al. 2018).

310 As far as known, two observations are new and call for attention. The first is the markedly low P
311 concentration in the rice tissue after P placements, despite the strong growth under the micro-dosed P. This
312 was most apparent when plotting shoot P concentrations against the yielded shoot dry matter, illustrating
313 that placements versus broadcast data separate out across all rates, soils, and genotypes (Figure 2, Figure
314 S3, Figure S4). The low P concentration in the tissue may indicate that micro-dose P placements enhanced
315 the internal P use efficiency of the rice at initial stages, following the fast growth boost (Vandamme et al.
316 2016a). The combination of a higher biomass with lower tissue nutrient concentration also points to a Piper-
317 Steenbjerg effect (Wikstrom 1994), which is explained as follows. Low tissue P concentrations occur when
318 the fast growth of plants grown in an initially higher P medium (locally after placement) eventually leads
319 to a more rapid depletion of external P than the slow growth of plants grown in an initially lower P medium.
320 However, this effect is less pronounced in more extremely deficient conditions, where the tissue P
321 concentrations without P amendments generally remain very low (i.e. Expt. 2). As the shoot P content
322 exceeds or approximates the amended dose of P by the placements after 52 DAS (Table 3, Expt. 1) this
323 study indicates that the available P from the micro-dose placements (both at an application rate of 12 and
324 24 mg P per planting hole) quickly becomes insufficient to the fast growing rice plants (roots and shoots),
325 resulting in the observed drop in shoot P concentration at later stages. Indeed, growth curves of the tiller

326 and leaf number under placements were observed to flatten off compared to P broadcasts at large rates,
327 from ca. 35 DAS in these pot trials and this was also observed for field-grown rice (De Bauw et al. 2019;
328 Vandamme et al. 2018). Such declining effects of micro-dose P placements over time compared to
329 broadcasts were also observed for millet (Muehlig-Versen et al. 2003) and maize (Eghball and Sander
330 1989). The latter decrease in growth indicates a P deficiency at later stages under P placements, and hence
331 special attention should be given in P deficient soils to avoid P limitations during the later stages of the rice
332 cropping cycle when placing micro-doses of P, possibly by additional P management at later growth stages.

333 The second new observation is that deep rooting of rice is stimulated by micro-dose P placements. It is well
334 known that plants enhance their rooting depth in response to dryer conditions (Comas et al. 2013). For
335 lowland rice an enhanced deep rooting was already observed in response to water saving techniques (De
336 Bauw et al., 2019). For upland rice, a response in root elongation and rooting depth to drought was
337 previously also observed (Asch et al. 2005; Kato et al. 2006; Kano et al. 2011; Suralta et al. 2016), and such
338 deep root response of upland rice to drying periods is now also confirmed in this work. The latter response
339 might have a two-fold reason since P availability in upper layers would also decrease under drying
340 conditions.

341 Interestingly, we observed that P placements also enhance deep rooting of upland rice, both in absolute and
342 relative terms (Figures 3 and 4; Tables 3 and 4). Such responses of deep rooting to P placements were
343 previously reported when P was banded in deeper layers (Singh et al. 2005; Nkebiwe et al. 2016; Hansel et
344 al. 2017), or when P was locally placed in deeper layers of the soil (Fatondji et al. 2008; Ibrahim et al. 2015;
345 Weerathne et al. 2015). Accordingly, morphological changes of rice roots to localized P applications were
346 previously observed by He et al. (2003), and they argued that the relative root allocation of rice is favored
347 in the soil layer with high-phosphorus supply. However, the enhancement of deep rooting in response to
348 micro-dose P placements in the planting hole was never reported before. The mechanisms contributing to
349 such deep rooting after basal micro-dose P placements have not yet been confirmed, but this deep rooting
350 might be explained by an osmotic response to the local higher salt concentration at the seedling base, as
351 drought and salt responses are strongly related within plants (Maheswari et al. 2012; Niu et al. 2016; Forni
352 et al. 2017). Another explanation would be that nodal root elongation over depth is stimulated over lateral
353 elongation, following the local P saturation at the root base. In other words, a localized P application after
354 placement results in a local P hotspot and a P deficient bulk soil. Hence, plants would not benefit from
355 extended root proliferation in such a deficient topsoil layer after P placements, resulting in a decrease of
356 root allocation to this layer so stimulating deep rooting. Further research would thus benefit from unraveling
357 these mechanistic effects of micro-dose P placements on root development and root distribution.

358 This response of deep rooting after P placements has strong implications for enhancing the drought
359 resilience of upland rice and possibly also in other crops, as deep rooting is known to enhance drought
360 avoidance (Gewin 2010; Gowda et al. 2011). Such effects of micro-dose placements on drought avoidance
361 were here not clearly presented in the shoot weights. However, in the field these effects are expected to
362 become larger than in pots because subsurface soils in the field may have more water than in the closed
363 pots for obvious reasons. In the field, micro-dose placements of fertilizers have been reported to result in
364 rapid early growth and better crop performance under drought conditions (Tabo et al. 2006, 2007), which
365 might be related to such an enhanced rooting depth. Additionally, micro-dose P placements in upland rice
366 were previously observed to induce end-of-season drought escape following faster maturity of the rice
367 under P placements (Vandamme et al. 2018). Hence, following these observed root responses and the fast
368 maturity after placements, this technique of micro-dose P placements could indeed be used as a sustainable
369 management practice to enhance the resilience of upland rice, and possibly also other crops to droughts.

