RESEARCH ARTICLE

Plasticity of root hair and rhizosheath traits and their relationship to phosphorus uptake in sorghum

Michael O. Adu[1] | Nathaniel Zigah[1] | David O. Yawson[2] |
Kwadwo K. Amoah[1] | Emmanuel Afutu[1] | Kofi Atiah[3] |
Alfred A. Darkwa[1] | Paul A. Asare[1]

[1]Department of Crop Science, School of Agriculture, College of Agriculture and Natural Sciences, University of Cape Coast, Cape Coast, Ghana

[2]Centre for Resource Management and Environmental Studies (CERMES), The University of the West Indies, Bridgetown, Barbados

[3]Department of Soil Science, School of Agriculture, College of Agriculture and Natural Sciences, University of Cape Coast, Cape Coast, Ghana

Correspondence
Michael O. Adu and Paul A. Asare, Department of Crop Science, School of Agriculture, College of Agriculture and Natural Sciences, University of Cape Coast, Cape Coast, Ghana.
Email: michael.adu@ucc.edu.gh and pasare@ucc.edu.gh

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Abstract

Sorghum is an essential crop for resilient and adaptive responses to climate change. The root systems of crop plants significantly contribute to the tolerance of abiotic stresses. There is little information on sorghum genotypes' root systems and plasticity to external P supply. In this paper, we investigated the variations in root systems, as well as the responses, trait relationships, and plasticity of two sorghum genotypes (Naga Red and Naga White), popularly grown in Ghana, to five external P concentrations ($[P]_{ext}$): 0, 100, 200, 300, and 400 mg P kg^{-1} soil. Sorghum plants were grown in greenhouse pots and harvested for root trait measurements at the five-leaf and growing point differentiation (GPD) developmental stages. The plants were responsive to $[P]_{ext}$ and formed rhizosheaths. The two genotypes showed similar characteristics for most of the traits measured but differed significantly in total and lateral root lengths in favor of the red genotype. For example, at the five-leaf growth stage, the lateral root length of the red and white genotypes was 22.8 and 16.2 cm, respectively, but 124 and 88.9 cm, at the GPD stage. The responses and plasticity of the root system traits, including rhizosheath, to $[P]_{ext}$ were more prominent, positive, and linear at the five-leaf stage than at the GPD growth stage. At the five-leaf growth stage, total root length increased by about 2.5-fold with increasing $[P]_{ext}$ compared to the unamended soil. At the GPD stage, however, total root length decreased by about 1.83-fold as $[P]_{ext}$ increased compared to the unamended soil. Specific rhizosheath weight correlated with RHD, albeit weakly, and together explained up to 59% of the variation in tissue P. Root hair density was more responsive to P supply than root hair length and showed a similar total and lateral root length pattern. Most desirable responses to P occurred at a rate of 200–300 mg P kg^{-1} soil. It is concluded that sorghum would form rhizosheath, and $[P]_{ext}$ could be critical for the early vigorous growth of sorghum's responsive root and shoot traits. Beyond the early days of development, additional P application might be necessary to sustain the responses and plasticity observed during the early growth period, but this requires further investigation, potentially under field conditions.

1 | INTRODUCTION

Sorghum (*Sorghum bicolor* [L.] Moench*)* is a C4 domesticated cereal cultivated for its grain, forage, and lignocellulosic biomass. Although sorghum is a staple food for over half a million people, mainly in Africa, it is also widely used in the bioethanol, fuel, brewing, sugar, or syrup industries (Brenton et al., 2016; Casa et al., 2008; Mace et al., 2013; Morris et al., 2013; National Research Council, 1996; Paterson et al., 2009). The pericarp of sorghum grains comes in various colors, from shades of white to red, making it a versatile human food and animal feed. Sorghum is the world's fifth most widely grown in terms of area, after maize, rice, wheat, and barley (Wojciechowski & Kant, 2021). In Africa, sorghum is the second most crucial cereal after maize (Taylor, 2004), with a total production of 25.6 million tons. Africa is the global leader in sorghum production (Pereira & Hawkes, 2022). Sorghum is grown in varied climates due to its tolerance to various environmental conditions. It is tolerant to drought and short periods of water-logging conditions, making it an exceptionally resilient crop in low-input agroecosystems and arid or semi-arid regions (Pereira & Hawkes, 2022; Wojciechowski & Kant, 2021) and for climate change adaptation in resource-poor environments.

Although Africa accounts for the largest share of global production and direct sorghum consumption, it has the lowest grain yield, estimated at 967 kg ha^{-1} (OECD, 2017). Even under optimal conditions, sorghum yields are lower than maize (Marsalis et al., 2010; Mason et al., 2008). Further increases in abiotic stresses' severity, frequency, and complexity would likely cause additional yield penalties, especially in regions already experiencing significant yield gaps. As sorghum is tolerant to water stresses (Monk et al., 2014; Staggenborg et al., 2008), soil fertility could be an essential target for stabilizing or improving yields. Low plant-available phosphorus (P) is already constraining African food production (Gemenet et al., 2016). A review by Gemenet et al. (2016) concluded that African sorghum production predominantly occurs on highly P-deficient soils. The soils are mostly highly weathered entisols and alfisols, characterized by low pH and cation exchange capacity (CEC). These soils typically have low total and available P levels, with an average total of 109 mg kg^{-1} and available soil P generally below 2 mg kg^{-1} (Manu et al., 1991). In addition, these soils have a low capacity to fix P, with P-sorption ranging from 27 to 252 mg kg^{-1} (Sanchez & Uehara, 1980). Some sorghum yield increases have been attributed to P fertilizer (Silveira et al., 2018). Compared to control plots, which had no P nor N fertilizer, sorghum grain yield rose by over 200% on Ethiopian soil (Hailu & Kedir, 2022). Meanwhile, P fertilizer use and use efficiency in Africa are among the lowest in the world, mainly due to poor access to P fertilizers (Ricker-Gilbert, 2020). As a result, selecting plant traits to improve the acquisition and use of soil P in sorghum should potentially increase sorghum yields.

In plants, alterations in root system architecture (RSA), including changes in geometry, morphology, topology, or growth dynamics, are among the most important adaptive responses to soil P dynamics. These modifications permit a more efficient and compelling exploration of the soil environment. On a macroscale, roots show these adaptations by altering their lengths, relative lengths, numbers, and densities. Root weight or length densities in compartments of the soil, which describe root distribution in the soil, are among the most crucial root traits in soil resource acquisition (Tajima, 2021). Plants adjust their insertion angles, diameters, surface areas, and volumes to increase their soil explorative and resource uptake capacity (Smith & De Smet, 2012). At the microscale, adaptive plants modify the numbers per unit area, lengths, and branching of root hairs to increase the surface area of RSAs to enable greater uptake of soil resources (Adu et al., 2017; Kohli et al., 2022; Maqbool et al., 2022). Root hairs are the tubular-shaped outgrowths of root epidermis cells that proliferate and elongate to expand the soil volume subject to the depletion of nutrients that diffuse to the root surface (Lynch & Brown, 2008). Root hairs contribute up to 80% to plant P uptake by increasing the root surface area or the contact space between root and soil for absorption (Kumar et al., 2019).

For all soil resources, but particularly for P, which is less mobile and low in most soils, the ability of root systems to explore the rhizosphere effectively without incurring substantial metabolic costs is ideal for efficient uptake (Lynch, 2015; Lynch & Brown, 2008). Although plants might incur a higher metabolic cost by investing more in root hair production and growth (Brown et al., 2012), root hairs are essential for acquiring P. Still, the utility of root hairs in P uptake may be superior in genotypes with shallow root growth angles than in genotypes with steep root growth angles (York et al., 2013). The utility of root hairs in improving P acquisition under low P conditions has been established for many crop plants, including Arabidopsis (Bates & Lynch, 2000), common bean (Miguel et al., 2015), cowpea (Mohammed et al., 2022; Opoku et al., 2022), maize (Zhu et al., 2010), soybean (Vandamme et al., 2013), and wheat and barley (Singh Gahoonia et al., 1997). Root hairs were implicated in achieving a high barley yield under P-deficient conditions (Brown et al., 2012). Although the studies characterizing sorghum RSA traits are relatively limited, data on sorghum root hair proliferation and growth in response to soil P availability is notably lacking. Most root hair studies in sorghum have focused on exudating the organic compound sorgoleone (Czarnota et al., 2003; Yang et al., 2004).

Related to root hair studies are the formation and functional roles of rhizosheath in soil resource acquisition. Aided by mucigel, soil aggregates enmesh in root hairs to form rhizosheath in many crop plants (Kohli et al., 2022). The size of a rhizosheath depends on many

factors, including lengths, density, and branching of root hairs (Haling et al., 2010); soil water content (Watt et al., 1994); and soil porosity and strength (Haling et al., 2014). Mycorrhizal associations, root and microbial mucilage, and microbial communities influence rhizosheath size (McCully, 1999; Tahir et al., 2015). Rhizosheaths form a functional link between plants and their rhizosphere to facilitate soil resource acquisition (Kohli et al., 2022). Rhizosheaths have become a pivotal root trait in enhancing crop nutrient status (Aslam et al., 2021). Barley genotypes showed an 18% larger rhizosheath mass (the amount of soil that remains physically adhered to the root system on excavation) under deficient P compared to replete P conditions (Brown et al., 2012). Rhizosheath formation improved P uptake by roots in white lupin under deficit P conditions (Aslam et al., 2021). In maize, rhizosheath formation confers substantial yield advantages on improved varieties compared to local landraces (Adu et al., 2017). Several shreds of evidence in essential crops establish the imperativeness of examining how root hair features produce useful rhizosheaths under P-limiting conditions. Yet, this area of research has not been explored in sorghum. Also, the need to understand how root traits differ among species, even among those in the same environment and at the same time, and how root traits change in response to their environments to facilitate resource acquisition has been noted.

