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INVITED REVIEW

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Root traits for low input agroecosystems in Africa: Lessons from three case studies

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Abstract

In many regions across Africa, agriculture is largely based on low-input and smallholder farming systems that use little inorganic fertilisers and have limited access to irrigation and mechanisation. Improving agricultural practices and developing new cultivars adapted to these environments, where production already suffers from climate change, is a major priority for food security. Here, we illustrate how breeding for specific root traits could improve crop resilience in Africa using three case studies covering very contrasting low-input agroecosystems. We first review how greater basal root whorl number and longer and denser root hairs increased P acquisition efficiency and yield in common bean in South East Africa. We then discuss how water-saving strategies, root hair density and deep root growth could be targeted to improve sorghum and pearl millet yield in West Africa. Finally, we evaluate how breeding for denser root systems in the topsoil and interactions with arbuscular mycorrhizal fungi could be mobilised to optimise water-saving alternate wetting and drying practices in West African rice agroecosystems. We conclude with a discussion on how to evaluate the utility of root traits and how to make root trait selection feasible for breeders so that improved varieties can be made available to farmers through participatory approaches.

KEYWORDS
arbuscular mycorrhizal symbiosis, rhizosphere, root anatomy, root architecture

1 | INTRODUCTION

The Green Revolution was driven by the development of novel cultivars along with government subsidised fertiliser inputs, mechanisation 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 et al., 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%–3% of the lands cultivated by smallholders are irrigated and no more than 10% of the households have irrigation capacity (Sheahan & Barrett, 2017). Concerning fertilisation, 41% of the cultivated plots in Nigeria, 17% in Niger and 3.2% in Uganda used inorganic fertiliser, 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

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suffers from degradation due to erosion, desertification, deforestation and poor agricultural practices (Eswaran et al., 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) For instance, phosphorus depletion from agricultural soils due to water erosion is 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 fertilisers (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 minimising expenditure (Fess et al., 2011; Gemenet et al., 2016; Joshi et al., 2016; Lynch, 2007). For this, identification of useful traits and their combinations for crops grown in low-input agroecosystems and their integration into breeding programmes is of major importance. Foremost among the challenges is developing and deploying phenotyping tools in these environments, understanding genotype by environment interactions (GxE, i.e., how the environment influences the response of different genotypes) and generating truly integrative phenotyping and selection approaches that ultimately increase yield and smallholder incomes (Reynolds et al., 2021) .

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

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

2 | 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 (Beebe, 2012; Wortmann et al., 1998). 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 (1) low phosphorus (P) availability in highly P fixing soils, (2) terminal and/or intermittent drought and (3) acid soil complexes, pathogens and insects limiting root growth and causing elevated root mortality (Lynch, 2019). These challenges are further complicated by irrigation systems, fertilisers and other soil amendments being poorly accessible 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. Farmers in Mozambique typically grow a variety of landraces along with a limited number of varieties including Doutor, Bonus, Manteiga and ICA Pijao, all released in the 1990s (Harries et al., 2009). They are known to be robust, in that they yield something in most years, but have relatively low yield potential and have sensitivity to low soil fertility, drought and disease. 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. While tradeoffs between low fertility tolerance and drought tolerance have been observed and linked to exploration of shallow versus deep soil zones, greater P acquisition efficiency is the more fundamental challenge in that particular context and may actually improve drought tolerance by improving overall plant growth as P is a major limiting factor (Lynch & Ho, 2005). Greater P acquisition is also related to increased biological nitrogen fixation and yield. With a larger shoot biomass shielding the soil, erosion is also reduced (Henry et al., 2009, 2010).

Greater basal root whorl number and longer and denser root hairs traits were targeted to increase common bean P acquisition efficiency. These traits have genetic control (Yan et al., 2004) and affect the zone of soil explored (Figure 1a), they can be easily and rapidly phenotyped in the field with resources readily available in less developed countries (Burridge et al., 2016), modifications of these traits do not require any change to the cropping system or farmer practices, and they have multi-scale impact.

Basal roots are a class of roots specific to dicots with epigeal germination and emerge from the transition zone between radicle and hypocotyl (Burridge et al., 2020). In common bean, basal roots emerge in whorls composed of four individual roots, due to its tetrarch vascular patterning (Figure 1b; Miguel et al., 2013). Basal root whorl number is under genetic control and ranges from 1 to 5, with two being the mode (Miguel et al., 2013). It can be phenotyped using low cost root roll-ups 5–9 days after germination (Figure 1b) and is associated with field phenotypes and field performance (Jochua et al., 2020; Strock, Burridge, et al., 2019). Varieties grown in Mozambique (Doutor, Bonus, Manteiga and ICA Pijao) have 2–3 basal root whorls. Greater basal root whorl number increases the vertical zone of soil explored, enabling the efficient exploration of both deep and shallow soil. It also affords a degree of root redundancy that is having multiple roots of a given type that can compensate for each other should one be lost to herbivory or disease. While root redundancy could reduce root system efficiency by increasing metabolic burden, the benefits of root redundancy likely outweigh the costs. In typical small-holder environments where roots are frequently lost due to biotic (pathogen or insect attack) or abiotic stresses, redundancy ensures that at least a few roots will survive to contribute to both deep and shallow resource acquisition (Strock, Schneider, et al., 2019).