370 *Agronomic implications on micro-dose P placement*

371 According to the P status of the soil, different rates of micro-dose P placements mattered for growth and P
372 content in Expt. 2, but not in Expt. 1 where differences in growth and P content between the two placement
373 rates were minor. Such minor differences among placement rates were previously also observed for rice in
374 De Bauw et al. (2019) and Vandamme et al. (2018), and this study now suggests that rate effects after P
375 placements will indeed only appear when the soil is extremely deficient in P. Lower rates of P placements
376 will result in a higher P use efficiency, and it was therefore argued that low placement rates are preferred
377 above higher rates (van der Eijk et al. 2006; Biielders and Gérard 2015; Aune et al. 2017). However, using
378 such small application rates of 12 mg P per plant (3 kg ha⁻¹) on the field, seasonal P balances of rice will
379 often be negative, while seasonal P balances were sometimes observed to be positive when placing rates of
380 24 mg P per plant (6 kg ha⁻¹) (De Bauw et al., 2019). Therefore, it was argued that micro-dosing increases
381 the risk of soil nutrient depletion in low-input cropping systems, and that seasonal balances should be
382 considered (Bagayoko et al. 2011; Ibrahim et al. 2016b; Blessing et al. 2017). Further research should thus
383 determine the appropriate application rates of micro-dose P placements for different soil types in order to
384 avoid P deficiency at later stages, and prevent further mining of the available P stocks in the already
385 deficient soils (De Bauw et al. 2019; Margenot et al. 2016). In this regard, larger placement rates should
386 not compromise on the emergence of the crop due to germination failure or salt injury of the seedlings
387 (Muehlig-Versen et al. 2003; Vandamme et al. 2018). To achieve this, larger rates or multiple doses of P
388 could possibly be placed further from the planting hole, or small rates of micro-dose P placements in the
389 planting hole could possibly be combined by additional broadcasts of locally available rock phosphate
390 (Muehlig-Versen et al. 2003), or practices of conservation agriculture such as organic amendments (Aune

391 and Coulibaly 2015). Additionally, it should be considered that the implementation of placements by
392 traditional manual methods is labor intensive, reducing the net profit (Vandamme et al. 2018). However,
393 the development of new mechanical tools like ‘Fertiseeders’ reduce labor input by 80% when placing
394 fertilizers together with seeds in the planting hole, thereby justifying the implementation of fertilizer
395 placements on the field (Africa Rice Center 2018).

396 Differences in P uptake efficiency and drought stress tolerance between rice varieties

397 The variety DJ123 indeed displays a faster growth and a higher absolute P uptake capacity (Vandamme et
398 al. 2016b, a) compared to NERIC4, likely following a fast root development (De Bauw et al. 2020).
399 However, despite the consistent higher P uptake capacity, the PAE of DJ123 often remains relatively low
400 compared to the inefficient variety NERICA4 (Table S1, Supplementary Information). For DJ123, these
401 results on PAE contradict those by Mori et al. (2016) and Wissuwa et al. (2020) who found that this
402 genotype generally displays a higher PAE than NERICA4 under P deficient conditions and suggested
403 DJ123 as a potential donor of traits towards enhanced root P uptake efficiency. This was recently also
404 contested by Rakotoson et al. (2020), and hence, our results additionally suggest that this hypothesis is not
405 consistently true.

406

407 Conclusions

408

409 This work highlights the opportunities of micro-dose P placements towards more efficient P management
410 in rice cultivation on low P upland soils as it strongly boosts rice establishment, while increasing the
411 fertilizer use efficiency and P recovery. We found that P placements enhance deep rooting of upland rice,
412 and hence the technique of P placements can serve as a management strategy to enhance P use in upland
413 rice, while mitigating effects of dry periods and increasing the resilience of upland rice to droughts.
414 Therefore, the technique of micro-dose P placement should be considered when developing new decision
415 support tools designing site-specific nutrient recommendations for rice (Bado et al. 2018; Saito et al. 2019).
416 Future field studies should be conducted to validate whether P placements can indeed mitigate drought
417 events in upland rice systems by improving root water acquisition on the field, and the observed root
418 responses to P placements should be assessed in other crops. The low P concentrations in the rice shoots
419 after P placements indicate that additional P management is needed to overcome P deficiency in the later
420 stages of the rice cropping cycle and to avoid further P mining when placing micro-doses of P in deficient
421 soils. To this end, multiple years of on-field validation trials are needed to draft sustainable and site-specific

422 recommendations on P management utilizing the technique of micro-dose P placement. Doing so,
423 contrasting rates of micro-dose P placements should be tested for multiple crops (Aune et al. 2017) along a
424 wide gradient of soil P availability.

425

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427

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435

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