Plasticity, or phenotypic plasticity, describes the variability of a trait in response to environmental stimuli or the ability of organisms to produce various phenotypes in response to their environment (Adu et al., 2022). Plasticity shows genetic variation and can be a heritable trait. It could also be an adaptive and acclimatization strategy occasioned by organisms' evolution in response to selection. Several plants exhibit root plasticity, with the ability to increase their roots in relatively fertile sections of the soil volume to enhance nutrient uptake (Grossman & Rice, 2012). Root plasticity is, therefore, a vital trait, especially in heterogeneous and poor soils. Root traits that show plastic responses must be known to leverage the benefits and maximize the trait for crop improvement and productivity. The present study, therefore, investigated the variations in root system responses of two sorghum genotypes currently grown in farmers' fields in Ghana to soil P supply. Specifically, the objectives of this study were to (i) evaluate the genotypic variation in RSA characteristics that are important for P uptake, (ii) quantify the differences in rhizosheath characteristics and assess the relationship between externally added P and rhizosheath characteristics of juvenile sorghum, and (iii) evaluate the response of the RSA characteristics to soil P concentration to determine the traits that enable plastic responses of juvenile sorghum plants under variable P conditions.

2 | MATERIALS AND METHODS

2.1 | Plant materials

Two commonly cultivated sorghum genotypes distinguished by the grain pericarp were obtained from sorghum farmers in the Upper West region of Ghana. The materials are high-yielding early maturing varieties called Naga Red and Naga White (hereafter referred to as Red Sorghum and White Sorghum), widely consumed and preferred by the locals for preparing beers and dishes, respectively. The cultivars were developed by mass selection (Kudadjie et al., 2004), with red and white sorghum landraces called Kazie and Kapiera (Buah et al., 2010), possibly providing the genetic background of Naga Red and Naga White. Information on the relatedness of these genotypes is lacking. Farmers have noted that the white cultivars are more vulnerable to stresses and require relatively high soil fertility, possibly pointing to differences in some physiological structures of these genotypes, including their root systems.

2.2 | Soil characteristics and environmental conditions

The soil for this work has previously been described by Opoku et al. (2022). It was topsoil (0–15 cm depth), Haplic Acrisol (sandy clay loam), typical of arable soils of the coastal savannah agroecological zone. It had a pH of 5.43, with 2.1% organic carbon, .08% total nitrogen (N), 7.00 cmol of charge per kg soil (cmolc kg^{-1}) P, .05 cmolc kg^{-1} potassium (K$^+$), 2.59 cmolc kg^{-1} calcium (Ca^{+2}), .87 cmolc kg^{-1} magnesium (Mg^{+2}), and a CEC of 7.3 cmolc kg^{-1}. The bulk density of the soil was 1.36 g cm^{-3}. The soil was air-dried and sieved with a 2-mm sieve. The experiments were conducted in the greenhouse of the Teaching and Research Farms, School of Agriculture, University of Cape Coast. The temperature and relative humidity in the greenhouse were approximately 24°C–32°C and 70%–80%, respectively. The experiments were conducted under the natural day length of the area, ranging from about 11.30 to 12.40 h.

2.3 | Experimental setup and treatments

Heaps of soil were either left un-amended or fertilized with potassium dihydrogen phosphate (KH$_2$PO$_4$) at four different rates: 100 mg P kg^{-1}, 200 mg P kg^{-1}, 300 mg P kg^{-1}, and 400 mg P kg^{-1} soil. The heaps of soil were watered to and kept at 80% field capacity (based on gravimetric water content) and incubated at ambient temperature for 28 days before planting. No other fertilizer amendment was applied to the soil. Nursery polybags (3600 cm^3) with drainage holes underneath were filled with the soil to a bulk density of approximately 1.1 g cm^{-3}. There were 10 replicates of genotype $\times$ [P]$_{ext}$ $\times$ sampling time combinations for a total of 200 experimental units or polybags. Two uniform-sized healthy seeds of the two sorghum genotypes were hand-sewn directly into the pots to a depth of about 2 cm. Upon emergence, the seedlings were thinned to one plant per polybag and allowed to grow for 14 or 28 days after sowing. These two periods correspond respectively to the five-leaf and the growing point differentiation (GPD) developmental stages of sorghum and are hereafter referred to as the five-leaf stage and the GPD growth stage. The fifth fully expanded leaf's collar is visible at the five-leaf growth stage of sorghum development,

and most post-emergent herbicides and fertilizer side dresses are recommended. The five-leaf growth stage is the second stage of sorghum development and is immediately followed by the GPD growth stage. The GPD growth stage is characterized by rapid growth and wilting of older leaves. In addition to soil nutrients, optimum soil moisture is critical at this stage since stress could harm the formation of seeds during flowering. The growth to the GPD stage was to assess the effect of the extended growth period on the microscale RSA features and rhizosheath traits. Soils in nursery polybags were watered on the day of sowing using tap water and maintained at approximately 80% field capacity determined gravimetrically. The nursery pots were frequently rearranged such that the positions of bags in the greenhouse would reduce the influence of gradients. At the five-leaf or GPD growth stage, six randomly selected plants for each genotype × $[P]_{ext}$ combination, for 60 plants for each sampling stage, were harvested and analyzed for differences in RSA features, shoot, and root biomass. A random sub-sample of three from the six replications was used for tissue P concentration analyses.

2.4 | Extraction of rhizosheath and RSA traits

Plants were harvested by gently cutting both sides of the polybag lengthwise. Rhizosheath mass was determined according to the procedure described by Adu et al. (2017) and (Opoku et al., 2022). The plants were carefully removed from the soil and shaken systematically so that loose bulk soil fell off, leaving the firmly attached sheath of soil on the root. Roots with attached soil were separated from shoots and weighed. The roots were gently washed out of the soil, taking care to minimize damage to the root hairs. The washed roots were systematically patted dry with tissue paper and weighed to obtain the weight without root sheaths. Rhizosheath weight (g) was calculated as the difference between the weight of the root with the rhizosheath and that of the cleansed roots. The ratio of rhizosheath weight to root weight and root length was used to compute relative rhizosheath weights (g g^{-1} and mg cm^{-1}).

Biomass traits measured included shoot and root biomass. Fresh roots and shoots were oven-dried for 3 days at 80°C to determine dry weights. Macroscale RSA traits, such as total root length (TRL), lateral root length (LRL), and mean lateral root diameter (LRD), were measured using image analyses. Other macroscale root features extracted include seminal root length (SRL), mean seminal root diameter (SRD), and mean total root diameter (TRD), which were measured using image analyses. We used a Canon EOS 70D DSLR camera (https://www.usa.canon.com/) to capture root images on a tripod 50 cm above roots. We achieved a good contrast level and minimized root overlap for the root imaging by suspending the roots in water in a rectangular glass dish with a black background. The *ImageJ* software (US National Institutes of Health, Bethesda, MD, USA, https://imagej.nih.gov/ij/) was used to extract RSA features from root images. Roots were traced with the SmartRoot root analyses software (Lobet & Draye, 2013) to extract root diameter features. In *ImageJ*, binary and skeletonization routines determined

TRL (Adu et al., 2015). Total LRL (TLRL) was determined by subtracting SRL from TRL.

We used the methods described by Adu et al. (2017) and Opoku et al. (2022) to extract root hair length (RHL) and root hair density (RHD). A 4–6 cm tip of randomly chosen seminal root axes of each RSA was severed and floated in water in a glass Petri dish. An AmScope compound microscope (×4 magnification; Irvine, California, USA, www.amscope.com/) fitted with a digital camera and linked to a computer was used to capture images of root hairs. Lengths of five root hairs on the 4–6 cm root tip were captured from three different positions. Thus, 15 RHLs were measured from each root tip. We traced and measured the root hairs using the freehand line tool in the *ImageJ* and calculated the mean of the 15 root hairs on each plant to get a single RHL value per plant sample. For RHD, we demarcated an area of a representative rectangle in *ImageJ* and manually counted the number of root hairs within the region. We divided the root hair count by the area to determine the number of root hairs per square millimeter.

2.5 | Determination of tissue P

We utilized the spectrophotometric determination of tissue P previously described in (Opoku et al., 2022). Whole shoot and root samples were milled with a domestic stainless-steel blender. The concentrations of P in diluted digests were determined based on the modified molybdenum blue method (Murphy & Riley, 1962). A spectrophotometer measured the tissue P on three replicates of oven-dried samples of both roots and shoots.

2.6 | Data analysis

Following data exploration, which demonstrated that normality assumptions could be upheld, a general analysis of variance (ANOVA) for a completely randomized design was used to test for differences among the means for various traits among the genotypes or $[P]_{ext}$ treatments. All root trait data are presented as the mean of six replicates, and means were compared by least significant difference (l.s.d.) ($p = .05$). Factors for the two-way ANOVA were sorghum genotype, $[P]_{ext}$ and the interaction of genotype and $[P]_{ext}$. Pearson's correlation coefficients between all trait combinations were computed. We fitted a simple linear regression to evaluate the relationships between tissue P and root/root hair/rhizosheath traits. To see if multiple roots traits explain a more considerable proportion of variation in tissue P, we subsequently fitted a multiple regression model (estimated using OLS) to predict tissue P with root and rhizosheath traits (formula: Rhoot P/Root P ~ TRL + RHL + RHD + RWT.g + SRWt.g g^{-1} + SRWT.cmg^{-1}). We undertook multivariate analyses employing a multiple-factor analysis (MFA), a procedure for analyzing datasets in which quantitative and qualitative variables describe individuals. We adopted the MFA procedure outlined in (Adu et al., 2022). We summarized the variables into two categorical

variables (genotype and P supply) and eight trait groupings based on biomass of shoot and root, length and diameter of roots, length and density of root hairs, rhizosheath, and tissue P. We used the R packages factoextra, FactoMineR (Lê et al., 2008), corrplot (Wei & Simko, 2021), and ggplot2 (Wickham, 2016) for Pearson's correlations, MFA, and graphics.