Root hairs are subcellular protrusions emerging from specialised epidermal cells on all root classes. Root hair length and density are under genetic control and have been related to greater P acquisition in multiple crops and experimental systems (Hanlon et al., 2018; Yan et al., 2004). Root hairs have minimal construction and maintenance

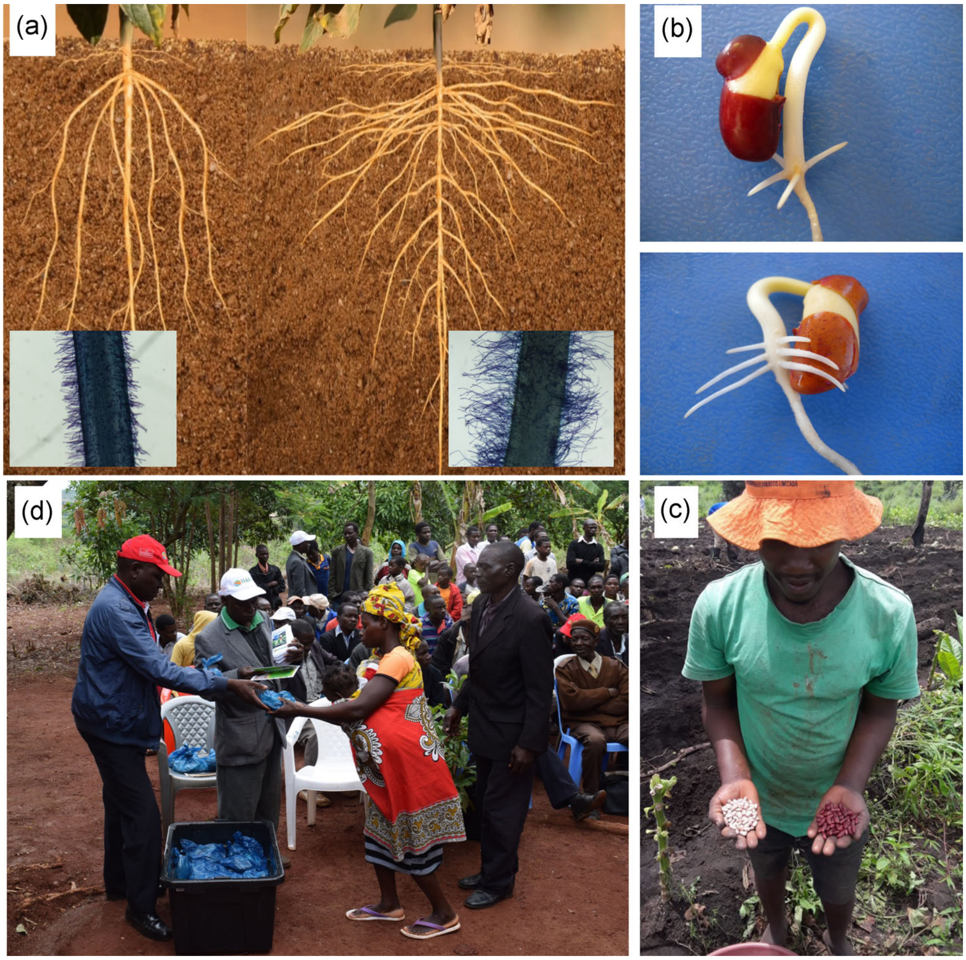

FIGURE 1 Greater basal root whorl number (BRWN) and longer and denser root hairs were selection targets to improve common bean production for small-holder farmers in Mozambique. (a) Root on left shows a typical older variety with fewer basal roots and short root hairs. Image on right represents the improved varieties with more BRWN and longer root hairs. (b) Bean seedling 4 days after imbibition showing 1 BRWN (top) and 3 BRWN (bottom). (c) Improved beans in hands of smallholder farmers generating certified seed. (d) Seed distribution in a Mozambican village as part of a pilot promotional campaign studied seed distribution, adoption and sharing. Image credits: a) still of movie sponsored by the CCRP and Mcknight Foundation (available at roots.psu.edu), photos of long and short root hairs courtesy of Anica Masas, (b) courtesy of Katy Barlow, (c) photo by Magalhaes Miguel, (d) photo of seed distribution by James Burridge

