1   **Root traits for low input agroecosystems in Africa: lessons from three case studies**

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Abstract

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15   In Africa, agriculture is largely based on low-input and small-holder farming systems that

16   use little inorganic fertilizers and have limited access to irrigation and mechanization.

17   Improving agricultural practices and developing new cultivars adapted to these low-input

18   environments, where production already suffers from climate change, is a major priority

19   for ensuring food security in the future. Root traits improving water and nutrient uptake

20   could represent a solution toward achieving these goals. In this review, we illustrate how

21   breeding for specific root traits could improve crop adaptation and resilience in Africa

22   using three case studies covering very contrasted low-input agroecosystems. First, we

23   review how targeted changes in root system architecture allowed a dramatic increase in

24   common bean yield in low input agroecosystems of South East Africa. We next discuss

25   how root traits could be targeted to improve the productivity and resilience of dryland

26   cereals in the face of climate change and soil degradation. Finally, we evaluate how root

27   traits could be mobilized to develop water-saving rice agroecosystems for West Africa.

28   We conclude with a discussion on how to prioritize target root traits, how they could be

29   validated and made available to breeders and farmers through participatory approaches.

Introduction

The Green Revolution was driven by the development of novel cultivars along with government subsidised fertilizer inputs, mechanization and irrigation and has dramatically increased crop yield globally but has excluded large parts of Africa (Pingali 2012). These changes required massive and coordinated investment across public and private institutions. As a consequence, most of the world enjoyed a significant increase in agricultural productivity while Africa and particularly its sub-Saharan parts, maintained the same degree of productivity (Johnson, Hazell & Gulati 2003). Recent surveys on agriculture practices in six sub-Saharan countries (Niger, Nigeria, Ethiopia, Malawi, Tanzania and Uganda) covering over 62,000 plots estimated that only 1 to 3 % of the lands cultivated by smallholders are irrigated and no more than 10% of the households have irrigation capacity (Sheahan & Barrett 2017). Concerning fertilization, 41% of the cultivated plots in Nigeria, 17% in Niger and 3.2% in Uganda used inorganic fertilizer, while 84% of the total studied area did not use agro-chemicals (pesticides, herbicides, fungicides and insecticides; Sheahan & Barrett 2017). Moreover, a large part of African soils suffers from degradation due to erosion, desertification, deforestation and poor agricultural practices (Eswaran, Lai & Reich 2001). Soil degradation is exacerbated by the increased frequency of extreme events such as heat waves, drought, flood or high wind associated with climate change (Olsson *et al.* 2019). Phosphorus depletion from agricultural soils due to water erosion are more predominant in regions with intensive extreme climates such as arid and semi-arid regions of Africa (Alewell *et al.* 2020). Poor soils along with climate change are serious threats to agricultural agroecosystems and crop production in Africa and are major impediments to achieve food security (ELD Initiative & UNEP, 2015).

In Africa, efforts to deal with low fertility soils are restricted by the challenges associated with transporting and applying massive amounts of fertilizers (organic or chemical) to dispersed and inaccessible farms. In contrast, improving agricultural practices and developing new cultivars of key food crops can have a substantial impact on food security, income production and agroecosystem dynamics while minimizing expenditure (Lynch 2007; Fess, Kotcon & Benedito 2011; Gemenet et al. 2016; Joshi et

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60   al. 2016). For this, identification of useful traits and their combinations for crops grown in
61   low-input agroecosystems and their integration into breeding programs is of major
62   importance. Foremost among the challenges is developing and deploying phenotyping
63   tools in these environments, understanding genotype by environment interactions (GxE,
64   i.e. how the environment influences the response of different genotypes) and generating
65   truly integrative phenotyping and selection approaches that ultimately increase yield and
66   smallholder incomes (Reynolds *et al.* 2021).

67   Root architectural and anatomical traits that increase the efficient acquisition of soil
68   resources, as defined by carbon investment per resource gained, are potentially valuable
69   selection targets. These traits can improve crop tolerance to the main primary constraints
70   in the low-input agroecosystems of Africa, namely water and phosphorus scarcity
71   (extensively reviewed in Lynch 2018, 2019; Schneider & Lynch 2020; Lynch et al. 2021).
72   However, trade-offs for specific traits have been identified due to the contrasting spatial
73   and temporal dynamics of these two resources. For example, shallow root growth
74   promotes topsoil foraging and P acquisition, while deep root growth promotes subsoil
75   foraging and water acquisition (Ho, Rosas, Brown & Lynch 2005; Lynch 2011). Root
76   ideotypes (target root phenotypes) for agroecosystems in Africa also need to consider
77   agricultural practices. The implementation of new sustainable approaches for water
78   saving and promotion of soil fertility through the use of beneficial root-soil microorganisms
79   interactions is another potentially fruitful option (de la Fuente Cantó et al. 2020). For
80   instance, improving nitrogen fixation by legumes would have a huge impact. This aspect
81   has been addressed in recent articles (Vanlauwe, Hungria, Kanampiu & Giller 2019;
82   Paliwal, Abberton, Faloye & Olaniyi 2020) and will not be discussed in our review.
83   Similarly, we will not address specific root traits related to root and tuber crops that play
84   an important role for food security in sub-Saharan Africa and were discussed in recent
85   reviews (Duque & Villordon 2019; Zierer, Rüscher, Sonnewald & Sonnewald 2021).

86   In this review, we will illustrate how breeding for specific root traits could improve
87   crop adaptation to low-input African agroecosystems subject to climate change using
88   three case studies. We then discuss how these traits and innovations could be validated,
89   made available to breeders and agronomists and finally adopted by farmers.

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Case study 1: improving phosphorus acquisition efficiency in common bean in South East Africa

Common bean (*Phaseolus vulgaris*) has critical food security, economic and agroecosystem value throughout South East Africa (Wortmann, Kirkby, Eledu & Allen 1998; Beebe 2012). It is fundamental for food security at the household level, as well as economically important at the household, village and regional level. Furthermore, common bean has a key agroecosystem role as a nitrogen (N) fixer. Bean in South East Africa is grown either as a sole crop or intercropped with maize, in both cases usually in rotation with the latter. The primary constraints to production in typical low-input small holder cropping systems in South East Africa include a) low phosphorus (P) availability in highly N fixing soils, b) terminal and/or intermittent drought and c) acid soil complexes, pathogens and insects limiting root growth and causing elevated root mortality (Lynch 2019). These challenges are further complicated by irrigation systems, fertilizers and other soil amendments being inaccessible due to cost and transportation limitations.

In Mozambique, researchers targeted root traits to develop novel varieties that substantially improved small-holder crop production and benefits to local agroecosystems. In this context, increasing P acquisition efficiency, defined by the ratio of carbon investment to P recovered, was identified as a key cross-cutting element because it impacts multiple aspects of plant productivity and agroecosystem function (Lynch & Ho 2005). For instance, shallow root growth has an advantage for the acquisition of soil resources with greater availability in shallow soil zones, particularly P. Greater P acquisition is in turn related to increased shoot growth, biological nitrogen fixation and yield. With a larger shoot biomass shielding the soil, erosion is also reduced (Henry, Kleinman & Lynch 2009; Henry, Chaves, Kleinman & Lynch 2010).

Greater basal root whorl number and longer and denser root hairs traits were targeted to increase common bean P acquisition efficiency. These traits affect the zone of soil explored (Fig. 1a), they can be easily and rapidly phenotyped in the field with resources readily available in less developed countries (Burridge, Jochua, Bucksch &

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119 Lynch 2016), modifications of these traits do not require any change to the cropping
120 system or farmer practices, and they have multi-scale impact.

121   Basal roots are a class of roots specific to dicots with epigeal germination and
122 emerge from the transition zone between radicle and hypocotyl (Burridge, Rangarajan &
123 Lynch 2020). In common bean, basal roots emerge in whorls composed of four individual
124 roots, due to its tetrarch vascular patterning (Fig. 1b; Miguel, Widrig, Vieira, Brown &
125 Lynch 2013). Basal root whorl number is under genetic control and ranges from one to
126 five, with two being the mode (Miguel *et al.* 2013). It can be phenotyped using low cost
127 root roll-ups five to nine days after germination (Fig. 1b) and is associated with field
128 phenotypes and field performance (Strock et al. 2019; Jochua, Strock & Lynch 2020).
129 Greater basal root whorl number increases the vertical zone of soil explored, enabling the
130 efficient exploration of both deep and shallow soil. It also affords a degree of root
131 redundancy. While root redundancy could reduce root system efficiency by increasing
132 metabolic burden, the benefits of root redundancy likely outweigh the costs. In typical
133 small-holder environments where roots are frequently lost due to biotic (pathogen or
134 insect attack) or abiotic stresses, redundancy ensures that at least a few roots will survive
135 to contribute to both deep and shallow resource acquisition (Strock *et al.* 2019).