The relative distance plasticity index method (RDPI) (Valladares et al., 2006) was used to identify traits responsible for plastic responses of sorghum to $[P]_{ext}$. The RDPI ranges from 0 (no plasticity) to 1 (maximum plasticity) and specifies the relative phenotypic distance or amount of change in a given trait between plants of the same genotype exposed to different $[P]_{ext}$. For each feature (x), $RDPI_{(x)}$ values were determined by the quotient of the sum ($x_{i'j'} + x_{ij}$) and the relative phenotypic distances across replicates ($d_{ij} \rightarrow ij\cdot$) of the same genotype grown in different $[P]_{ext}$. The total number of distances was denoted as n, and an RDPI, ranging from 0 to 1, was calculated for each genotype using Equation 1.

$$RDPI = \sum \left(d_{ij} \rightarrow i'j' / \left(x_{i'j'} + x_{ij} \right) \right) / n \qquad (1)$$

3 | RESULTS

3.1 | Descriptive data and genotypic variation in traits

In both experiments, the dispersions in the data were small to large for various characteristics (Table 1). Most traits had a more extensive range at the GPD growth stage than at the five-leaf growth stage. Generally, biomass traits presented smaller ranges, and root length

traits showed more extensive ranges. Except for a few features, as expected, the mean values were considerably higher for traits measured at the GPD growth stage than at the five-leaf growth stage. The two experiments' coefficients of variation (CVs) were broadly comparable in the various characteristics. The CV for the five-leaf and the GDD growth stages ranged from 10.24% (RW) to 86.73% (LRD) and 33.68% (RHL) to 98.57% (LRD). The CVs of other root diameter-related traits were exceptionally high and were 76.55 and 88.18% (TRD) and 47.04 and 66.9% (SRD) for the five-leaf and the GDD growth stages, respectively. Both experiments' CVs of root length-related traits were moderately high, ranging from 40.77% for TRL to 66.65% for LRL (Table 1). On the other hand, the CV for RW was relatively small in both experiments (Table 1). At the five-leaf growth stage only, there was a significant effect of genotype (p < .05) in three traits, including TRL and LRL (Table 2). The red genotype obtained 18.3% and 29% more TRL and LRL, respectively, than the white genotype.

3.2 | Effect of P supply

Significant (p < .05 or p < .01) responses to $[P]_{ext}$ occurred in over 73% and 80% of traits in the five-leaf and the GPD growth stages, respectively. In both experiments, RDW and RHL were not affected by $[P]_{ext}$, but the significant effect of $[P]_{ext}$ on SRW (g cm^{-1}) at the five-leaf growth stage was short-lived, as this was not evident when the plants were grown to the GPD growth stage. Genotype and $[P]_{ext}$ interactions were uncommon and occurred in only two traits (SFW and SRL) at the five-leaf growth stage and one (SRL) at the GPD growth stage (Table 2).

TABLE 1 Descriptive statistics of 15 measured traits (13 root traits and two shoot traits) in two sorghum genotypes grown in pots for 14 days (five-leaf stage) and 28 d (GPD stage).

Measure (unit)	Abbreviation	Five-leaf growth stage			GPD growth stage		
		Mean	Range	CV (%)	Mean	Range	CV (%)
Mean lateral root diameter (mm)	LRD	.363	1.41	86.73	2.198	9.495	98.57
Lateral root length (cm)	LRL	19.46	55.67	66.65	106.5	351.3	63.96
Root dry weight (g)	RDW	.016	.02	4.19	.398	1.08	51.27
Root fresh weight (g)	RFW	.107	.21	39.78	3.042	8.04	51.89
Root hair density (count mm^{-2})	RHD	8.296	17.41	43.76	18.03	40.92	37.57
Root hair length (um)	RHL	229	467.6	48.23	2,118	301.8	33.68
Specific rhizosheath weight (g cm^{-1})	SRW (g cm^{-1})	14.22	28.82	52.82	17.5	39.13	49.19
Rhizosheath weight (g)	RW (g)	1.931	.8	10.24	10.72	13.35	34.57
Specific rhizosheath weight (g g^{-1})	SRW (g g^{-1})	139.8	171	37.8	34.88	174.3	76.56
Shoot dry weight (g)	SDW	.06	0.1	30.81	1.087	2.07	45.05
Shoot fresh weight (g)	SFW	.578	.78	32.73	8.744	18.28	48.19
Mean seminal root diameter (mm)	SRD	.05	.112	47.04	.325	1.064	66.9
Seminal root length (cm)	SRL	8.013	19.8	50.14	46.28	108.3	49.04
Mean total root diameter (mm)	TRD	.412	1.436	76.55	2.52	9.706	88.18
Total root length (cm)	TRL	27.28	59.06	52.62	169.8	331.7	40.77

TABLE 2 Analysis of variance of responses of the shoot and root traits of two sorghum genotypes to varying rates of external P application.

| | Five-leaf growth stage | | | | | | | | GPD growth stage | | | | | | | | |
| | Means | | p values | | | l.s.d | | | Means | | p values | | | l.s.d | | |
Traits	Red	White	Gen.	$[P]_{ext}$	Gen. × $[P]_{ext}$	Geno.	$[P]_{ext}$	Geno × $[P]_{ext}$	Red	White	Geno.	$[P]_{ext}$	Gen. × $[P]_{ext}$	Geno.	$[P]_{ext}$	Gen. × $[P]_{ext}$
LRD	.392	.334	.452	.034	.482	.16	.25	.35	2.39	2	.451	.007	.617	1.038	1.647	2.354
LRL	22.8	16.2	.009	<.001	.459	4.90	7.77	11.10	124	88.9	.032	.022	.453	32.16	51.02	72.93
RDW	.01633	.01567	.689	.083	.987	.00	.01	.01	0.4	.393	.839	.086	.829	.105	.166	.2378
RFW	.1103	.104	.586	.695	.892	.02	.04	.05	3.09	3	.815	.014	.553	.769	1.22	1.743
RHD	7.88	8.71	.359	.014	.981	.89	1.42	2.02	18.4	17.61	.599	.014	.074	3.151	4.999	7.145
RHL	184	222	.135	.606	.339	50.8	80.4	113.7	229	1952	.064	.074	.712	353	56	800.3
SRW (g cm⁻¹)	15.47	12.97	.049	<.001	.573	2.49	3.95	5.64	19.7	15.3	.041	.178	.259	4.21	6.68	9.54
SRW (g g⁻¹)	140	139.7	.978	<.001	.913	24.60	39.03	55.79	31.4	38.4	.276	.008	.574	12.73	20.2	28.87
RW (g)	1.946	1.915	.527	.005	.996	.10	.15	.22	10.7	10.77	.88	<.001	.265	1.489	2.362	3.377
SDW	.0637	.057	.131	.044	.071	.01	.01	.02	1.13	1.041	.403	<.001	.747	.218	.345	.4935
SFW	.613	.543	.086	<.001	.015	.08	.13	.18	9.2	8.28	.305	<.001	.851	1.786	2.834	4.05
SRD	.047	.0532	.305	.774	.074	.01	.02	.03	.31	.341	.477	<.001	.286	.092	.145	.2077
SRL	7.72	8.3	.468	<.001	.033	1.58	2.51	3.59	45.5	47.1	.752	.001	.029	9.95	15.78	22.55
TRD	.438	.386	.504	.034	.541	.16	.25	.35	2.7	2.34	.489	.003	.67	1.05	1.665	2.38
TRL	30	24.5	.044	<.001	.632	5.33	8.45	12.08	193	146.3	.002	<.001	.227	29.29	46.48	66.43

Note: The $[P]_{ext}$ included 0, 100, 200, 300, and 400 mg P kg⁻¹ soil with KH2PO4. Analyses were done on six replicates.