costs making them an extremely efficient means to increase root volume and acquire immobile soil resources such as P, with no known trade-offs (Lynch, 2019). They are relatively easy to phenotype at the seedling stage using a low-cost root roll-up protocol (Vieira et al., 2007). Substantial synergy between greater root hairs and basal root growth angle have been observed in common bean in which the advantage of longer and denser root hairs is magnified when paired with shallow basal root growth (Miguel et al., 2015). Shallower basal root growth angle and longer and increased density of root hairs traits are ideal selection targets for improving P acquisition efficiency (Figure 2a).

In Mozambique, the selection strategy for improving P acquisition efficiency varieties involved extensive phenotyping of varieties and breeding lines to identify accessions possessing high basal root whorl number as well as long and dense root hairs (Burridge et al., 2019). These superior lines were then crossed with common varieties either already grown in Mozambique or to varieties with similar and desirable agronomic and market characteristics, such as seed colour and size. Several early generations of these lines were grown at the experimental stations with non-limiting conditions to select them for acclimation, grain quality, shoot architecture, disease and pest tolerance. Subsequently, seeds from F4 plants were evaluated for key root hair traits with those possessing longer and denser root hairs being advanced. Targeted field-based selection of varieties took place first on multiple stations across Mozambique with single constraints, such as low soil phosphorus or terminal drought. Simultaneously, selections were made on more remote stations and farmers' fields with multiple, interacting constraints. A final set of 40 varieties were included in a round of on-farm participatory variety selection using a citizen science approach in which each farmer received a random pack of three varieties to evaluate on their farm and under their management practices. Data were analysed on a regional basis. This dispersed and low risk technology evaluation and dissemination methodology, called triadic comparison of technology options (tricot) helps to identify the most suitable varieties for local agricultural conditions (van Etten et al., 2019). As a result, three new varieties of common bean, named Kufuna, Tiyela, and Matina, have been released in Mozambique. Trials on station and on farmer's fields suggest these lines have roughly double the yield of local varieties when grown with or without P fertiliser (Table 1). This is a noteworthy achievement, in part because no new varieties had been

TABLE 1 Summary of yield and income impact of P efficient common bean varieties

	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%

Note: Fixed costs of production mean twice as much yield has more than twice as much impact on income. Data from documents submitted to the Mozambican Seed Release committee.

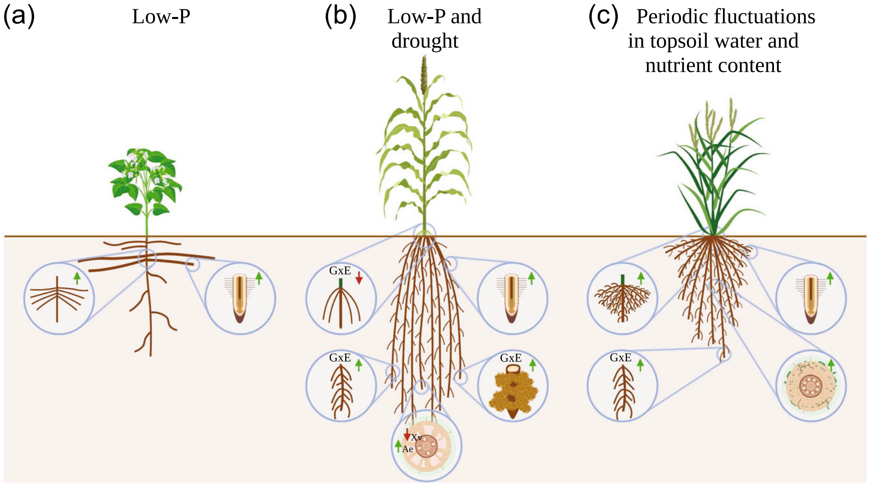

FIGURE 2 Root traits to optimise resources acquisition in common bean (left), sorghum (middle) and rice (right) when grown in low-input environments. For common bean grown in low-P soils, increased basal root whorl number and longer and denser root hairs were targeted to improve P acquisition efficiency. Proposed selection targets for sorghum grown in drought-prone regions with low-P soils in Sahelian Africa include greater root hair length and density for increased P acquisition, decreased crown root number and more aerenchyma (Ae) for decreased carbon cost of root tissues and deep growth plasticity, potentially combined with reduced xylem vessel (Xv) diameter or number for increased water use efficiency. Plasticity (GxE) in crown root number and lateral root branching at depth as well as rhizosheath formation are potential drought adaptive responses. In alternate wet and dry rice agroecosystems, proposed adaptive responses to periodic topsoil fluctuations in water and nutrient content include root hair development, increased crown root number and lateral branching in topsoil, combined with greater beneficial interactions with arbuscular-mycorrhizal fungi and deep root growth and branching plasticity. Figure was created with BioRender.com [Color figure can be viewed at wileyonlinelibrary.com]

released in Mozambique for over 12 years, and none of those previously released were bred specifically for Mozambique.