136   Root hairs are subcellular protrusions emerging from specialized epidermal cells
137 on all root classes (Bhosale *et al.* 2018). Root hair length and density are under genetic
138 control and have been related to greater P acquisition in multiple crops and experimental
139 systems (Ma, Walk, Marcus & Lynch 2001; Yan, Liao, Beebe, Blair & Lynch 2004; Hanlon
140 et al. 2018). Root hairs have minimal construction and maintenance costs making them
141 an extremely efficient means to increase root volume and acquire immobile soil resources
142 such as P (Lynch 2019). They are relatively easy to phenotype at the seedling stage using
143 a low-cost root roll-up protocol (Vieira, Jochua & Lynch 2007). Substantial synergy
144 between greater root hairs and basal root growth angle have been observed in common
145 bean in which the advantage of longer and denser root hairs is magnified when paired
146 with shallow basal root growth (Miguel, Postma & Lynch 2015). Shallower basal root

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147 growth angle and longer and increased density of root hairs traits are ideal selection
148 targets for improving P acquisition efficiency (Fig. 2A).

149   In Mozambique, the selection strategy for improving P acquisition efficiency
150 varieties involved extensive phenotyping of varieties and breeding lines in order to identify
151 accessions possessing high basal root whorl number as well as long and dense root hairs
152 (Burridge *et al.* 2019). These superior lines were then crossed with common varieties
153 either already grown in Mozambique or to varieties with similar and desirable agronomic
154 and market characteristics, such as seed colour and size. Several early generations of
155 these lines were grown at the experimental stations with non-limiting conditions to select
156 them for acclimation, grain quality, shoot architecture, disease and pest tolerance.
157 Subsequently, seeds from F4 plants were evaluated for key root hair traits with those
158 possessing longer and denser root hairs being advanced. Targeted field-based selection
159 of varieties took place first on multiple stations across Mozambique with single
160 constraints, such as low soil phosphorus or terminal drought. Simultaneously, selections
161 were made on more remote stations and farmers' fields with multiple, interacting
162 constraints. A final set of 40 varieties were included in a round of on-farm participatory
163 variety selection using a citizen science approach called the triadic comparison of
164 technology options (tricot) to allow farmers to identify the most suitable varieties for their
165 local agricultural conditions (van Etten *et al.* 2019). Each of many individual farmers
166 received a random pack of three varieties to evaluate on their farm and under their
167 management practices. As a result, three new varieties of common bean, named Kufuna,
168 Tiyela and Matina, have been released in Mozambique. Trials on station and on farmer's
169 fields suggest these lines have roughly double the yield of local varieties when grown with
170 or without P fertilizer (Table 1). This is a noteworthy achievement, in part because no new
171 varieties had been released in Mozambique for over 12 years, and none of those
172 previously released were bred specifically for Mozambique.

173   To further promote and study how new varieties are shared and impact yield, food
174 security and local economies, a pilot promotional campaign was organized in three
175 different regions and compared to three regions that received the improved varieties but
176 not the promotional campaign (Fig. 1c&d). Stocks of breeder and pre-basic seed are

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177 maintained by the Mozambican Agricultural Research Institute and a collaborative model
178 involving the Mozambican Agricultural Research Institute, farmers organization, and seed
179 companies was used to amplify these varieties from zero to 45 tons of seeds in just 3
180 years from 2018 to 2021. This amount of seeds will enable 3,600 hectares of improved
181 P-efficient varieties to be planted in the 2021-2022 season, up from zero in the 2018-
182 2019 season. This mixed public, private and farmer organization model promotes the
183 maximum penetration of the new varieties and promotes long-term sustainability for both
184 companies and farmer organizations. Other varieties of common bean are in various
185 stages of development with some nearly ready for release and others in on-farm trials.

186 The accomplishments in Mozambique demonstrate the utility of a root trait oriented
187 selection strategy traits, which was followed by on-station trials targeting specific abiotic
188 constraints and soil types and then on-farm trials with multiple biotic and abiotic
189 constraints and the use of local practices. Similar systems have proved successful and
190 continue to offer great potential (Humphries et al. 2015; Ryan et al. 2018; van Etten et al.
191 2019). Other key legumes, namely cowpea, groundnut and chickpea have very similar
192 food security, economic and agroecosystem roles across broad swaths of Africa. Lessons
193 from common bean can be in large applied to these other legumes due to similar root
194 system, phenology as well as seed saving, sharing and buying systems.

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196 **Case study 2: Improving water and nutrient acquisition in dryland cereals in West**
197 **Africa**
198 Sorghum (*Sorghum bicolor* [L.] Moench) and pearl millet (*Pennisetum glaucum* [L.] R. Br.)
199 are the fifth and sixth most important cereal crop in the World (FAOSTAT 2021). They are
200 well adapted to arid and semi-arid environments found in sub-Saharan Africa and India.
201 In these regions, they are usually grown one cycle a year during the rainy season by
202 smallholder farmers and represent a major source of micronutrient protein for humans
203 and fodder for livestock. They are usually sown at low density (around 10,000 plants per
204 hectare, Pearson, Norman & Dixon 1995) before or right after the first rain of the season
205 and grown with no or low inputs simply because water and fertilizers are inaccessible
206 and/or unaffordable (Matlon 1990; vom Brocke et al. 2010). Although sorghum and pearl

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207 millet prevail in these environments where other mainstream crops tend to fail, their
208 cultivation is increasingly threatened by high temperature and intermittent drought caused
209 by climate change and soil degradation caused by loss of nutrients and soil organic
210 carbon, a phenomenon accentuated by desertification and erosion (Jones et al. 2013;
211 Sultan, Defrance & Iizumi 2019). Therefore, improving the resilience of sorghum and pearl
212 millet is particularly important for food security in arid and semi-arid regions of Africa and
213 for adaptation of African agriculture to future climates.

214 Sorghum and pearl millet root systems are characterized by a single embryonic
215 seminal root (Singh et al. 2010; Passot et al. 2016). In sorghum and pearl millet, as in
216 their genetic relative maize, multiple post-embryonic crown and brace roots that originate
217 from the belowground and aboveground nodes, respectively, can be observed (Tsuji *et*
218 *al.* 2005; Chopart, Sine, Dao & Muller 2008; Singh *et al.* 2010; Faye *et al.* 2019). Primary,
219 seminal and nodal roots all have lateral roots. In pearl millet, as in maize, three different
220 types of lateral roots have been identified that differ by length, diameter and internal
221 structures (Varney, Canny, Wang & Mccully 1991; Passot et al. 2016), as well as by their
222 growth dynamics (Passot et al. 2018). In sorghum, large variability in crown root angle
223 and root area was observed in diversity panels, backcross nested association mapping
224 (BCNAM) populations and recombinant inbred lines (Mace et al. 2012; Joshi et al. 2017).
225 Similarly, diversity in primary root growth and root branching (Passot *et al.* 2016), and
226 root length density (Faye *et al.* 2019) was observed in pearl millet. Despite this observed
227 root phenotypic diversity and the fact that several authors have proposed root traits as
228 breeding targets for improvement of sorghum and pearl millet (Gemenet et al. 2016; Joshi
229 et al. 2016), selection strategies involving root traits have not been deployed in breeding
230 programmes so far.

231 Architectural traits such as deep rooting might be particularly interesting for
232 drought tolerance of sorghum and pearl millet grown in sub-Saharan Africa where soils
233 are generally deep and sandy with low water retention (Joshi *et al.* 2016). In maize,
234 reducing crown root number or lateral root density was associated with deeper root
235 growth, greater water capture at depth and improved plant water status and yield under
236 drought (Zhan, Schneider & Lynch 2015; Gao & Lynch 2016). This response is linked to

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237 a carbon allocation mechanism in which plants that develop fewer roots are able to invest
238 more carbon in individual roots that can grow deeper (Lynch 2013, 2018; Van Oosterom
239 et al. 2016). Another means for a plant to grow deeper roots is to develop nodal roots with
240 steeper growth angle (Lynch 2013). In sorghum, quantitative trait loci (QTLs) for steep
241 nodal root angle co-localizing with previously identified stay-green and grain yield QTLs
242 showed synteny with previously identified root angle QTLs in maize (Mace et al. 2012;
243 Borrell et al. 2014). In fact, conserved genetic control of root architectural traits have been
244 observed in sorghum and maize (Zheng *et al.* 2020), suggesting that comparative
245 analyses of root traits from both species could be useful for improvement of their root
246 functions (Lynch 2018).