3.3 | Biomass and tissue P concentration

Biomass of both genotypes responded positively ($p < .001$) to increasing $[P]_{ext}$ in both experiments (Figure 1). At the five-leaf growth stage, the maximum increase in fresh and oven-dried shoot biomass, which occurred at $[P]_{ext}$ of 300 mg P kg^{-1} soil, was 47.7 and 32.6%, respectively, for the red genotype and 42.3% and 40% for the white genotype (Figure 1a). At the GDD growth stage, the shoot dry weight increased significantly ($p < .05$) to an asymptote with increasing $[P]_{ext}$, peaking at 200 mg P kg^{-1} soil (Figure 1b). The percentage increases in shoot biomass were higher at the GPD growth stage. Fresh and oven-dried weights increased by 66.1% and 61%, respectively, for the red
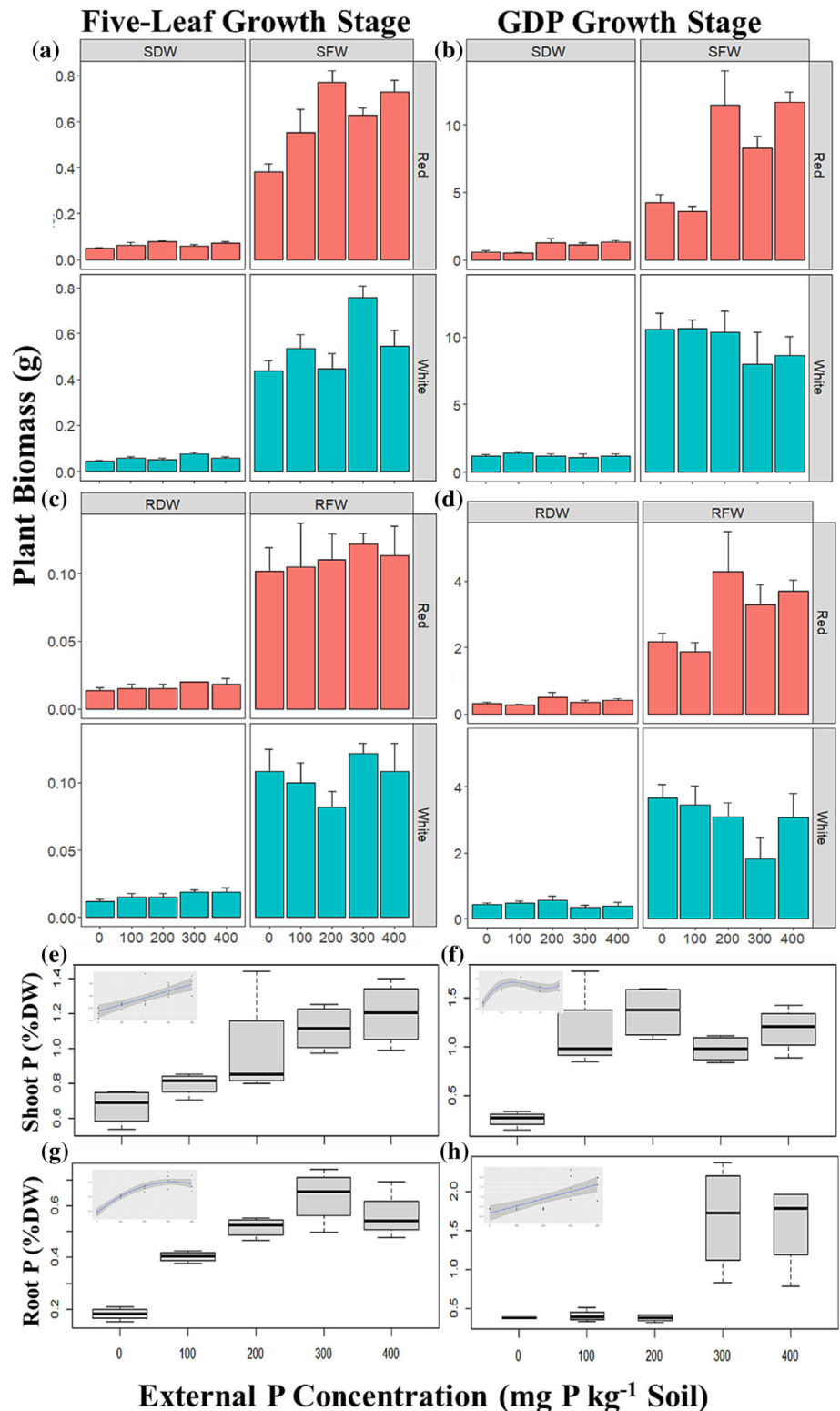
FIGURE 1 Response of biomass and tissue P of juvenile sorghum plants to an increasing amount of P added to the soil in a greenhouse experiment. (a, b) shoot biomass, (c, d) root biomass, (e, f) shoot P concentration, and (g, h) root P concentration. Insets in e–h show the relationships between tissue P concentration with soil P concentration. Values are the mean of six a–d replicates and three e–h replicates. Bars represent standard errors of the mean. Acronyms are defined in Table 1. GPD is the growing point differentiation growth stage, and Red and White refer to the two sorghum genotypes.

genotype and 61.1% and 57.4% for the white genotype (Figure 1b). For root biomass, a significant ($p < .05$) response to $[P]_{ext}$ occurred only in RFW (Figure 1c,d). About a 40% increase was recorded in the root biomass of plants raised in soil fertilized with 400 mg P kg^{-1} compared with the root biomass of plants grown in the unamended soil (Figure 1d).

The shoot P concentration increased significantly ($p < .05$) with adding P to the soil. However, the trends were inconsistent for the two experiments. At the five-leaf growth stage, the shoot P concentration did not reach an asymptote and was described by a linear relationship. A polynomial relationship with P supply represented the root P concentration (Figure 1e). At the GPD growth stage, an exponential rise to a maximum characterized the response of shoot P concentration, but the relationship was linear for root P (Figure 1f).

Abbreviations: GPD, growing point differentiation; SRD, mean seminal root diameter; SRL, seminal root length; TRD, mean total root diameter; TRL, total root length;

3.4 | Macroscale root system traits

There were significant differences ($p < .05$) in most of the macroscale root system traits between $[P]_{ext}$ treatments for both the five-leaf and the GPD growth stages (Figure 2). Phosphorus supply affected TRL in both experiments, but the trend was inconsistent. At the five-leaf growth stage, TRL increased with increasing $[P]_{ext}$ by 2- and 2.5-fold more significantly for the red and white genotypes than plants grown on 0-added P soil (Figure 2a). For both growth periods and genotypes, the mean diameter of the whole root system increased with increasing $[P]_{ext}$ to an asymptote at $[P]_{ext}$ rate of 200 mg P kg^{-1} soil and then declined at the high $[P]_{ext}$ level (Figure 2a,b). The response of LRL to $[P]_{ext}$ was similar to that of TRL in the separate experiments (Figure 2c,d).

At the five-leaf growth stage, there was 2.4- and 2.5-fold significantly higher LRL, respectively, for the red and white genotypes of plants grown in high P conditions compared to those in no $[P]_{ext}$ conditions (Figure 2c). Perhaps, expectedly, the mean diameter of lateral roots responded similarly to that of the TRL (Figure 2c,d). There was a 37.7% and 56.2% difference for the red and white genotypes, respectively, between the SRL on low P soils and those from high $[P]_{ext}$ soils. The SRL measured from the intermediate $[P]_{ext}$ were generally similar for both genotypes (Figure 2e). Phosphorus supply did not significantly affect SRD (Figure 2e).

At the GPD growth stage, TRL appeared to decrease with increasing $[P]_{ext}$, with -1.83- and -1.6-fold change for the red and white genotypes compared to genotypes of plants grown on 0-added P soil (Figure 2b). There was a 1.5- and 1.6-fold significantly lower LRL, respectively, for the red and white genotypes, in plants grown on high $[P]_{ext}$ soils compared to those in low P conditions (Figure 2d). The SRL generally declined with increasing $[P]_{ext}$, with the red and the white sorghum plants recording 57.8% and 39.9% longer seminal roots, respectively, at low $[P]_{ext}$ than at high $[P]_{ext}$ conditions (Figure 2f). The

SRD declined with increasing $[P]_{ext}$, with a 3.2- and 3.9-fold difference between low and high P for the red and white sorghum genotypes (Figure 2f).

3.5 | Microscale root system and rhizosheath traits

The two sorghum genotypes produced many root hairs averaging $\sim$200 and $\sim$212 μm at the five-leaf and the GPD growth stages, respectively. The microscopic images suggested no or minor damage to the root hairs during the harvesting and washing. In the present study, RHD (but not RHL) showed a significant response to $[P]_{ext}$ application (Figure 3a,b). Figure 4 provides photographic evidence of the differences in RHD between the $[P]_{ext}$ rates. After washing, soil (rhizosheath) was occasionally entangled within the root hairs (Figure 4). In both experiments, measures of rhizosheath did not have significant relationships with RHL, although some trends were evident (data not shown).

At the five-leaf growth stage, the red and white sorghum genotype recorded 34.7% and 24.8% more root hairs per square millimeter, respectively, in the low $[P]_{ext}$ treatment than in the high $[P]_{ext}$ treatment (Figure 3a). There was an insignificant relationship between measures of rhizosheath and RHD. Figure 3e exemplifies the relationship between measures of rhizosheath and RHD, with specific rhizosheath weight (g g^{-1}). The total rhizosheath weights of the old red and white sorghum genotypes were, respectively, $\sim$40% and $\sim$66% smaller at high $[P]_{ext}$ than at low $[P]_{ext}$ ($p < .001$; Figure 4c).

When grown to the GPD growth stage, RHD decreased with increasing P supply in both genotypes. However, the magnitude of the decline between low and high P was more considerable in the red (43.5%) than the white (10.5%) sorghum genotype (Figure 3b). Similar responses were observed for the absolute and relative rhizosheath weights, with smaller rhizosheaths generally kept at a higher P supply for both genotypes and experiments (Figure 3c,d). The total rhizosheath weights of the red and white sorghum genotypes were, respectively, $\sim$24% and $\sim$31% smaller at high $[P]_{ext}$ than at low $[P]_{ext}$ ($p < .001$; Figure 3d). However, variation in specific rhizosheath weight per gram of root produced a weak, positive relationship ($R^2 = .1247$, $p < .05$, Figure 3f) when correlated with RHD.

3.6 | Relationships between measured traits

Significant correlations were observed among the 15 measured traits, some of which were weak, moderate, or strong. Significant correlations were fewer at the GPD growth stage (Figure 5a,b). At the five-leaf growth stage, TRL was strongly positively correlated with LRL and SRW (g cm^{-1}) but moderately positively correlated with SRL. A moderate, positive association was observed between shoot biomass and all the length-related traits (TRL, LRL, and SRL), SRW (g cm^{-1}), and root biomass. There were few significant, negative correlations among features, such as between RHD and shoot biomass, between SRW (g g^{-1}) and SRW (g cm^{-1}), and between TRL and root biomass