To further promote and study how new varieties are shared and impact yield, food security and local economies, a pilot promotional campaign was organised in three different regions and compared to three regions that received the improved varieties but not the promotional campaign (Figure 1c,d). Data are still being collected and analysed. Stocks of breeder and pre-basic seed are maintained by the Mozambican Agricultural Research Institute and a collaborative model involving the Mozambican Agricultural Research Institute, farmers organisation, and seed companies were used to amplify these varieties from zero to 45 tons of seeds in just three years from 2018 to 2021. This amount of seeds will enable 3600 hectares of improved P-efficient varieties to be planted in the 2021–2022 season, up from zero in the 2018–2019 season. This mixed public, private and farmer organisation model promotes the maximum penetration of the new varieties and promotes long-term sustainability for both companies and farmer organisations. Other varieties of the common bean are in various stages of development with some nearly ready for release and others in on-farm trials.

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

3 | CASE STUDY 2: IMPROVING WATER AND NUTRIENT ACQUISITION IN DRYLAND CEREALS IN WEST AFRICA

Sorghum (*Sorghum bicolor* [L.] Moench) and pearl millet (*Pennisetum glaucum* [L.] R. Br.) are the fifth and sixth most important cereal crops in the World (FAOSTAT 2021). They are well adapted to arid and semi-arid environments found in sub-Saharan Africa. In these regions, they are grown one cycle a year during the rainy season by smallholder farmers and represent a major source of micronutrient protein for humans and fodder for livestock. They are usually sown at low density (around 10,000 plants per hectare; Pearson, Norman, Dixon 1995) before or right after the first rain of the season and grown with no or low inputs simply because water and fertilisers are inaccessible and/or unaffordable (Matlon 1990; vom Brocke et al., 2010). Although sorghum and pearl millet prevail in these environments where other mainstream crops tend to fail, their yield remains low and is increasingly threatened by high temperature and intermittent drought caused by climate change and soil degradation caused by loss of nutrients and soil organic carbon, a phenomenon accentuated by desertification and erosion (Sultan et al., 2019). Therefore, improving the resilience of sorghum and pearl millet is particularly important for food security in arid and semi-arid regions of Africa and for adaptation of African agriculture to future climates.

Sorghum and pearl millet root systems are characterised by a single embryonic seminal root (Passot et al., 2016; Singh et al., 2010). In sorghum and pearl millet, as in their genetic relative maize, multiple post-embryonic crown and brace roots that originate from the belowground and aboveground nodes, respectively, can be observed (Chopart et al., 2008; Faye et al., 2019; Singh et al., 2010; Tsuji et al., 2005). Primary, seminal and nodal roots all have lateral roots. In pearl millet, as in maize, three different types of lateral roots have been identified that differ by length, diameter and internal structures (Passot et al., 2016; Varney et al., 1991), as well as by their growth dynamics (Passot et al., 2018). In sorghum, large variability in crown root angle and root area was observed in diversity panels, backcross nested association mapping (BCNAM) populations and recombinant inbred lines (Joshi et al., 2017; Mace et al., 2012). Similarly, diversity in primary root growth and root branching (Passot et al., 2016), and root length density (Faye et al., 2019) was observed in pearl millet. This suggests that root traits could be breeding targets for improvement of sorghum and pearl millet (Joshi et al., 2016).

In dry and hot climates of Western Africa, improving transpiration efficiency (biomass produced/water transpired) over the entire crop cycle has been demonstrated as important for drought tolerance, especially when occurring at reproductive stage (Kholová et al., 2010; Vadez et al., 2013). Reduced xylem conductance capacity has been targeted in strategies aiming at improving transpiration efficiency (Vadez et al., 2014). In wheat for instance, reduced xylem diameter and the associated reduced root hydraulic conductance resulted in plants with more conservative water use that yielded 11% more grains under drought conditions (Richards & Passioura, 1989). Sorghum lines with higher number of xylem vessels showed higher transpiration rate, suggesting that reducing xylem vessel numbers in this crop is associated with water saving strategies (Salih et al., 1999). Recent genome wide association studies on root metaxylem area and number in barley (Oyiga et al., 2020) and in rice (Kadam et al., 2017) identified potential interesting candidate genes controlling these traits, including the barley *ZIFL2* and the rice *SCARECROW* whose homologous in *Arabidopsis thaliana* control auxin transport and radial anatomy, respectively (Di Laurenzio et al., 1996; Remy et al., 2013). Another means of improving transpiration efficiency consists in restriction of transpiration in response to increasing vapour pressure deficit (Sinclair et al., 2005; Vadez et al., 2014). In pearl millet, transpiration restriction to VPD has been linked to modulation of aquaporin functions in roots and leaves (Reddy et al., 2017) but the precise role of root-related traits in this response remains to be explored.