247 Anatomical traits such as reduced root cortical cell file number and cortical cell size
248 were also hypothesized to reduce the metabolic cost of soil exploration and be beneficial
249 for drought tolerance (Lynch 2018). Maize lines with reduced root cortical cell file number
250 and greater cortical cell size showed reduced root respiration, increased root growth at
251 depth, better shoot growth and water status, and significant increase in yield under
252 drought as compared to lines with greater root cortical cell file number and reduced
253 cortical cell size (Burton, Brown & Lynch 2013; Jaramillo, Nord, Chimungu, Brown &
254 Lynch 2013; Chimungu, Brown & Lynch 2014). Similarly, maize lines with more root
255 cortical aerenchyma showed decreased root respiration, increased deep rooting, shoot
256 growth and yield (Zhu, Brown & Lynch 2010; Chimungu et al. 2015). Root cortical
257 aerenchyma formation was observed both in sorghum and pearl millet indicating that this
258 trait could be explored for diversity, genetic control and used for improving drought
259 tolerance (Promkhambut, Polthanee, Akkasaeng & Younger 2011; Jaffuel et al. 2016;
260 Passot et al. 2016). No information exists however on root cortical cell file number and
261 cortical cell size diversity nor their impacts in sorghum and pearl millet drought response.

262 Reduced xylem conductance capacity has been targeted in strategies aiming at
263 improving transpiration efficiency (biomass produced/water transpired), the latter being
264 also associated with drought tolerance (Vadez, Kholova, Medina, Kakkera & Anderberg
265 2014). In wheat for instance, reduced xylem diameter and the associated reduced root
266 hydraulic conductance resulted in plants with more conservative water use that yielded

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267   11% more grains under drought conditions (Richards & Passioura 1989). In fact, annual

268   crop plants adapted to drought stress environments tend to favour smaller xylem diameter

269   as a water conservation strategy (Henry, Cal, Batoto, Torres & Serraj 2012; Kadam, Yin,

270   Bindraban, Struik & Jagadish 2015; Grondin, Mauleon, Vadez & Henry 2016). Sorghum

271   lines with higher number of xylem vessels showed higher transpiration rate, suggesting

272   that reducing xylem vessel number in this crop is associated with water saving strategies

273   (Salih *et al.* 1999). Improving transpiration efficiency over the entire crop cycle, possibly

274   by restricting maximum transpiration at high vapor pressure deficit, through reduction in

275   root xylem diameter, could conserve soil water for the critical reproduction and grain filling

276   stage (Kholová et al. 2010; Vadez, Kholová, Yadav & Hash 2013; Vadez 2014).

277   Root hairs are well-known to improve P acquisition from the soil by increasing the

278   absorption area of the root system (Lynch 2019). In sorghum and pearl millet,

279   characterization of root hair density and length, genotypic variation, as well as their role

280   in P uptake, remains limited. However, a recent study of the genetic architecture of

281   phosphorus efficiency in sorghum showed colocalization between QTLs for P acquisition

282   efficiency, grain yield, total root surface area and individual root diameter (Bernardino *et*

283   *al.* 2019). Interestingly, one of these sorghum QTL located close to the homolog of the

284   rice serine/threonine kinase *OsPSTOL1*, which was previously found to enhance early

285   root growth and grain yield in rice under low-P (Gamuyao et al. 2012; Bernardino et al.

286   2019). Increasing exploration of shallow soil by increasing root hair length and density

287   might be beneficial for P capture.

288   There are clear trade-offs between root traits beneficial for drought and P

289   acquisition. In environments where P scarcity is always a constraint but drought is often

290   intermittent, increased top-soil root hair length and density combined with drought-

291   inducible plasticity in deeper root growth possibly through reduced top-soil root carbon

292   cost (more root cortical aerenchyma for instance) could co-optimize drought and low-P

293   tolerance. Drought-related root plastic response has been described in *Setaria italica* (a

294   close relative of sorghum and pearl millet), where an interruption in crown root growth

295   under drought was observed (Sebastian *et al.* 2016). This plastic response appeared to

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be conserved in sorghum and pearl millet where nodal root length was significantly reduced when grown in split-pot system where the seminal root grew in moist soil while the crown roots grew in dry soil (Rostamza, Richards & Watt 2013). These observations suggest that root plasticity in response to drought exists, and could be exploited to improve drought tolerance. Intercropping systems where root systems of neighbouring plants (sorghum/pearl millet and cowpea/groundnut for instance) could have complementary interactions in terms of water and nutrient availability without competing with each other may also help reducing these trade-offs (Brooker *et al.* 2015).

Beyond root architectural and anatomical traits, targeting the rhizosphere could be another future avenue to improve dryland cereals performance (de la Fuente Cantó *et al.* 2020). The rhizosphere is the volume of soil around the root under the influence of the root system, i.e. whose physico-chemical and biological properties are modified by the root, which, in turn, impacts plant nutrition, development and physiology (York, Carminati, Mooney, Ritz & Bennett 2016; de la Fuente Cantó et al. 2020). One potential rhizosphere target trait in sorghum and pearl millet would be rhizosheath formation, i.e. the aggregation of soil particles around the roots (Ndour, Heulin, Achouak, Laplaze & Cournac 2020). This fraction of the soil firmly attached to the roots corresponds to the most biologically active fraction of the rhizosphere. First described in desert grasses, rhizosheath formation has since been reported in many cereal crops including sorghum and pearl millet (Duell & Peacock 1985; Brown, George, Neugebauer & White 2017; Ndour et al. 2017). A positive impact of rhizosheath on water and mineral nutrition was reported for several plants in laboratory conditions and could be in part explained by improved contact between the soil and the root surface (Ndour *et al.* 2020). Phenotyping for rhizosheath size is high throughput and this trait is largely under plant genetic control and large variability exists in the germplasm in pearl millet thus making it a potential target for breeding (Ndour *et al.* 2021). However, rhizosheath formation can represent a significant carbon sink, and further work is needed to demonstrate the impact of a larger rhizosheath on dryland cereals in field conditions.

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In conclusion, greater root hair length and density for increased P acquisition, combined with more aerenchyma for decreased carbon cost of root tissues and potentially reduced xylem vessel diameter for increased water use efficiency are potential selection targets for dryland cereals grown in low-P soils and drought-prone regions of West Africa (Fig. 2B). Plasticity (GxE) in crown root number and lateral root branching at depth as well as rhizosheath formation may be considered potential drought adaptive responses (Fig. 2B).

Case study 3: Water-saving rice agroecosystems for West Africa

Rice is the most consumed cereal in West-Africa and demand for rice is strongly increasing mostly due to population growth and changes in consumption pattern linked to increased urbanization (Elbehri, Kaminski, Koroma, Iafrate & Benali 2013; ECOWAS 2019). Currently, local production covers only roughly 60% of the demand, the remainder being met by imports that strongly impact the region's economy and increase vulnerability to price changes in the global commodity market (ECOWAS 2019). Since a majority of West Africans are projected to live in urban areas in the future, demand for rice is expected to strongly increase (ECOWAS 2019). Several programs have been launched to increase local production to meet this future demand and guarantee food sovereignty. As a consequence, total rice production in West Africa increased by 104,3% from 2009 to 2019 through an increase in total cultivated surface (FAOSTAT 2021) and a further 79,4% increase will be needed between 2019 and 2025 to fully meet the projected demand (ECOWAS 2019). In West Africa, roughly 12% of the rice harvested area is irrigated, with large areas cultivated along the Senegal, the Niger and the Benue rivers (You, Wood, Wood-Sichra & Wu 2014). Irrigated rice is the most productive agroecosystem and 2 cycles of culture can be conducted per year so that irrigated rice contributes strongly to local rice production (van Oort & Zwart 2018). Moreover, interannual yield variability is about two times less in irrigated than in rainfed systems and with the adoption of adaptation measures irrigated rice systems could play a major role for rice production resilience in response to climate change in the region (van Oort &

353   Zwart 2018). As a consequence, some countries such as Senegal, are strongly investing
354   to increase the surface of irrigated paddies.

355   However, irrigated rice cultivation requires a large amount of freshwater. It was
356   estimated that in a dry environment with an evaporation rate higher than precipitation rate,
357   as is found in large parts of West Africa, traditional irrigated rice cultivation requires
358   between 700 to 1,500 mm of water to produce 1 kg of rice per year (Bhuiyan 1992).
359   Furthermore, climate change is trending towards a hotter and dryer atmosphere in the
360   region, which will increase evaporative demand. With increased competition from
361   industries and city growth for freshwater and increased uncertainty in precipitation
362   patterns resulting in reduced water availability in the region, it will not be possible to meet
363   the growing demand with local rice production using the conventional irrigated rice
364   cultivation system (Nie *et al.* 2012). Several water-saving alternatives have been
365   suggested including alternate wetting and drying or aerobic cultivation in order to reduce
366   water consumption and increase cultivated surfaces. While these practices can save up
367   to 50% of the water used for rice production, they often incur a yield penalty with the
368   current varieties that have been selected for irrigated agro-ecosystems (Bouman, Peng,
369   Castañeda & Visperas 2005; Peng et al. 2006; Kreye et al. 2009; Sasaki et al. 2010).