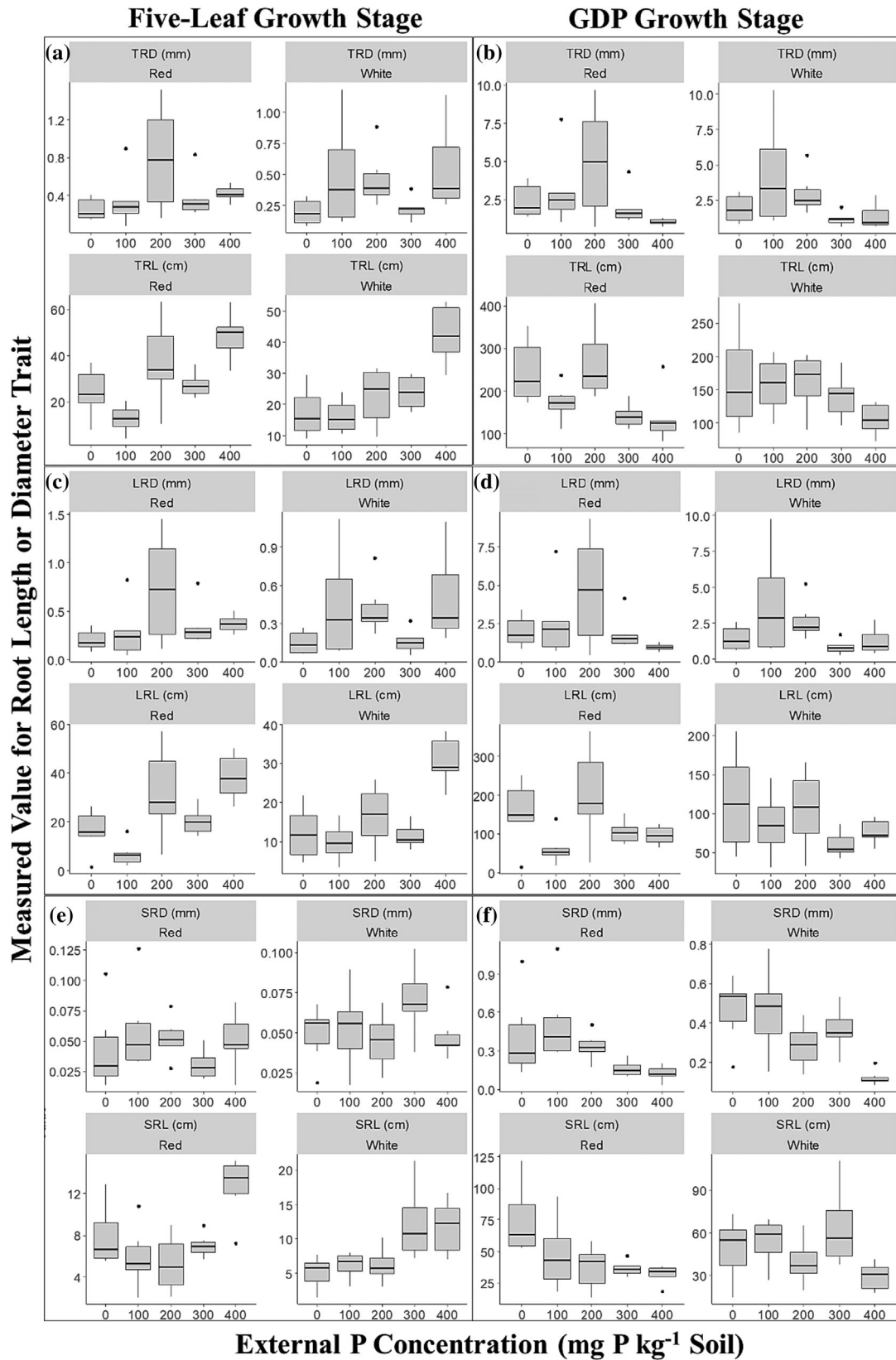**FIGURE 2** Variation in macroscale root system traits of two sorghum genotypes (red and white grain sorghum). (a, b) Total root length and diameter. (c, d) Lateral root length and diameter. (e, f) Seminal root length and diameter. Data are the mean of six replicates. Root traits acronyms are defined in Table 1. GPD is the growing point differentiation growth stage, and Red and White refer to the two sorghum genotypes.
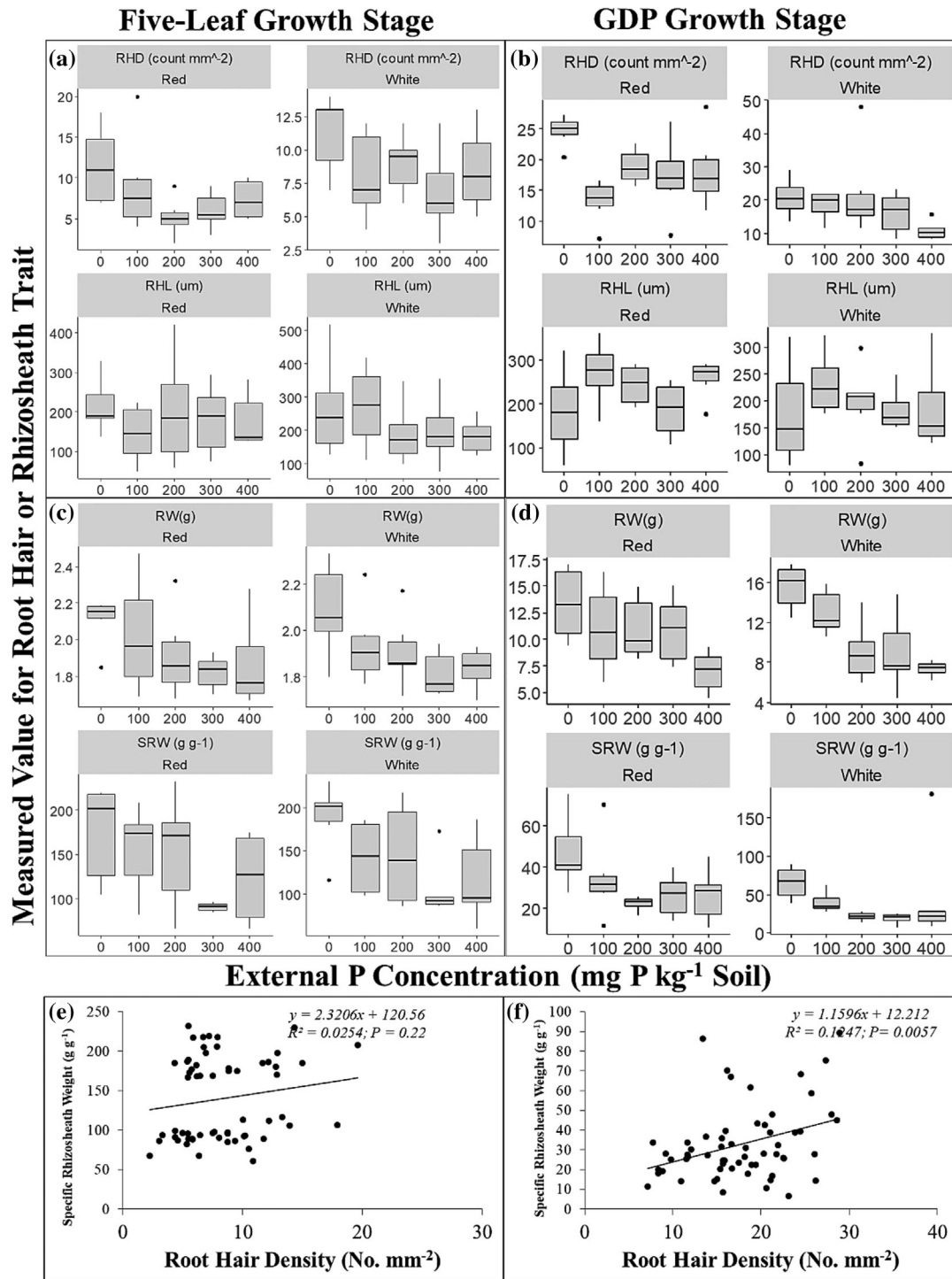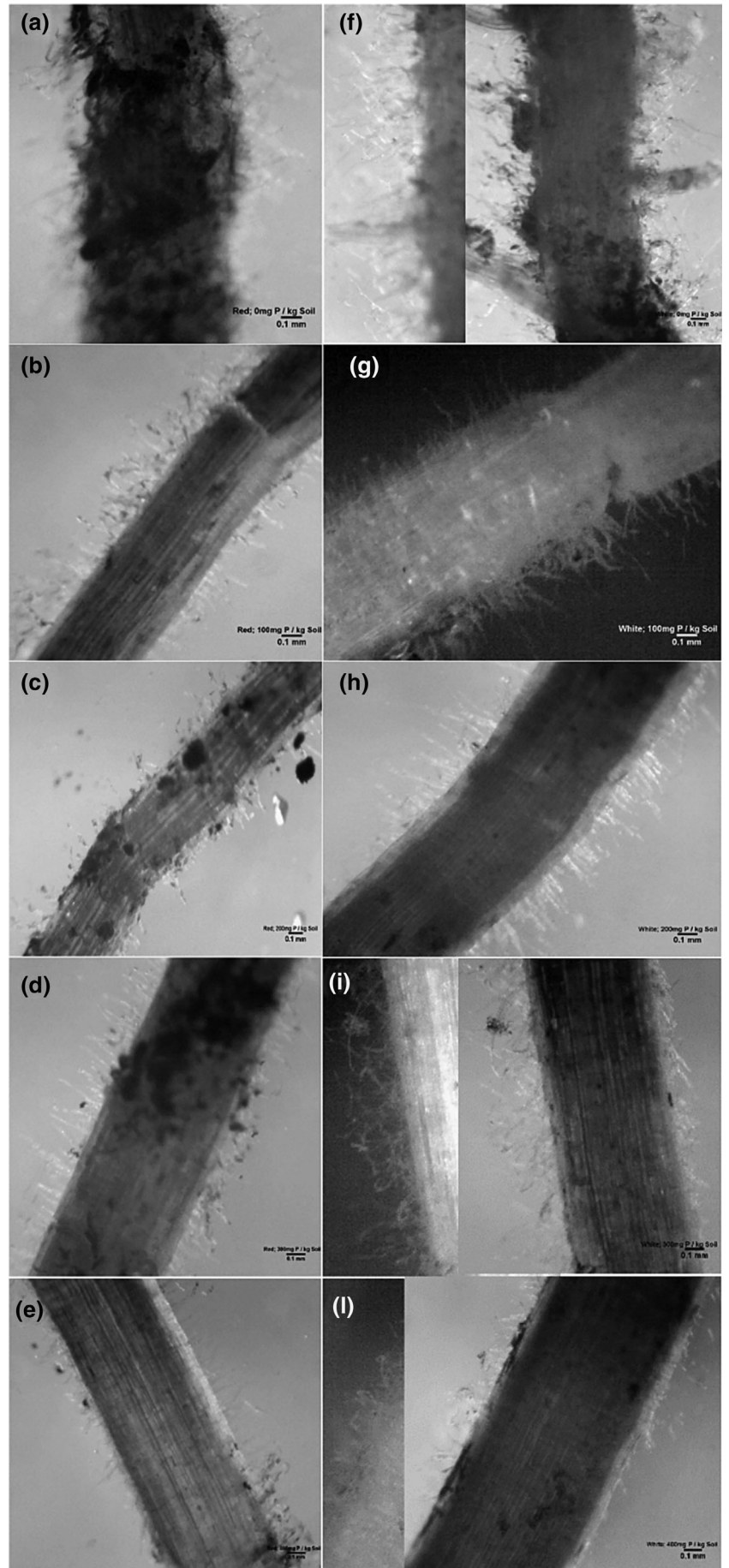
FIGURE 3 Variation and relationship between microscale root system traits of two sorghum genotypes grown for 14 days (five-leaf growth stage) and 28 days (GPD growth stage) in unamended soil and in the soil to which 100, 200, 300, and 400 mg KH_2PO_4 kg^{-1} had been added. (a, b) Root hair length and density. (c, d) Rhizosheath weight (g) and specific rhizosheath weight (g g^{-1}). Data are the mean of six replicates, with error bars representing the s.e.m. (e, f) Relationship between root hair density (root count mm^{-2}) and specific rhizosheath weight (g g^{-1} root) at (e) the five-leaf growth stage (d) and (f) the GPD growth stage. Acronyms are defined in Table 1. GPD is the growing point differentiation growth stage, and Red and White refer to the two sorghum genotypes.