Growing deeper roots might be another interesting trait for drought tolerance of sorghum and pearl millet grown in sub-Saharan Africa where soils are generally deep and sandy with low water retention (Joshi et al., 2016). Means for a plant to grow deeper roots relates to its ability to develop nodal roots with steeper growth angle (Lynch 2013). In sorghum, quantitative trait loci (QTLs) for steep nodal root angle colocalizing with previously identified stay-green and grain yield QTLs showed synteny with previously identified root angle QTLs in maize (Borrell et al., 2014; Mace et al., 2012). In fact, conserved genetic control of root architectural traits have been observed in sorghum and maize (Zheng et al., 2020), suggesting that comparative analyses of root traits from both species could be useful for improvement of their root functions (Lynch, 2018). In this regard, the sorghum homologue of *CALCINEURIN B-LIKE PROTEIN (CBL)-INTERACTING SERINE/THREONINE-PROTEIN KINASE 15* (*ZmCIPK15*) identified as quantitatively controlling root angle in maize may be of interest (Schneider et al., 2021). Other means of growing deeper roots relates to root metabolic cost and optimisation of root carbon allocation (Lynch 2013, 2018; van Oosterom et al., 2016) that can be achieved either by reducing crown root number or lateral root density in shallow soils (Gao & Lynch 2016; Zhan et al., 2015), reducing root cortical cell file number (Burton et al., 2013; Jaramillo et al., 2013), increasing cortical cell size (Chimungu et al., 2014) or increasing root cortical aerenchyma (Chimungu et al., 2015; Zhu et al., 2010). In maize, such traits were associated with deeper root growth, greater water capture at depth and improved plant water status and yield under drought (Lynch, 2018).

Low available P in soils is another key limiting factor for crop yield in West Africa. A recent study of the genetic architecture of phosphorus efficiency in sorghum showed colocalization between QTLs for P acquisition efficiency, grain yield, total root surface area and individual root diameter (Bernardino et al., 2019). One of these sorghum QTL located close to the homologue of the rice serine/threonine kinase *OsPSTOL1*, which was previously found to enhance early root growth and grain yield in rice under low-P (Bernardino et al., 2019; Gamuyao et al., 2012). However, since P tends to accumulate in shallow soils and water in deep soils, there are trade-offs between root traits beneficial for water and P acquisition. Therefore, increased shallow soil root hair length and density combined with drought-inducible deep root growth plasticity could co-optimise low P and drought tolerance.

Plasticity in response to drought has been observed for nodal root growth in sorghum and pearl millet, with a reduction of nodal root length in dry soil in pots (Rostamza et al., 2013). Similar responses have been observed in field conditions in improved elite varieties of sorghum (Soumba from Mali in particular) where root length density was reduced in shallow soil and increased in deep soils in plants growing under drought as compared to plants growing under irrigated conditions (Gano et al., 2021). In pearl millet, increased deep root growth was also observed in variety SL28 (a dual purpose variety from Senegal selected for fodder and grain yield) under drought (Faye et al., 2019). A recent study characterised the genetics of root architectural plasticity in maize using association genetics (Schneider, Klein, Hanlon, Nord, et al., 2020).

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, that is whose physico-chemical and biological properties are modified by the root, which, in turn, impacts plant nutrition, development and physiology (de la Fuente Cantó et al., 2020). One potential rhizosphere target trait in sorghum and pearl millet would be rhizosheath formation, that is, the aggregation of soil particles around the roots (P. M. S. Ndour et al., 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 (Brown et al., 2017; Duell & Peacock, 1985; P. M. S. Ndour et al., 2017). A positive impact of the rhizosheath on water and mineral nutrition was reported for several plants in laboratory conditions and could be partly explained by improved contact between the soil and the root surface (P. M. S. 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 (P. M. S. Ndour et al., 2021) even if it seems to be under complex genetic control in pearl millet (de la Fuente Canto et al., submitted). As rhizosheath formation is positively correlated with root hair length in wheat and barley, QTLs increasing root hair length and/or density to improve P capture could also indirectly improve rhizosheath formation (Delhaize et al., 2015; George et al., 2014). However, rhizosheath formation could represent a significant carbon sink, and further work is needed to demonstrate the impact of a larger rhizosheath on dryland cereals in West African field conditions.