370   Aerobic rice cultivation aims to maximize crop water use efficiency by growing
371   plants in soil without flooding or puddling (Matsunami, Matsunami & Kokubun 2009;
372   Matsuo & Mochizuki 2009). It allows greater water savings and can be deployed in regions
373   without access to irrigation water but has a high yield penalty and is associated with
374   increased weed management and risks of nematodes. In this system, periodic drought
375   stress may reduce yield stability and yield potential (Sandhu *et al.* 2019). For these
376   reasons, aerobic rice has not become popular among farmers in irrigated areas (Meena,
377   Bhusal, Kumar, Jain & Jain 2019). On the other hand, alternate wetting and drying is a
378   simple practice where, instead of keeping the fields permanently flooded, irrigation is
379   periodically stopped until the soil water table reaches a certain depth, easily measured
380   using a pipe set in the soil, and then re-started until the field is flooded again (Bouman &
381   Tuong 2001). Alternate wetting and drying cycles are repeated either during the
382   vegetative or flowering stage or throughout the rice cultivation cycle, although keeping

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383   paddies flooded in hot environments during the flowering stage help avoid the problems
384   linked to heat sensitivity though the cooling effect of evaporation (Jagadish, Murty & Quick
385   2015). Two types of alternate wetting and drying have been described: moderate
386   alternate wetting and drying when field water level is allowed to drop down to 15 cm below
387   the soil surface, and severe alternate wetting and drying when soils are allowed to dry
388   beyond −20 kPa (Carrijo, Lundy & Linquist 2017). Alternate wetting and drying can be
389   easily adopted in these areas as it does not change the cultivation practices, is not
390   associated with increased labour needs and can contribute to a reduction in water
391   consumption of 5 to 30%, depending on the season and soil, as well as reduce methane
392   emissions and grain arsenic levels (Linquist et al. 2015; Carrijo et al. 2017). In general,
393   alternate wetting and drying has a limited yield penalty (5.4% in a meta-analysis of 56
394   studies, Carrijo et al. 2017) but the yield decrease is more important in severe alternate
395   wetting and drying or if alternate wetting and drying is maintained throughout the crop
396   cycle (Carrijo *et al.* 2017). The impact on yield is also very dependent on the genotype
397   and most of the currently used high-yield varieties show yield reduction in alternate
398   wetting and drying (Carrijo et al. 2017; Sandhu et al. 2017). Thus, there is a clear need
399   to develop new varieties to optimize yield in alternate wetting and drying rice
400   agroecosystems.

401   The use of root traits has been little explored in such agroecosystems, but could
402   support increased water use efficiency, phosphorus (P) use efficiency and nitrogen (N)
403   use efficiency, thus reducing inputs globally alternate wetting and drying. Indeed,
404   alternate wetting and drying results in periodic changes in water content in the topsoil but
405   also changes the dynamics of nutrient availability and in particular of N and P availability
406   (Wang et al. 2016; Acosta-Motos et al. 2020). For instance, it increases topsoil P
407   availability and has been linked with changes in the soil microbiota and the stimulation of
408   aerobic P-solubilizing bacteria in the aerobic topsoil compartment (Li *et al.* 2018).
409   Conversely, N availability seemingly decreases upon alternate wetting and drying due to
410   increased denitrification, volatilisation and leaching although these losses can be avoided
411   by timely N application (Tan et al. 2013; Djaman et al. 2018). Water and N signalling are
412   known to interact in ways that affect root traits for synergistic or antagonistic resource

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413   uptake (reviewed in (Araus, Swift, Alvarez, Henry & Coruzzi 2020). Hence, varieties for

414   alternate wetting and drying agro-ecosystems need to be adapted to fluctuations in soil

415   water and nutrient content in the topsoil.

416   Root traits could be mobilized to that end as a large genetic diversity for these traits

417   is available in rice (Ahmadi *et al.* 2014). Root traits that increase the volume of topsoil

418   exploration and promote P uptake should be prioritized to improve rice yields in alternate

419   wetting and drying systems. Traits   that merit investigation include crown root number,

420   lateral root density (there are two types of lateral roots in rice, thin and determinate short

421   lateral roots and indeterminate long lateral roots; (Rebouillat *et al.* 2009), and root hair

422   length and density.

423   A recent large-scale study by (Sandhu *et al.* 2017) is consistent with nodal root

424   number and lateral root density positively impacting yield in alternate wetting and drying

425   . Evaluation of new rice varieties derived from crosses between popular varieties and

426   drought-tolerant accessions was performed in fully-irrigated and alternate wetting and

427   drying systems in seven sites across Asia (Sandhu *et al.* 2017). Out of 82 lines tested in

428   at least three sites, lines with stable and high yield in alternate wetting and drying

429   conditions compared to irrigated conditions were identified. Comparison of the root

430   phenotype of a subset of these stable high-yielding lines and the control line IR64 (high

431   yield variety that shows a reduction in yield in alternate wetting and drying) showed that

432   higher nodal root number and root dry weight at 10–20 cm depth played an important role

433   in maintaining grain yield under alternate wetting and drying (Sandhu *et al.* 2017).

434   Interestingly, quantitative changes in these root traits induced after initiation of alternate

435   wetting and drying cycle, i.e. plasticity response of the (Catolos *et al.* 2017) root system,

436   were shown to be important for yield stability (Sandhu *et al.* 2017).

437   Alternate wetting and drying seems to have a positive effect on root development

438   as indicated by increased root biomass and maximum root length (Wang et al. 2016;

439   Acosta-Motos et al. 2020). This might simply be a positive response to a mild water stress

440   on root growth potentially mediated by ABA (Miao *et al.* 2021). These observations are in

441   agreement with previous analyses describing the important role of root system plasticity

442   for drought and low P tolerance in field and controlled conditions (Sandhu *et al.* 2016). In

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443   the best performing lines under alternate wetting and drying (initially selected as drought

444   tolerant breeding lines), the number of nodal roots below 20 cm and deep root length at

445   the flowering stage appear to have a positive effect on yield. Therefore, while root

446   branching plasticity in the topsoil improved P uptake in these lines, root growth plasticity

447   in deeper soil layers may have improved water and nitrogen acquisition (Fig. 2C).

448   Similarly, a study performed using a combination of pot experiments and functional-

449   structural plant model indicated that root system P acquisition efficiency is improved by

450   increased root branching both in irrigated and water stress conditions (De Bauw *et al.*

451   2020). In alternate wetting and drying, P acquisition was shown to occur mainly at the

452   root tip and led to P depletion along the root due to the low mobility of P in the soil (De

453   Bauw *et al.* 2020).

454   Root interactions with soil symbiotic microbes such as arbuscular mycorrhizal

455   fungi, which are inhibited by flooding, might also improve water and nutrient acquisition

456   in the topsoil in alternate wetting and drying (Vallino, Fiorilli & Bonfante 2014; Mbodj et

457   al. 2018). Furthermore, arbuscular mycorrhizal fungi were shown to confer drought

458   tolerance in rice (Chareesri, De Deyn, Sergeeva, Polthanee & Kuyper 2020).

459   Interestingly, arbuscular mycorrhizal fungi colonization was also shown to reduce P loss

460   from paddy fields, thus improving P use efficiency and reducing environmental impacts

461   (Zhang *et al.* 2020). Thus, root traits that promote arbuscular mycorrhizal fungi infection

462   in topsoil such as increased number of crown roots and large lateral roots with more

463   cortex cells and less aerenchyma to accommodate intracellular fungal structures may

464   lead to improved water and nutrient uptake. Moreover, rice response to arbuscular

465   mycorrhizal fungi infection is dependent on the plant genotype and could be targeted for

466   plant breeding (Diedhiou et al. 2016; Huang et al. 2020; Lefebvre 2020).

467   Overall, improving root traits in rice for alternate wetting and drying systems could

468   lead to improved water use efficiency but also P use efficiency (Acosta-Motos *et al.* 2020)

469   and N use efficiency (Wang *et al.* 2016b) through synergistic interactions between water

470   and nutrients, thus leading to more sustainable rice agroecosystems with reduced water

471   and fertilizer consumption. Lines adapted to aerobic conditions that show root plasticity

472   in response to alternate wetting and drying in topsoil (increased branching) could be

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473   interesting materials to test. Rhizosphere traits could also be targeted to improve water
474   and nutrient acquisition efficiency in this system.

475

476   **Conclusion**

477   We propose two main root trait-based strategies to accelerate the development of new
478   cultivars better adapted to low-input environments in Africa.

479   The first is to identify simple traits that have the broadest positive influence on
480   enhanced performance and that minimize trade-offs. First and foremost, long and dense
481   root hairs are promising selection criteria as greater root hair length and density promotes
482   soil exploration and nutrient acquisition with minimal cost. Additionally, root plasticity traits
483   could be another potential selection criteria as for topsoil root branching plasticity could
484   be beneficial upon partial dry-down, especially for rice in alternate wetting and drying
485   agroecosystems. Subsoil root length plasticity could be beneficial during prolonged
486   drought stress particularly in the reproduction and grain filling stage (for sorghum and
487   pearl millet in arid and semi-arid agroecosystems for example).