(Figure 4a). Most of these associations were not evident at the GPD growth stage. The associations between SRW (g g^{-1}) and all biomass-related traits were negative (Figure 5b).

A two-factor ANOVA for tissue P concentration found a significant interaction ($p < .05$) between $[P]_{ext}$ and genotypes. Simple linear regression of shoot P concentration for plants grown at the five-leaf

FIGURE 4 Sample images of root hairs of two sorghum genotypes captured at ×4 magnification with an AmScope compound microscope. Images represent P supply's impact on root hair density in the red (a–e) and white (f–j) sorghum genotypes. Panels a and f, b and g, c and h, d and i, and e and j represent images of root hairs of plants grown in soils with 0, 100, 200, 300, and 400 mg KH$_2$PO$_4$ kg^{-1}. The scale bar represents .1 mm.

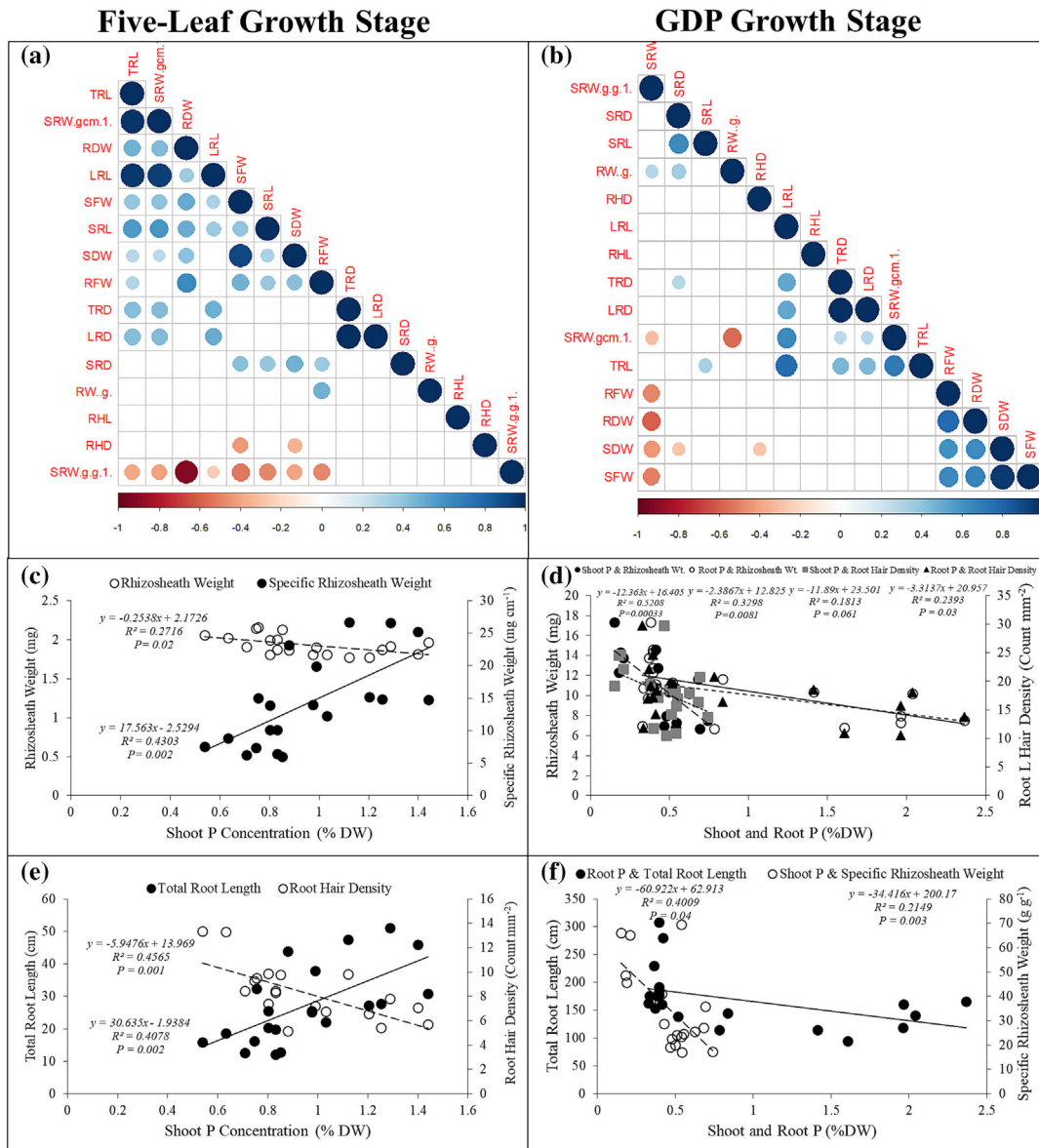## Five-Leaf Growth Stage   GDP Growth Stage

FIGURE 5 Correlation between traits and relationship between tissue P concentration and rhizosheath, root hair density, and root length for two sorghum genotypes grown to the five-leaf and the growth point differentiated growth (GPD) stages in soil to which 0, 100, 200, 300, and 400 mg KH_2PO_4 kg^{-1} had been added. (a, b) Phenotypic correlations between traits. The color of the circles represents the correlation value, and the scale is indicated in the bar below the matrix. Blank boxes indicate non-significant relationships ($p > .05$). Acronyms are defined in Table 1. (c) Shoot P concentration plotted against rhizosheath weight (mg; open markers) and specific rhizosheath weight (mg cm^{-1}; filled markers). (d) Shoot P and root P concentration plotted against rhizosheath and RHD, shoot P against rhizosheath weight (mg; closed circle markers), root P against rhizosheath weight (mg; open circle markers), shoot P against root hair density (closed gray square markers), and root P against root hair density (closed triangle markers). (e) Shoot P concentration plotted against TRL (cm; closed markers) and root hair density (root count mm^{-2}; open markers). (f) Shoot P and root P concentration plotted against total root length and specific rhizosheath weight; root P against TRL (cm; closed markers) and shoot P against specific rhizosheath weight (g g^{-1}). Data show means of $n = 3$. The lines are derived from linear correlations and show the best-fit lines from which the R^2 was derived. GPD is the growing point differentiation growth stage.

growth stage against measures of rhizosheath (Figure 5c) and RHD and TRL (Figure 5e) showed significant correlations. The relationships suggested that these traits explained between 27% and 46% of the variation in shoot P concentration (Figure 5c,e). At the GPD growth stage, the root features explained 18%–52% of the variation in tissue P concentration (Figure 5d,f). The multiple regression linear model to

predict tissue P concentration with roots, root hair, and rhizosheath traits at both growth stages explained a statistically and substantial significant proportion of the variance. At the five-leaf growth stage, the model explained 53% of the variation in shoot P ($F_{[6,13]} = 4.55$, $p = .011$, adj. $R^2 = .53$), but it was statistically insignificant for root P ($F_{[6,13]} = .67$, $p = .674$, adj. $R^2 = -.12$). Even so, only the RHD

predictor had a statistically significant and negative effect in the full model for shoot P ($\beta = -.06$, 95% CI [$-.11$, $-.00458$], $t_{[13]} = -2.35$, $p = .035$). At the GPD growth stage, the model explained 59% and 55% of the shoot P ($F_{[6,13]} = 5.53$, $p = .005$, adj. $R^2 = .59$) and root P ($F_{[6,13]} = 4.90$, $p = .008$, adj. $R^2 = .55$) variation, respectively. Even so, only the specific rhizosheath weight ($\beta = -.441$, 95% CI [-00851, -000311], $t_{[13]} = -2.32$, $p = .037$) and RHL ($\beta = -.69$, 95% CI [-1.24, $-.13$], $t_{[13]} = -2.66$, $p = .020$) predictors had significant effects in the full model for the shoot and root P, respectively.