In conclusion, lessons learnt mostly from studies on maize indicate that greater root hair length and density in shallow soil for increased P acquisition, combined with deeper root growth through improved root metabolic cost (more aerenchyma for instance) for increased water acquisition, and reduced xylem vessel diameter for improved water use efficiency could be interesting selection targets for dryland cereals grown in low P soils and drought-prone regions of West Africa (Figure 2b, Table 2). Plasticity (GxE) in deep root lateral branching through reduced crown root number as well as rhizosheath formation may represent drought adaptive responses (Figure 2b, Table 2).

4 | CASE STUDY 3: WATER-SAVING RICE AGROECOSYSTEMS FOR WEST AFRICA

Rice is the most consumed cereal in West-Africa and demand for rice is increasing rapidly, mostly due to population growth and changes in consumption pattern linked to increased urbanisation (ECOWAS 2019; Elbehri et al., 2013). Currently, local production covers only roughly 60% of the demand (ECOWAS, 2019). Several programmes have been launched to increase local production leading to a surge in total rice production in West Africa by 104,3% from 2009 to 2019 through an increase in total cultivated area (FAOSTAT, 2021). A further 79.4% increase will be needed between 2019 and 2025 to fully meet the projected demand (ECOWAS, 2019).

TABLE 2 Summary of the proposed target traits to improve common bean, sorghum, pearl millet and rice adaptation to low P, drought and fluctuations in topsoil water and nutrient content respectively

		Common bean	Sorghum and pearl millet	Rice	
Low P	Increased number of basal/nodular roots	✓		X	Burridge et al. (2019) Zhang et al. (2016) Sandhu et al. (2017)
	Longer and denser root hairs	✓	X	X	Miguel et al. (2015)
	Root branching in topsoil			X	De Bauw et al. (2020) Sandhu et al. (2017)
Drought	Rhizosphere interactions	X	X	X	P. M. S. Ndour et al. (2020)
	Low root metabolic cost		X		Jaramillo et al. (2013) Chimungu et al. (2014) Chimungu et al. (2015)
	Reduced xylem diameter		X		Richards and Passioura (1989)
	Deep root growth plasticity		X	X	-

Note: ✓ indicates traits that were validated in the corresponding species while X indicates proposed targets.

In West Africa, roughly 12% of the harvested rice area is irrigated (You et al., 2014). Irrigated rice is the most productive agroecosystem and two 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 & Zwart 2018).

However, irrigated rice cultivation requires a large amount of freshwater. In a dry environment as is found in large parts of West Africa, traditional irrigated rice cultivation requires between 700 and 1500 mm of water to produce 1 kg of rice per year (Bhuiyan 1992). Furthermore, climate change is trending towards a hotter and dryer atmosphere in the region, which will increase evaporative demand. With increased competition from industries and city for freshwater and increased uncertainty in precipitation patterns, it will not be possible to meet the growing demand using the conventional irrigated rice cultivation system (Nie et al., 2012).

Several water-saving alternatives have been suggested to reduce water consumption and increase cultivated surfaces. Aerobic rice cultivation aims to maximise crop water use efficiency by growing plants in soil without flooding or puddling (Matsunami et al., 2009; Matsuo et al., 2009). It allows greater water savings and can be deployed in regions without access to irrigation water but has a high yield penalty and is associated with increased weed management and risks of nematodes (Meena et al., 2019).

Alternate wetting and drying is an intermediate cropping system where intermittent irrigation co-optimises yield potential and water usage. In this system irrigation is periodically stopped until the soil water table reaches a certain depth, easily measured using a pipe set in the soil, and then re-started until the field is flooded again (Bouman & Tuong, 2001). Alternate wetting and drying cycles are repeated either during the vegetative or flowering stage or throughout the rice cultivation cycle, although keeping paddies flooded in hot environments during the flowering stage help avoid the problems linked to heat sensitivity through the cooling effect of evaporation (Jagadish et al., 2015).

Two types of alternate wetting and drying have been described: moderate alternate wetting and drying when field water level is allowed to drop down to 15 cm below the soil surface, and severe alternate wetting and drying when soils are allowed to dry beyond −20 kPa (Carrijo et al., 2017). Alternate wetting and drying can be easily adopted as it does not change the cultivation practices, is not associated with increased labour needs and can contribute to a reduction in water consumption of 5%–30%, depending on the season and soil, as well as reduced methane emissions and grain arsenic levels (Carrijo et al., 2017; Linquist et al., 2015). Alternate wetting and drying has a limited yield penalty (5.4% in a meta-analysis of 56 studies, Carrijo et al., 2017) but the yield decrease is more important in severe alternate wetting and drying or if alternate wetting and drying is maintained throughout the crop cycle (Carrijo et al., 2017). The impact on yield is also very dependent on the genotype and most of the currently used high-yield varieties such as the popular IR64 variety show yield reduction in alternate wetting and drying (Carrijo et al., 2017; Sandhu et al., 2017). Thus, there is a clear need to develop new varieties to optimise yield in alternate wetting and drying rice agroecosystems.