488   The second major strategy is to understand and target trait synergisms and
489   integrated phenotypes. Synergisms between root traits are defined as interactions that
490   have more than additive effect, as in the case of long and dense root hairs paired with
491   shallow root system architecture for P acquisition (Miguel *et al.* 2015). Integrated
492   phenotypes would clearly affect the utility of selecting for a single component trait
493   without selecting for their complementary phenotypes. For example, the utility of high
494   conductance capacity xylem likely depends on root traits that affect rooting depth since
495   deep roots can access and thus transport greater volumes of soil water (Strock, Burridge,
496   Niemiec, Brown & Lynch 2020). The development of root structural and functional models
497   for crops such as sorghum or pearl millet that can evaluate the effects of architectural and
498   anatomical traits as well as trait combinations in changing soil environments will be
499   particularly useful (Ndour, Pradal & Lucas 2017). Other less well characterized trait
500   assemblages, especially those involving transpiration, should be further investigated and
501   validated in particular stress scenarios (Strock et al. 2019; Klein, Schneider, Perkins,
502   Brown & Lynch 2020). Considering resource acquisition and use, especially that of water
503   within the context of phenology, leads to acknowledging the importance of interactions

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504 among roots and shoots for timely water use across the crop cycle (Vadez *et al.* 2014).
505 In that regard, combining root models with crop models could potentially link above-
506 ground traits to root traits, the former serving as a proxy for root function (Benes *et al.*
507 2020).

508   In order to make these innovations readily available to breeders, researchers and
509 breeders need to work together to validate trait utility, develop phenotyping protocols
510 (including field sites) and the type of genetic material to work with (e.g. recombinant inbred
511 lines, near isogenic lines, tester lines, germplasm deployment strategy) and ultimately
512 identify marker or genes controlling beneficial traits. As in the case of common bean (case
513 study 1) demonstrated, identifying traits and deploying a selection strategy at a particular
514 stage of cultivar development, is important. To maximize deployment of improved
515 cultivars and to then secure the adoption of those improved cultivars, social scientists and
516 farmers should be integrated in the selection process (Amelework *et al.* 2016). The
517 inclusion of useful root traits in such approaches may help to stimulate a new Green
518 Revolution in Africa.
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References

Acosta-Motos J.R., Rothwell S.A., Massam M.J., Albacete A., Zhang H. & Dodd I.C. (2020) Alternate wetting and drying irrigation increases water and phosphorus use efficiency independent of substrate phosphorus status of vegetative rice plants. *Plant Physiology and Biochemistry* **155**, 914–926.

Ahmadi N., Audebert A., Bennett M.J., Bishopp A., de Oliveira A., Courtois B., … Xu J. (2014) The roots of future rice harvests. *Rice* **7**, 29.

Alewell C., Ringeval B., Ballabio C., Robinson D.A., Panagos P. & Borrelli P. (2020) Global phosphorus shortage will be aggravated by soil erosion. *Nature Communications* **11**, 4546.

Amelework B.A., Shimelis H.A., Tongoona P., Mengistu F., Laing M.D. & Ayele D.G. (2016) Sorghum production systems and constraints, and coping strategies under drought-prone agro-ecologies of Ethiopia. *South African Journal of Plant and Soil* **33**, 207–217.

Araus V., Swift J., Alvarez J.M., Henry A. & Coruzzi G.M. (2020) A balancing act: How plants integrate nitrogen and water signals. *Journal of Experimental Botany* **71**, 4442–4451.

De Bauw P., Mai T.H., Schnepf A., Merckx R., Smolders E. & Vanderborght J. (2020) A functional-structural model of upland rice root systems reveals the importance of laterals and growing root tips for phosphate uptake from wet and dry soils. *Annals of Botany* **126**, 789–806.

Beebe S. (2012) Common bean breeding in the tropics. In *Plant Breeding Reviews*, First Edit. (ed J. Janick), John Wiley & Sons, Inc.

Benes B., Guan K., Lang M., Long S.P., Lynch J.P., Marshall-Colón A., … Turk M.J. (2020) Multiscale computational models can guide experimentation and targeted measurements for crop improvement. *Plant Journal* **103**, 21–31.

Bernardino K.C., Pastina M.M., Menezes C.B., De Sousa S.M., Maclel L.S., Geraldo Carvalho G.C., … Magalhaes J. V. (2019) The genetic architecture of phosphorus efficiency in sorghum involves pleiotropic QTL for root morphology and grain yield under low phosphorus availability in the soil. *BMC Plant Biology* **19**, 1–15.

Bhosale R., Giri J., Pandey B.K., Giehl R.F.H., Hartmann A., Traini R., … Swarup R. (2018) A mechanistic framework for auxin dependent Arabidopsis root hair elongation to low external phosphate. *Nature Communications* **9**, 1–9.

20

565 Bhuiyan S.I. (1992) Water management in relation to crop production: case study on
566   rice. *Outlook on Agriculture* **21**, 293–299.

567 Borrell A.K., Mullet J.E., George-Jaeggli B., Van Oosterom E.J., Hammer G.L., Klein
568   P.E. & Jordan D.R. (2014) Drought adaptation of stay-green sorghum is associated
569   with canopy development, leaf anatomy, root growth, and water uptake. *Journal of*
570   *Experimental Botany* **65**, 6251–6263.

571 Bouman B. a. M. & Tuong T.P. (2001) Field water management to save water and
572   increase its productivity in irrigated lowland rice. *Agricultural Water Management*
573   **1615**, 1–20.

574 Bouman B.A.M., Peng S., Castañeda A.R. & Visperas R.M. (2005) Yield and water use
575   of irrigated tropical aerobic rice systems. *Agricultural Water Management* **74**, 87–
576   105.

577 vom Brocke K., Trouche G., Weltzien E., Barro-Kondombo C.P., Gozé E. & Chantereau
578   J. (2010) Participatory variety development for sorghum in Burkina Faso: Farmers'
579   selection and farmers' criteria. *Field Crops Research* **119**, 183–194.

580 Brooker R.W., Bennett A.E., Cong W.F., Daniell T.J., George T.S., Hallett P.D., …
581   White P.J. (2015) Improving intercropping: A synthesis of research in agronomy,
582   plant physiology and ecology. *New Phytologist* **206**, 107–117.

583 Brown L.K., George T.S., Neugebauer K. & White P.J. (2017) The rhizosheath – a
584   potential trait for future agricultural sustainability occurs in orders throughout the
585   angiosperms. *Plant and Soil* **418**, 115–128.

586 Burridge J., Jochua C.N., Bucksch A. & Lynch J.P. (2016) Legume shovelomics: High-
587   Throughput phenotyping of common bean (*Phaseolus vulgaris* L.) and cowpea
588   (*Vigna unguiculata* subsp*, unguiculata*) root architecture in the field. *Field Crops*
589   *Research* **192**, 21–32.

590 Burridge J.D., Findeis J.L., Jochua C.N., Miguel M.A., Mubichi-Kut F.M., Quinhentos
591   M.L., … Lynch J.P. (2019) A case study on the efficacy of root phenotypic selection
592   for edaphic stress tolerance in low-input agriculture: Common bean breeding in
593   Mozambique. *Field Crops Research* **244**, 107612.

594 Burridge J.D., Rangarajan H. & Lynch J.P. (2020) Comparative phenomics of annual
595   grain legume root architecture. *Crop Science* **60**, 2574–2593.

596 Burton A.L., Brown K.M. & Lynch J.P. (2013) Phenotypic diversity of root anatomical
597   and architectural traits in *Zea* species. *Crop Science* **53**, 1042–1055.

21

598 Carrijo D.R., Lundy M.E. & Linquist B.A. (2017) Rice yields and water use under
599   alternate wetting and drying irrigation: A meta-analysis. *Field Crops Research* **203**,
600   173–180.

601 Catolos M., Sandhu N., Dixit S., Shamsudin N.A.A., Naredo M.E.B., McNally K.L., …
602   Kumar A. (2017) Genetic loci governing grain yield and root development under
603   variable rice cultivation conditions. *Frontiers in Plant Science* **8**, 1–17.

604 Chareesri A., De Deyn G.B., Sergeeva L., Polthanee A. & Kuyper T.W. (2020)
605   Increased arbuscular mycorrhizal fungal colonization reduces yield loss of rice
606   (*Oryza sativa* L.) under drought. *Mycorrhiza* **30**, 315–328.

607 Chimungu J.G., Brown K.M. & Lynch J.P. (2014) Reduced root cortical cell file number
608   improves drought tolerance in maize. *Plant Physiology* **166**, 1943–1955.