3.7 | Multifactor analyses

Figures 6 and 7 illustrate MFA plots showing coordinates, contributions, and interrelationships of trait groups and quantitative traits at the five-leaf and GPD growth stages. The correlation plot between groups and dimensions is shown in Figure S1a. Six active groups resolved on the first dimension at the five-leaf growth stage, with root diameters having the highest coordinate. Root biomass was the dominant trait in the second dimension (Figure 6a). Four active groups that contributed above average to the first dimension were root diameters, root lengths, shoot biomass, and RHD (Figure S1a). Still, the coordinates of the root lengths, shoot biomass, and RHD were almost identical, suggesting these contributed similarly to the first dimension (Figures S1a and S1c). Two groups, root biomass and rhizosheath, had the highest contribution to the second dimension (Figure S1b).

However, four groups (shoot and root biomass, rhizosheath, and root diameters trait groups) contributed above the average cutoff point to the variability in the first two dimensions (Figure 6b). There were moderate associations between shoot and root biomass (RV = .58), root diameters and RHL/RHD (RV = .41 and .43, respectively), rhizosheath and RHD/root length (RV = .44 and .53, respectively) (Figure 6c). There were also moderate associations between various trait groups and tissue P, including associations with RHD (RV = .44), root diameters (RV = .51), shoot biomass (RV = .55), and root biomass (RV = .53). The relations between root lengths (RV = .23), RHL (RV = .22) and rhizosheath (RV = .18), and tissue P were low at this growth stage (Figure 6c). The RV coefficients for the mean configuration of the MFA for groups of traits representing shoot biomass, root biomass, root lengths, root diameters, RHL, RHD, rhizosheath, and tissue P were .64, .46, .60, .68, .51, .59, .61, and .65, respectively. Thus, albeit moderate, root diameters recorded a closer RV coefficient (.68) to the mean configuration of the MFA (Figure 6c).

Three factors had eigenvalues of ≥1, providing a three-factor solution, which explained approximately 77.8% of the variance. Most of the quantitative variables were separated along the PC1 axis, with 43.9% of variance explained (Figure 6d). The second and third dimensions explained 22.2% and 11.8% of the variance, respectively. Increasing shoot P was associated with increased root length and diameter traits, which had high positive loadings along the axis of the first dimension. Increasing root P was closely associated with an increase in root biomass, which had high positive loadings along the

FIGURE 6 Results of multiple factor analysis (MFA) for plants grown to the five-leaf growth stage, showing (a) loading scores of variable groups; (b) contribution of variable groups to the first two dimensions; (c) RV coefficients, which computes the similarity coefficients and reflects the correlation between two groups of traits, with coefficients approaching 1 indicating stronger relationships; (d) biplot illustrating the correlation between quantitative variables and dimensions by groups of attributes; (e) coordinates of quantitative variables; and (f) contribution of individual quantitative variables to the first and second dimensions. Acronyms for variables are defined in Table 1.

axis of the second dimension (Figure 6d). The quantitative variable coordinates (Figure 6e) indicated that the variation in the first axes was primarily explained by 10 of the 17 traits factorized for the MFA, including shoot biomass, and features for root length diameter and root hairs. Three root traits that described the variation on the second dimension include root biomass rhizosheath weight. Correlations of traits with PCs and significance levels are presented in Supplementary Table S1. The most significantly associated variables with PC1 included shoot P, SFW, TRD, LRL, and TRL, and those significantly associated variables with PC2 were root biomass, root P, and rhizosheath weight (Table S1). Root hair and shoot biomass traits contributed dominantly to the first dimension, whereas root biomass and rhizosheath weight traits contributed above average to the second dimension. The ranking order of quantitative traits that contributed above average to the variability in PC1 is RHD > RHL > SFW > TRD > LRD > SDW (Figure S2). When the first two dimensions were combined, root hair and biomass-related traits contributed above the average cutoff point to the variability (Figure 6f). The projections of the individuals in the PC1–PC2 plane differed depending, to a large extent, on genotype (Figure S3).

At the GPD growth stage, across genotypes and $[P]_{ext}$, the first two PCs of the MFA performed on the eight trait groupings, with eigenvalue ≥1, together explained 72% of the total variance in the phenotypic space (PC1 and PC3 explained 41.6% and 30.4%, respectively). The correlation plot between groups and dimensions is shown in Figure S4a. Four positively correlated trait groups contributed the most to PC1 (Figure 7a). The trait groups associated with PC1 included biomass and rhizosheath traits. Three groups, comprising biomass and rhizosheath features, mainly contributed to the first dimension (Figure S4b). Four groups, encompassing root length, diameter, and root hair trait groups, contributed to the second PC (Figure S4c). However, three groups (shoot and root biomass and root length trait groups) contributed above the average cutoff point to the variability in the first two dimensions (Figure 7b). Low (.1) to high (.9) RV coefficients were recorded (Figure 7c). There were moderate associations between tissue P and RHD (RV = .41), root biomass and rhizosheath (RV = .50), and RHL and root length traits (RV = .46). The RVs for the association between root lengths and tissue P (.30) and rhizosheath and tissue P (.20) were low (Figure 7c). The RV coefficients for the mean configuration of the MFA for groups of traits representing shoot biomass, root biomass, root lengths, root diameters, RHL, RHD, rhizosheath, and tissue P were .97, .92, .79, .66, .71, .70, .80, and .43, respectively. Thus, shoot biomass recorded a closer RV coefficient (.97) to the mean configuration of the MFA (Figure 7c).

According to the MFA scores, three main positively correlated groups are seen in the biplot of PC1 and 2 (Figure 7d). The first group includes root length, RHL, root diameter traits, and biomass traits positively correlated to PC1. Although not very well represented on the quantitative variables factor map, specific rhizosheath weight is positively connected to PC1, which resolved in the second quadrant with tissue P and root biomass, suggesting a positive correlation between these traits. Root hair density, rhizosheath weight (g), and specific

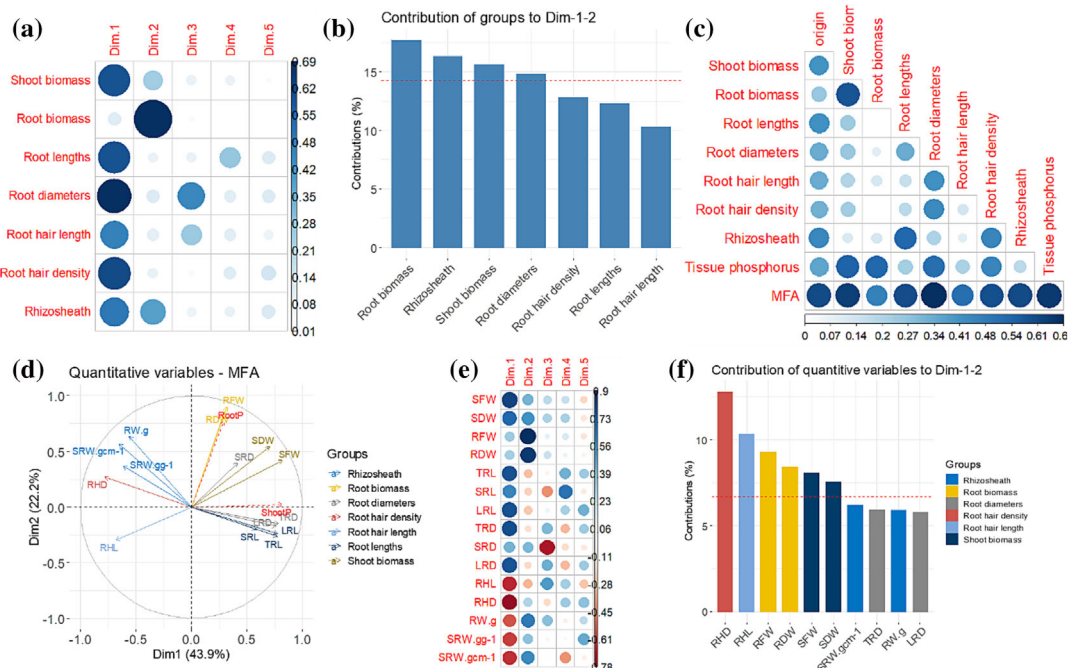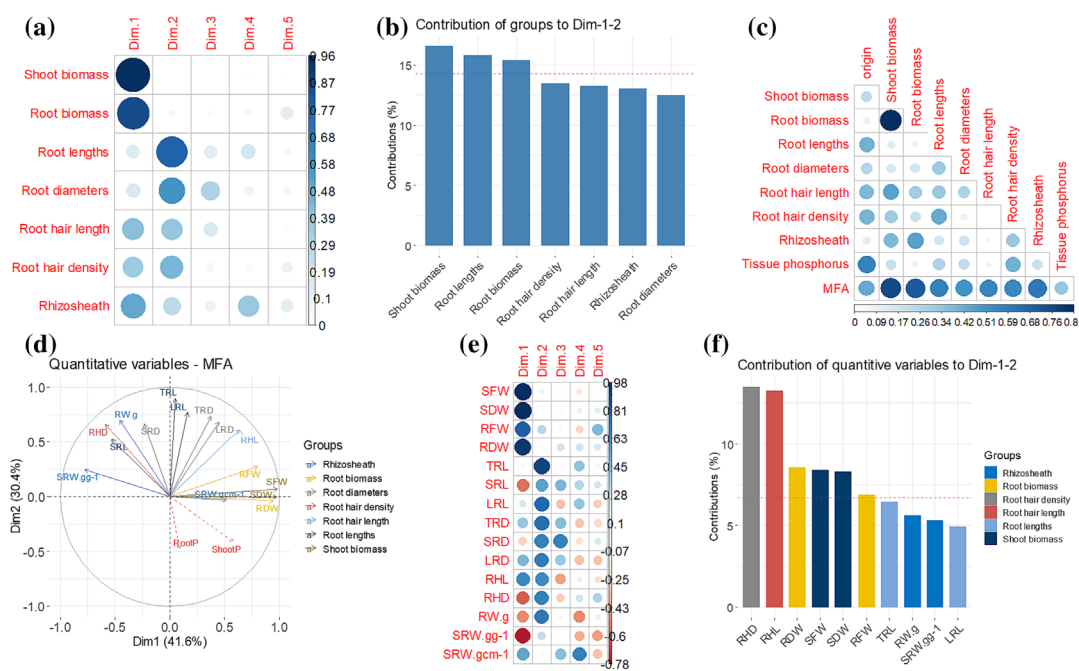**FIGURE 7** Results of multiple factor analysis (MFA) for a plant grown to the GPD growth stage, showing (a) loading scores of variable groups; (b) contribution of variable groups to the first two dimensions; (c) RV coefficients, which computes the similarity coefficients and reflects the correlation between two groups of traits, with coefficients approaching 1 indicating stronger relationships; (d) biplot illustrating the correlation between quantitative variables and dimensions by groups of attributes; (e) coordinates of quantitative variables; and (f) contribution of individual quantitative variables to the first and second dimensions. Acronyms for variables are defined in Table 1.