Alternate wetting and drying results in periodic changes in water content in the topsoil but also changes the dynamics of nutrient availability and in particular of N and P availability (Acosta-Motos et al., 2020; Wang, Zhao, et al., 2016). For instance, it increases topsoil P availability and has been linked with changes in the soil microbiota and the stimulation of aerobic P-solubilizing bacteria in the aerobic topsoil compartment (Li et al., 2018). Conversely, N availability seemingly decreases upon alternate wetting and drying due to increased denitrification, volatilisation and leaching although these losses can be avoided by timely N application (Djaman et al., 2018; Tan et al., 2013). Water and N signalling are known to interact in ways that affect root traits for synergistic or antagonistic resource uptake (reviewed in Araus et al., 2020). Hence, varieties for alternate wetting and drying agroecosystems need to be adapted to fluctuations in soil water and nutrient content in the topsoil.

The use of root traits has been little explored in such agroecosystems, but could support increased water, phosphorus (P) and nitrogen (N) use efficiency. Large genetic diversity for root traits is available in rice (Ahmadi et al., 2014). Root traits that increase the volume of topsoil explored and promote P uptake should be prioritised to improve rice yields in alternate wetting and drying systems. Traits that merit investigation include nodal root number, lateral root density (there are two types of lateral roots in rice, thin and determinate short lateral roots and indeterminate long lateral roots; Rebouillat et al., 2009), and root hair length and density.

A recent large-scale study by Sandhu et al. (2017) is consistent with nodal root number and lateral root density positively impacting yield in alternate wetting and drying agroecosystems. Evaluation of new rice varieties derived from crosses between popular varieties and drought-tolerant accessions was performed in fully irrigated and alternate wetting and drying systems in seven sites across Asia (Sandhu et al., 2017). Out of 82 lines tested in at least three sites, lines with stable and high yield in alternate wetting and drying conditions compared to irrigated conditions were identified. Analyses of the root phenotype of a subset of these stable high-yielding lines and the control line IR64 (popular high yield lowland variety widely grown in Asia and part of Africa that shows a reduction in yield in alternate wetting and drying) showed that increased nodal root number and root dry weight at 10–20 cm depth (dependent on nodal root number and root branching) were associated with maintained grain yield under alternate wetting and drying (Sandhu et al., 2017). Similarly, a study performed using a combination of pot experiments and functional-structural plant model indicated that root system P acquisition efficiency is improved by increased root branching both in irrigated and water stress conditions (De Bauw et al., 2020). In alternate wetting and drying, P acquisition was shown to occur mainly at the root tip and led to P depletion along the root due to the low mobility of P in the soil (De Bauw et al., 2020). An increased number of root tips (through increased nodal root number and branching) would therefore improve P uptake. As mentioned in other case studies, increased root hair length would also be desirable.

Alternate wetting and drying seems to have a positive effect on root growth as indicated by increased root biomass and maximum root length (Acosta-Motos et al., 2020; Wang, Zhang, et al., 2016). This might simply be a positive response to a mild water stress on root growth potentially mediated by ABA (Miao et al., 2021). Interestingly, these quantitative changes in root traits induced after initiation of alternate wetting and drying cycle, that is plasticity response of the root system, were shown to be important for yield stability (Sandhu et al., 2017). In the best performing lines under alternate wetting and drying (initially selected as drought-tolerant breeding lines), the number of nodal roots below 20 cm and deep root length at the flowering stage appears to have a positive effect on yield. Therefore, while increased nodal root number and root branching in the topsoil improved P uptake in these lines, root growth plasticity in deeper soil layers may improve water and nitrogen acquisition (Figure 2c). Selecting for increased deep root growth and branching in response to alternate wetting and drying (plasticity) would reduce the tradeoff linked to a constitutively extensive root system (such as high metabolic cost, reduced root growth, etc).