609 Chimungu J.G., Maliro M.F.A., Nalivata P.C., Kanyama-Phiri G., Brown K.M. & Lynch
610   J.P. (2015) Utility of root cortical aerenchyma under water limited conditions in
611   tropical maize (*Zea mays* L.). *Field Crops Research* **171**, 86–98.

612 Diedhiou A.G., Mbaye F.K., Mbodj D., Faye M.N., Pignoly S., Ndoye I., … Champion A.
613   (2016) Field trials reveal ecotype-specific responses to mycorrhizal inoculation in
614   rice. *PLoS ONE* **11**, 1–17.

615 Djaman K., Mel V., Ametonou F., El-Namaky R., Diallo M. & Koudahe K. (2018) Effect
616   of nitrogen fertilizer dose and application timing on yield and nitrogen use efficiency
617   of irrigated hybrid rice under semi-arid conditions. *Journal of Agricultural Science*
618   *and Food Research* **9**, 1–7.

619 Duell R.W. & Peacock G.R. (1985) Rhizosheaths on mesophytic grasses 1. *Crop*
620   *Science* **25**, 880–883.

621 Duque L.O. & Villordon A. (2019) Root branching and nutrient efficiency: Status and
622   way forward in root and tuber crops. *Frontiers in Plant Science* **10**, 1–8.

623 ECOWAS Commission (2019) Directorate of agriculture and rural development, The
624   ECOWAS Rice Factbook 1st Edition.

625 ELD Initiative & UNEP (2015) The economics of land degradation in Africa: Benefits of
626   action outweigh the costs. *Available from www.eld-initiative.org*

627 Eswaran H., Lai R. & Reich P. (2001) Land degradation: An overview. In: Bridges, E.M.,
628   Hannam, I.D., Oldeman, L.R., Pening de Vries, F.W.T., Scherr, S.J., Sompatpanit,
629   S. (eds.), Responses to Land Degradation. Proceedings of 2nd International
630   Conference on Land Degradation and Desertification, Khon Kaen, Thailand. Oxford
631   Press, New Delhi, India.

632 van Etten J., de Sousa K., Aguilar A., Barrios M., Coto A., Dell'Acqua M., … Steinke J.
633   (2019) Crop variety management for climate adaptation supported by citizen
634   science. *Proceedings of the National Academy of Sciences of the United States of*
635   *America* **116**, 4194–4199.

636 FAOSTAT (2021) Statistical division of the UN Food and Agriculture Organization (FAO)
637   *Available at: http://faostat.fao.org/*

638 Faye A., Sine B., Chopart J.-L., Grondin A., Lucas M., Diedhiou A.G., … Laplaze L.
639   (2019) Development of a model estimating root length density from root impacts on
640   a soil profile in pearl millet (*Pennisetum glaucum* (L.) R. Br). Application to measure
641   root system response to water stress in field conditions. *Plos One* **14**, e0214182.

642 Fess T.L., Kotcon J.B. & Benedito V.A. (2011) Crop breeding for low input agriculture: A
643   sustainable response to feed a growing world population. *Sustainability* **3**, 1742–
644   1772.

645 Gamuyao R., Chin J.H., Pariasca-Tanaka J., Pesaresi P., Catausan S., Dalid C., …
646   Heuer S. (2012) The protein kinase Pstol1 from traditional rice confers tolerance of
647   phosphorus deficiency. *Nature* **488**, 535–539.

648 Gao Y. & Lynch J.P. (2016) Reduced crown root number improves water acquisition
649   under water deficit stress in maize (*Zea mays* L.). *Journal of Experimental Botany*
650   **67**, 4545–4557.

651 Gemenet D.C., Leiser W.L., Beggi F., Herrmann L.H., Vadez V., Rattunde H.F.W., …
652   Haussmann B.I.G. (2016) Overcoming phosphorus deficiency overcoming
653   phosphorus deficiency in West African pearl millet and sorghum production
654   systems: Promising options for crop improvement. *Frontiers in Plant Science* **7**, 1–
655   10.

656 Grondin A., Mauleon R., Vadez V. & Henry A. (2016) Root aquaporins contribute to
657   whole plant water fluxes under drought stress in rice (*Oryza sativa* L.). *Plant, Cell*
658   *and Environment* **39**, 347–65.

659 Hanlon M.T., Ray S., Saengwilai P., Luthe D., Lynch J.P. & Brown K.M. (2018) Buffered
660   delivery of phosphate to Arabidopsis alters responses to low phosphate. *Journal of*
661   *Experimental Botany* **69**, 1207–1219.

662 Henry A., Cal A.J., Batoto T.C., Torres R.O. & Serraj R. (2012) Root attributes affecting
663   water uptake of rice (*Oryza sativa*) under drought. *Journal of Experimental Botany*
664   **63**, 4751–4763.

665 Henry A., Chaves N.F., Kleinman P.J.A. & Lynch J.P. (2010) Will nutrient-efficient
666   genotypes mine the soil? Effects of genetic differences in root architecture in

23

667 common bean (*Phaseolus vulgaris* L.) on soil phosphorus depletion in a low-input
668 agro-ecosystem in Central America. *Field Crops Research* **115**, 67–78.

669 Henry A., Kleinman P.J.A. & Lynch J.P. (2009) Phosphorus runoff from a phosphorus
670 deficient soil under common bean (*Phaseolus vulgaris* L.) and soybean (*Glycine*
671 *max* L.) genotypes with contrasting root architecture. *Plant and Soil* **317**, 1–16.

672 Ho M.D., Rosas J.C., Brown K.M. & Lynch J.P. (2005) Root architectural tradeoffs for
673 water and phosphorus acquisition. *Functional Plant Biology* **32**, 737–748.

674 Huang R., Li Z., Mao C., Zhang H., Sun Z., Li H., … Duanmu D. (2020) Natural variation
675 at *OsCERK1* regulates arbuscular mycorrhizal symbiosis in rice. *New Phytologist*
676 **225**, 1762–1776.

677 Humphries S., Rosas J.C., Gómez M., Jiménez J., Sierra F., Gallardo O., … Barahona
678 M. (2015) Synergies at the interface of farmer-scientist partnerships: Agricultural
679 innovation through participatory research and plant breeding in Honduras.
680 *Agriculture and Food Security* **4**, 1–17.

681 Jaffuel S., vom Brocke K., Hamadou T.V.C., Dardou A., Vidal A. & Trouche G. (2016)
682 Anatomical features of an African sorghum landrace adapted to flooded conditions.
683 *Australian Journal of Crop Science* **10**, 1489–1495.

684 Jagadish S.V.K., Murty M.V.R. & Quick W.P. (2015) Rice responses to rising
685 temperatures - challenges, perspectives and future directions. *Plant, Cell and*
686 *Environment* **38**, 1686–1698.

687 Jaramillo R.E., Nord E.A., Chimungu J.G., Brown K.M. & Lynch J.P. (2013) Root cortical
688 burden influences drought tolerance in maize. *Annals of Botany* **112**, 429–437.

689 Jochua C.N., Strock C.F. & Lynch J.P. (2020) Root phenotypic diversity in common
690 bean reveals contrasting strategies for soil resource acquisition among gene pools
691 and races. *Crop Science* **60**, 3261–3277.

692 Johnson M., Hazell P. & Gulati A. (2003) The role of intermediate factor markets in
693 Asia's Green Revolution: Lessons for Africa? *American Journal of Agricultural*
694 *Economics* **85**, 1211–1216.

695 Jones A., Breuning-Madsen H., Brossard M., Dampha A., Deckers J., Dewitte O., …
696 Zougmoré R., eds. (2013) Soil Atlas of Africa. Luxembourg: European Commission.

697 Joshi D., Singh V., van Oosterom E., Mace E., Jordan D. & Hammer G. (2016) Genetic
698 manipulation of root system architecture to improve drought adaptation in Sorghum.
699 In: Rakshit S., Wang Y.H. (eds) The Sorghum Genome. Compendium of Plant
700 Genomes. Springer.

24

701 Joshi D.C., Singh V., Hunt C., Mace E., van Oosterom E., Sulman R., … Hammer G.
702   (2017) Development of a phenotyping platform for high throughput screening of
703   nodal root angle in sorghum. *Plant Methods* **13**, 1–12.

704 Kadam N.N., Yin X., Bindraban P.S., Struik P.C. & Jagadish K.S.V. (2015) Does
705   morphological and anatomical plasticity during the vegetative stage make wheat
706   more tolerant of water deficit stress than rice? *Plant Physiology* **167**, 1389–1401.

707 Kholová J., Hash C.T., Kumar P.L., Yadav R.S., Kocová M. & Vadez V. (2010) Terminal
708   drought-tolerant pearl millet [*Pennisetum glaucum* (L.) R. Br.] have high leaf ABA
709   and limit transpiration at high vapour pressure deficit. *Journal of experimental*
710   *botany* **61**, 1431–40.

711 Klein S.P., Schneider H.M., Perkins A.C., Brown K.M. & Lynch J.P. (2020) Multiple
712   integrated root phenotypes are associated with improved drought tolerance. *Plant*
713   *Physiology* **183**, 1011–1025.

714 Kreye C., Bouman B.A.M., Reversat G., Fernandez L., Vera Cruz C., Elazegui F., …
715   Llorca L. (2009) Biotic and abiotic causes of yield failure in tropical aerobic rice.
716   *Field Crops Research* **112**, 97–106.

717 de la Fuente Cantó C., Simonin M., King E., Moulin L., Bennett M.J., Castrillo G. &
718   Laplaze L. (2020) An extended root phenotype: the rhizosphere, its formation and
719   impacts on plant fitness. *Plant Journal* **103**, 951–964.

720 Lefebvre B. (2020) An opportunity to breed rice for improved benefits from the
721   arbuscular mycorrhizal symbiosis? *New Phytologist* **225**, 1404–1406.

722 Li Z., Li Z., Letuma P., Zhao H., Zhang Z., Lin W., … Lin W. (2018) A positive response
723   of rice rhizosphere to alternate moderate wetting and drying irrigation at grain filling
724   stage. *Agricultural Water Management* **207**, 26–36.

725 Linquist B.A., Anders M.M., Adviento-Borbe M.A.A., Chaney R.L., Nalley L.L., da Rosa
726   E.F.F. & van Kessel C. (2015) Reducing greenhouse gas emissions, water use,
727   and grain arsenic levels in rice systems. *Global Change Biology* **21**, 407–417.

728 Lynch J.P. (2007) Roots of the second green revolution. *Australian Journal of Botany*
729   **55**, 493–512.

730 Lynch J.P. (2011) Root phenes for enhanced soil exploration and phosphorus
731   acquisition: Tools for future crops. *Plant Physiology* **156**, 1041–1049.

732 Lynch J.P. (2013) Steep, cheap and deep: An ideotype to optimize water and N
733   acquisition by maize root systems. *Annals of Botany* **112**, 347–357.

Lynch J.P. (2018) Rightsizing root phenotypes for drought resistance. *Journal of Experimental Botany* **69**, 3279–3292.

Lynch J.P. (2019) Root phenotypes for improved nutrient capture: an underexploited opportunity for global agriculture. *New Phytologist* **223**, 548–564.

Lynch J.P. & Ho M.D. (2005) Rhizoeconomics: Carbon costs of phosphorus acquisition. *Plant and Soil* **269**, 45–56.

Lynch J.P., Strock C.F., Schneider H.M., Sidhu J.S., Ajmera I., Galindo-Castañeda T., … Hanlon M.T. (2021) *Root anatomy and soil resource capture*. Plant Soil, https://doi.org/10.1007/s11104-021-05010-y

Ma Z., Walk T.C., Marcus A. & Lynch J.P. (2001) Morphological synergism in root hair length, density, initiation and geometry for phosphorus acquisition in Arabidopsis thaliana: A modeling approach. *Plant and Soil* **236**, 221–235.

Mace E.S., Singh V., van Oosterom E.J., Hammer G.L., Hunt C.H. & Jordan D.R. (2012) QTL for nodal root angle in sorghum (*Sorghum bicolor* L. Moench) co-locate with QTL for traits associated with drought adaptation. *Theoretical and Applied Genetics* **124**, 97–109.

Matlon P.J. (1990) Improving productivity in sorghum and pearl millet in semi-arid Africa. *Food Research Institute Studies* **22**, 1–43.

Matsunami M., Matsunami T. & Kokubun M. (2009) Growth and yield of new rice for africa (NERICAs) under different ecosystems and nitrogen levels. *Plant Production Science* **12**, 381–389.

Matsuo N. & Mochizuki T. (2009) Growth and yield of six rice cultivars under three water-saving cultivations. *Plant Production Science* **12**, 514–525.

Mbodj D., Effa-Effa B., Kane A., Manneh B., Gantet P., Laplaze L., … Grondin A. (2018) Arbuscular mycorrhizal symbiosis in rice: Establishment, environmental control and impact on plant growth and resistance to abiotic stresses. *Rhizosphere* **8**, 12–26.

Meena R.K., Bhusal N., Kumar K., Jain R. & Jain S. (2019) Intervention of molecular breeding in water saving rice production system: aerobic rice. *3 Biotech* **9**, 1–12.

Miao R., Yuan W., Wang Y., Garcia-Maquilon I., Dang X., Li Y., … Xu W. (2021) Low ABA concentration promotes root growth and hydrotropism through relief of ABA INSENSITIVE 1-mediated inhibition of plasma membrane H$^+$-ATPase 2. *Science Advances* **7**, 1–15.

26

Miguel M.A., Postma J.A. & Lynch J.P. (2015) Phene synergism between root hair length and basal root growth angle for phosphorus Acquisition. *Plant Physiology* **167**, 1430–1439.

Miguel M.A., Widrig A., Vieira R.F., Brown K.M. & Lynch J.P. (2013) Basal root whorl number: A modulator of phosphorus acquisition in common bean (*Phaseolus vulgaris*). *Annals of Botany* **112**, 973–982.

Ndour A., Pradal C. & Lucas M. (2017) Virtual plants need water too: Functional-structural root system models in the context of drought tolerance breeding. *Frontiers in Plant Science* **8**, 1577.

Ndour P.M.S., Barry C.M., Tine D., De la Fuente Cantó C., Gueye M., Barakat M., … Cournac L. (2021) Pearl millet genotype impacts microbial diversity and enzymatic activities in relation to root-adhering soil aggregation. *Plant and Soil* **464**, 109–129

Ndour P.M.S., Gueye M., Barakat M., Ortet P., Bertrand-Huleux M., Pablo A.-L., … Cournac L. (2017) Pearl millet genetic traits shape rhizobacterial diversity and modulate rhizosphere aggregation. *Frontiers in Plant Science* **8**, 1–14.

Ndour P.M.S., Heulin T., Achouak W., Laplaze L. & Cournac L. (2020) The rhizosheath: from desert plants adaptation to crop breeding. *Plant and Soil* **456**, 1–13.

Nie L., Peng S., Chen M., Shah F., Huang J., Cui K. & Xiang J. (2012) Aerobic rice for water-saving agriculture. A review. *Agronomy for Sustainable Development* **32**, 411–418.

Olsson L., Barbosa H., Bhadwal S., Cowie A., Delusca K., Flores-Renteria D., … Stringer L. (2019) Land Degradation. *Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems*, 345–436.

van Oort P.A.J. & Zwart S.J. (2018) Impacts of climate change on rice production in Africa and causes of simulated yield changes. *Global Change Biology* **24**, 1029–1045.

Van Oosterom E.J., Yang Z., Zhang F., Deifel K.S., Cooper M., Messina C.D. & Hammer G.L. (2016) Hybrid variation for root system efficiency in maize: Potential links to drought adaptation. *Functional Plant Biology* **43**, 502–511.

Paliwal R., Abberton M., Faloye B. & Olaniyi O. (2020) Developing the role of legumes in West Africa under climate change. *Current Opinion in Plant Biology* **56**, 242–258.

799 Passot S., Gnacko F., Moukouanga D., Lucas M., Guyomarc'h S., Ortega B.M., …
800   Laplaze L. (2016) Characterization of pearl millet root architecture and anatomy
801   reveals three types of lateral roots. *Frontiers in plant science* **7**, 829.

802 Passot S., Moreno-Ortega B., Moukouanga D., Balsera C., Guyomarc'h S., Lucas M., …
803   Guédon Y. (2018**)** A new phenotyping pipeline reveals three types of lateral roots
804   and a random branching pattern in two cereals. *Plant Physiology* **177**, 896-9.

805 Pearson C.J., Norman D.W., Dixon J. (1995) Sustainable dryland cropping in relation to
806   soil productivity. *FAO Soils Bulletin* **72**, 157.

807 Peng S., Bouman B., Visperas R.M., Castañeda A., Nie L. & Park H.K. (2006)
808   Comparison between aerobic and flooded rice in the tropics: Agronomic
809   performance in an eight-season experiment. *Field Crops Research* **96**, 252–259.

810 Pingali P.L. (2012) Green revolution: Impacts, limits, and the path ahead. *Proceedings*
811   *of the National Academy of Sciences of the United States of America* **109**, 12302–
812   12308.

813 Promkhambut A., Polthanee A., Akkasaeng C. & Younger A. (2011) Growth, yield and
814   aerenchyma formation of sweet and multipurpose sorghum (*Sorghum bicolor* L.
815   Moench) as affected by flooding at different growth stages. *Australian Journal of*
816   *Crop Science* **5**, 954–965.

817 Rebouillat J., Dievart A., Verdeil J.L., Escoute J., Giese G., Breitler J.C., … Périn C.
818   (2009) Molecular genetics of rice root development. *Rice* **2**, 15–34.