Root interactions with soil symbiotic microbes such as arbuscular mycorrhizal fungi, which are inhibited by flooding, might also improve water and nutrient acquisition in the topsoil in alternate wetting and drying (Mbodj et al., 2018; Vallino et al., 2014). Accordingly, symbiosis with arbuscular mycorrhizal fungi were shown to confer drought tolerance in rice (Chareesri et al., 2020). Arbuscular mycorrhizal fungi colonisation was also shown to reduce P loss from paddy fields, thus improving P use efficiency and reducing environmental impacts (Zhang et al., 2020). Thus, root traits that promote arbuscular mycorrhizal fungi infection in topsoil such as increased number of nodal roots and large lateral roots with more cortex cells and less aerenchyma to accommodate intracellular fungal structures may lead to improved water and nutrient uptake. Interestingly, these are the same root architectural traits that increase water and nutrient use efficiency in alternate wetting and drying. Moreover, rice response to arbuscular mycorrhizal fungi infection is dependent on the plant genotype and could be targeted for breeding plants with improved symbiosis efficiency (Diedhiou et al., 2016; Huang et al., 2020; Lefebvre, 2020).

Overall, lessons learnt from the available studies indicate that improving root traits in rice for alternate wetting and drying systems could lead to improved water use efficiency but also P use efficiency (Acosta-Motos et al., 2020) and N use efficiency (Wang, Zhang, et al., 2016), thus leading to more sustainable rice agroecosystems with reduced water and fertiliser consumption. Main target traits are increased nodal root number and branching in the topsoil as well as increased nodal root growth and branching in deep soil in response to alternate wetting and drying (plasticity; Figure 2c, Table 2). QTLs for crown root number have already been reported in rice (e.g. as Phung et al., 2016) well as QTLs for root traits plasticity in response to water deficit (Kadam et al., 2017; Sandhu et al., 2016) and could be mobilised for breeding. Rhizosphere traits could also be targeted to improve water and nutrient acquisition efficiency in this system.

5 | CONCLUSION

Learning from past research, we propose two main root trait-based strategies to accelerate the development of new cultivars better adapted to low-input environments in Africa.

The first is to characterise the primary constraints of the target agroecosystem and identify selectable root traits that have robust positive impact on performance and minimal tradeoffs. First and foremost, long and dense root hairs are promising selection criteria as greater root hair length and density promotes soil exploration and nutrient acquisition with minimal cost. Specific root plasticity traits could be useful potential selection criteria in particular cases. In alternate wetting and drying rice agroecosystems topsoil root branching plasticity could co-optimise water and nutrient uptake during the drying period. Subsoil root length plasticity could be beneficial during prolonged drought stress particularly during grain filling (for sorghum and pearl millet in arid and semi-arid agroecosystems for example).

The second major strategy is to understand and target trait synergisms and integrated phenotypes. Synergisms between root traits are defined as interactions that have more than additive effect, as in the case of long and dense root hairs paired with shallow root system architecture for P acquisition (Miguel et al., 2015). Integrated phenotypes would clearly affect the utility of selecting for a single component trait without selecting for their complementary phenotypes. For example, the utility of high conductance capacity xylem likely depends on root traits that affect rooting depth since deep roots can access and thus transport greater volumes of soil water (Strock et al., 2020). The development of root structural and functional models for crops such as sorghum or pearl millet that can evaluate the effects of architectural and anatomical traits as well as trait combinations in changing soil environments will be particularly useful (A. Ndour et al., 2017). Other less well-characterised trait assemblages, especially those involving transpiration, should be further investigated and validated in particular stress scenarios (Gano et al., 2021; Klein et al., 2020; Strock, Burridge, et al., 2019). Considering the dynamics of resource acquisition and use, especially that of water within the context of phenology, leads to acknowledgement of the importance of interactions among roots and shoots for timely water use across the crop cycle (Vadez et al., 2014). In that regard, combining root models with crop models could potentially link aboveground traits to root traits, the former serving as a proxy for root function (Benes et al., 2020).

To make these innovations readily available to breeders, researchers and breeders need to work together to validate trait utility, develop phenotyping protocols (including field sites) and the type of genetic material to work with (e.g., recombinant inbred lines, near isogenic lines, tester lines, and germplasm deployment strategy) and ultimately identify markers or genes controlling beneficial traits. Given our current understanding of crop adaptation to low input agroecosystems, a breeding strategy combining trait based and field evaluation, similar to that outlined in case study 1, is the most likely to result in the rapid generation of new, more resilient varieties. This breeding strategy starts with identification of favourable traits, then moves to selection of parental materials that offer a combination of local adaptation and the key trait(s) to be improved. Following is direct phenotypic selection of progeny for the trait(s) of primary interest and then field trials evaluating adaptability and performance. In the longer term, as more QTLs and genes controlling the target root traits and their plasticity will be characterised, marker assisted selection and ultimately genomic selection could be used. To maximise deployment of improved cultivars and to then secure the adoption of those improved cultivars, social scientists and farmers should be integrated in the selection process (Amelework et al., 2016). The inclusion of useful root traits in such approaches may help to stimulate a new Green Revolution in Africa.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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