819 Reynolds M., Atkin O.K., Bennett M., Cooper M., Dodd I.C., Foulkes M.J., … Wittich
820   P.E. (2021) Addressing research bottlenecks to crop productivity. *Trends in plant*
821   *science* **26**, 607–630.

822 Rostamza M., Richards R.A. & Watt M. (2013) Response of millet and sorghum to a
823   varying water supply around the primary and nodal roots. *Annals of Botany* **112**,
824   439–446.

825 Ryan S.F., Adamson N.L., Aktipis A., Andersen L.K., Austin R., Barnes L., … Dunn R.R.
826   (2018) The role of citizen science in addressing grand challenges in food and
827   agriculture research. *Proceedings of the Royal Society B: Biological Sciences* **285**,
828   20181977.

829 Salih A.A., Ali I.A., Lux A., Luxova M., Cohen Y., Sugimoto Y. & Inanaga S. (1999)
830   Rooting, water uptake, and xylem structure adaptation to drought of two sorghum
831   cultivars. *Crop Science* **39**, 168–173.

832 Sandhu N., Anitha Raman K., Torres R.O., Audebert A., Dardou A., Kumar A. & Henry
833   A. (2016) Rice root architectural plasticity traits and genetic regions for adaptability
834   to variable cultivation and stress conditions. *Plant Physiology* **171**, 2562–2576.

835 Sandhu N., Dixit S., Swamy B.P.M., Raman A., Kumar S., Singh S.P., … Kumar A.
836   (2019) Marker assisted breeding to develop multiple stress tolerant varieties for
837   flood and drought prone areas. *Rice* **12**, 8.

838 Sandhu N., Subedi S.R., Yadaw R.B., Chaudhary B., Prasai H., Iftekharuddaula K., …
839   Kumar A. (2017) Root traits enhancing rice grain yield under alternate wetting and
840   drying condition. *Frontiers in Plant Science* **31**, 1879.

841 Sasaki Y., Hosen Y., Peng S., Nie L., Rodriguez R., Agbisit R., … Bouman B.A.M.
842   (2010) Do abiotic factors cause a gradual yield decline under continuous aerobic
843   rice cultivation? A pot experiment with affected field soils. *Soil Science and Plant*
844   *Nutrition* **56**, 476–482.

845 Schneider H.M. & Lynch J.P. (2020) Should root plasticity be a crop breeding target?
846   *Frontiers in Plant Science* **11**, 1–16.

847 Sebastian J., Yee M.-C., Goudinho Viana W., Rellán-Álvarez R., Feldman M., Priest
848   H.D., … Dinneny J.R. (2016) Grasses suppress shoot-borne roots to conserve
849   water during drought. *Proceedings of the National Academy of Sciences* **113**,
850   8861–8866.

851 Sheahan M. & Barrett C.B. (2017) Ten striking facts about agricultural input use in Sub-
852   Saharan Africa. *Food Policy* **67**, 12–25.

853 Singh V., van Oosterom E.J., Jordan D.R., Messina C.D., Cooper M. & Hammer G.L.
854   (2010) Morphological and architectural development of root systems in sorghum
855   and maize. *Plant and Soil* **333**, 287–299.

856 Strock C.F., Burridge J., Massas A.S.F., Beaver J., Beebe S., Camilo S.A., … Lynch
857   J.P. (2019) Seedling root architecture and its relationship with seed yield across
858   diverse environments in *Phaseolus vulgaris*. *Field Crops Research* **237**, 53–64.

859 Strock C.F., Burridge J.D., Niemiec M.D., Brown K.M. & Lynch J.P. (2020) Root
860   metaxylem and architecture phenotypes integrate to regulate water use under
861   drought stress. *Plant Cell and Environment* **44**, 49–67.

862 Sultan B., Defrance D. & Iizumi T. (2019) Evidence of crop production losses in West
863   Africa due to historical global warming in two crop models. *Scientific Reports* **9**, 1–
864   15.

865 Tan X., Shao D., Liu H., Yang F., Xiao C. & Yang H. (2013) Effects of alternate wetting
866   and drying irrigation on percolation and nitrogen leaching in paddy fields. *Paddy*
867   *and Water Environment* **11**, 381–395.

868 Vadez V. (2014) Root hydraulics: The forgotten side of roots in drought adaptation.
869   *Field Crops Research* **165**, 15–24.

870 Vadez V., Kholova J., Medina S., Kakkera A. & Anderberg H. (2014) Transpiration
871   efficiency: New insights into an old story. *Journal of Experimental Botany* **65**, 6141–
872   6153.

873 Vadez V., Kholová J., Yadav R.S. & Hash C.T. (2013) Small temporal differences in
874   water uptake among varieties of pearl millet (*Pennisetum glaucum* (L.) R. Br.) are
875   critical for grain yield under terminal drought. *Plant and Soil* **371**, 447–462.

876 Vallino M., Fiorilli V. & Bonfante P. (2014) Rice flooding negatively impacts root
877   branching and arbuscular mycorrhizal colonization, but not fungal viability. *Plant,*
878   *Cell and Environment* **37**, 557–572.

879 Vanlauwe B., Hungria M., Kanampiu F. & Giller K.E. (2019) The role of legumes in the
880   sustainable intensification of African smallholder agriculture: Lessons learnt and
881   challenges for the future. *Agriculture, Ecosystems and Environment* **284**, 106583.

882 Varney G.T., Canny M.J., Wang X.L. & Mccully M.E. (1991) The branch roots of *Zea*. I.
883   First order branches, their number, sizes and division into classes. *Annals of*
884   *Botany* **67**, 357–364.

885 Vieira R.F., Jochua C.N. & Lynch J.P. (2007) Method for evaluation of root hairs of
886   common bean genotypes. *Pesquisa Agropecuaria Brasileira* **42**, 1365–1368.

887 Wang Y., Zhao X., Wang L., Zhao P.H., Zhu W. Bin & Wang S.Q. (2016a) Phosphorus
888   fertilization to the wheat-growing season only in a rice–wheat rotation in the Taihu
889   Lake region of China. *Field Crops Research* **198**, 32–39.

890 Wang Z., Zhang W., Beebout S.S., Zhang H., Liu L., Yang J. & Zhang J. (2016b) Grain
891   yield, water and nitrogen use efficiencies of rice as influenced by irrigation regimes
892   and their interaction with nitrogen rates. *Field Crops Research* **193**, 54–69.

893 Wortmann C.S., Kirkby R.A., Eledu C.A. & Allen D.J. (1998) *Atlas of common bean*
894   *(Phaseolus vulgaris L.) production in Africa*, CIAT publication. CIAT publication,
895   Cali, Colombia.

896 Yan X., Liao H., Beebe S.E., Blair M.W. & Lynch J.P. (2004) QTL mapping of root hair
897   and acid exudation traits and their relationship to phosphorus uptake in common
898   bean. *Plant and Soil* **265**, 17–29.

899 York L.M., Carminati A., Mooney S.J., Ritz K. & Bennett M.J. (2016) The holistic
900   rhizosphere: Integrating zones, processes, and semantics in the soil influenced by
901   roots. *Journal of Experimental Botany* **67**, 3629–3643.

902 You L., Wood S., Wood-Sichra U. & Wu W. (2014) Generating global crop distribution
903   maps: From census to grid. *Agricultural Systems* **127**, 53–60.

904 Zhan A., Schneider H. & Lynch J.P. (2015) Reduced lateral root branching density
905   improves drought tolerance in maize. *Plant Physiology* **168**, 1603–1615.

906 Zhang S., Guo X., Yun W., Xia Y., You Z. & Rillig M.C. (2020) Arbuscular mycorrhiza
907   contributes to the control of phosphorus loss in paddy fields. *Plant and Soil* **447**,
908   623–636.

909 Zheng Z., Hey S., Jubery T., Liu H., Yang Y., Coffey L., … Schnable P.S. (2020) Shared
910   Genetic control of root system architecture between *Zea mays* and *Sorghum*
911   *bicolor*. *Plant Physiology* **182**, 977–991.

912 Zhu J., Brown K.M. & Lynch J.P. (2010) Root cortical aerenchyma improves the drought
913   tolerance of maize (*Zea mays* L.). *Plant, Cell and Environment* **33**, 740–749.

914 Zierer W., Rüscher D., Sonnewald U. & Sonnewald S. (2021) Tuber and tuberous root
915 development. *Annual Review of Plant Biology* **72**, 551–580
916

917 **Table 1.** Summary of yield and income impact of P efficient varieties. Fixed costs of
918   production mean twice as much yield has more than twice as much impact on
919   income. Data from documents submitted to Mozambican Seed Release committee.

	Local variety	P-efficient variety
Yield, no P fert	737 kg / ha	1412 kg / ha
Yield, with P fert	1484 kg / ha	2844 kg / ha
Income gain, no P fert	-	249%
Income gain, with P fert	-	148%

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