rhizosheath weight (g g^{-1}), seminal root-related traits were positively associated, and these were negatively related to other traits, including tissue P (Figure 7d). Two sets of quantitative traits were linked to PC1 (Figure S5a; see Supplementary Table S2 for correlations of traits with PCs and significance levels). The first set comprised biomass traits, and the second was specific rhizosheath. Four sets of quantitative traits were linked to PC2. The first set comprised root length traits (TRL and LRL); the second comprised root diameter traits (TRD, SRD, and LRD); the third and fourth sets were rhizosheath weight and RHD (Figure 7e). Quantitative traits that contributed to above average to variability in PC1 were biomass traits, root hair traits, and specific rhizosheath (g g^{-1}). All these traits and root length and diameter contributed above average to PC2 (Figure S5a,b). However, root hair and biomass-related traits contributed above the average cutoff point to the variability in the first two dimensions (Figure 7f). The projections of the individuals in the PC1–PC2 plane differed enormously depending on genotype than on the external P level (Figure S6).

3.8 | Relative distance plasticity index

The relative distance plasticity indices (RDPIs) showed that plasticity depended on the measured trait (Figure 8). There was no significant difference in the RDPI between the two genotypes. Still, the RDPI for the red genotype appeared higher in about 66% and 40% of the characteristics measured in the five-leaf and GPD growth stages, respectively (Figure 8). The RDPI for the two experiments was comparable and could be classified as low (≤.3) to moderate (.3–.5). Five traits, including TRD, TRL, SRW (g cm^{-1}), LRD, and LRL, had moderate RDPI at the five-leaf growth stage (Figure 8a). The experiment at the five-leaf growth stage had a 7-fold difference between the lowest and the highest RDPI. The RDPI ranged from .066 ± .00241 (RW) to .425 ± .014 (LRL) for the red sorghum and .048 ± .00199 (RW) to .428 ± .0129 (LRD) for the white sorghum (Figure 8a). Six traits in the red genotype recorded moderate RDPI at the GPD growth stage. These were SDW, SFW, RFW, TRD, LRL, SRD, and LRD. In the white
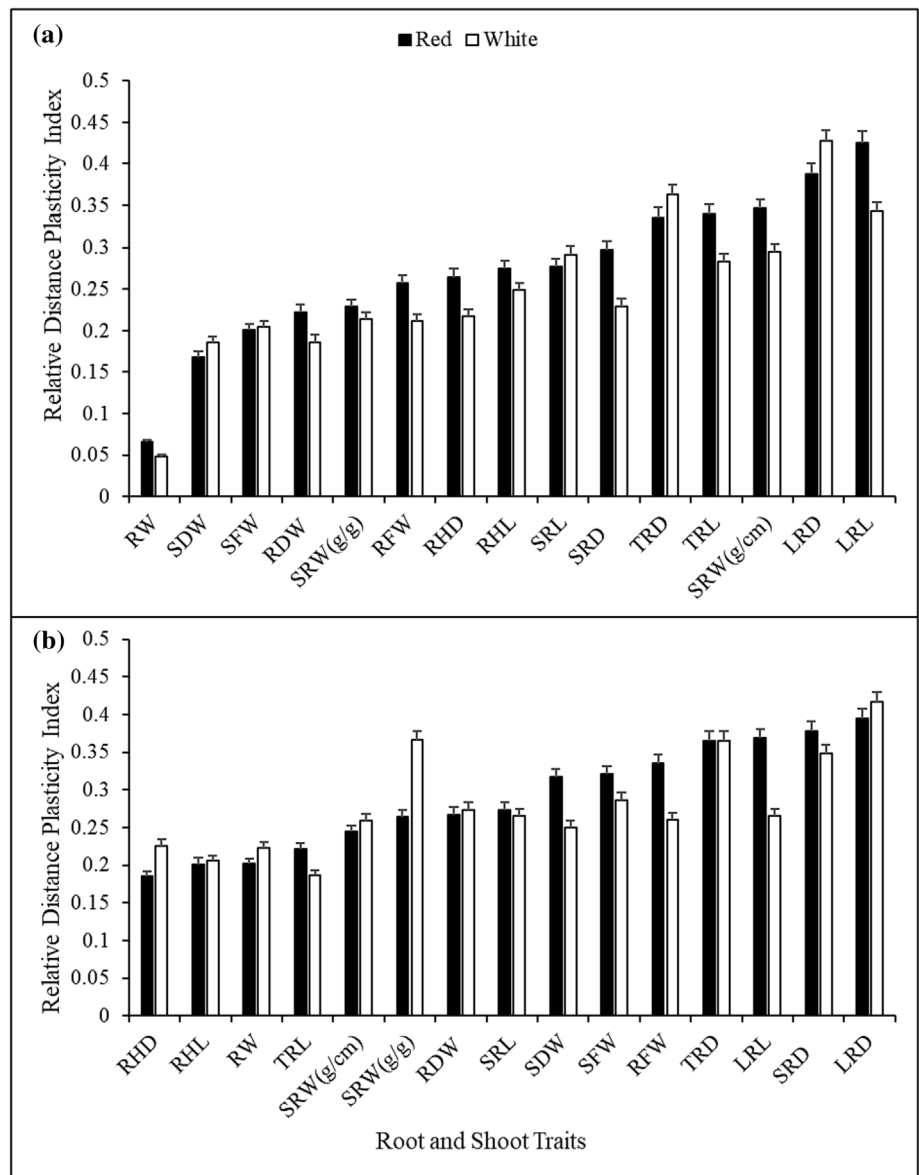

FIGURE 8   Relative distance plasticity indices (RDPI) for the quantitative root traits for two sorghum genotypes grown to (a) the five-leaf growth stage and (b) the growth point differentiated growth stage in unamended soil and soils to which 100, 200, 300, and 400 mg KH$_2$PO$_4$ kg^{-1} had been added.

genotype, four characteristics, including SRW (g g^{-1}), TRD, SRD, and LRD, recorded moderate RDPI (Figure 8b). There was a ∼2-fold difference between the lowest and the highest RDPI. The RDPI ranged from .185 ± .00725 (RHD) to .395 ± .0128 (LRD) for the red sorghum and .187 ± .00666 (TRL) to .416 ± .0131 (LRD) for the white sorghum (Figure 8b).

4 | DISCUSSION

4.1 | Genotypic variations in RSA and P uptake

The red and white sorghum genotypes used in the present study generally require very fertile soils or intensive fertilization to attain higher yields (Kudadjie, 2006). The more comprehensive cultivation of these varieties by sorghum farmers could incur fertilizer costs or yield penalties. The farmers' choice of these genotypes might be due to several reasons. Firstly, these early-maturing genotypes, as opposed to late-maturing ones, could better adapt to the prevailing climatic conditions of erratic rainfall and extensive drought. Beyond this adaptive reason, these genotypes are amenable to several uses, including animal feed and direct human food. Their short cycle contributes to livelihood resilience and coping with hunger during the lean seasons (Kudadjie et al., 2004).

The red sorghum (Naga red) performs slightly better under various soil conditions than the white genotype (Kudadjie et al., 2004). This advantage could be attributed to better soil exploration capacity in the red genotype. To the best of our knowledge, there has not been any assessment of the genetic diversity in root traits between the two genotypes and about variations in the acquisition of critical soil resources such as P. The results of the present study suggest that the two genotypes do not differ significantly in most of the traits measured. The absence of significant variations in many root features could reflect the limited genetic diversity that breeders had at their disposal when these genotypes were developed, the marginalization of root traits during selection, or selection under similar conditions.

However, the two genotypes differed significantly only in length-related traits of the root system, namely, the TRL and LRL. The root system of the red genotype was nearly 30% longer than that of the white genotype. These variations were observed only at the five-leaf growth stage (Table 2). This does not strongly suggest a demonstration and persistence of variability in given root traits to serve as criteria for the systematic improvement of the root systems. The slightly higher yield of the red genotype, reported by farmers, could be due to its soil exploration capacity conferred by a relatively larger root size. This suggestion requires further studies for validation, using replicated trials under field conditions and growing to maturity or by indexing the genotype against standard or efficient genotypes used in genetic studies and breeding programs. It is important to note that the advantages of the more extensive root system in soil exploration may be negated by the excessive allocation of biomass to root classes that are more metabolically demanding. Crop genotypes having lower metabolic costs of soil exploration, according to Lynch (2015), would have better soil resource uptake.

4.2 | Biomass and tissue P concentration responded to P supply

The results demonstrated that juvenile sorghum, grown on soils typical of the coastal savannah agroecosystem of Ghana, is responsive to adding P fertilizer (Figure 1). Thus, both the sorghum and the soil responded to external P. This responsiveness suggests that variations in soil P supply could be critical for the early growth and establishment of sorghum, and soil P supplements will be required to attain growth close to the physiological maximum for the crop. Early vigorous growth and establishment of crops contribute to resource use efficiency and resilience to abiotic stresses beyond the establishment phase. In the current study, the shoot biomass increased to an asymptote with increasing P addition to the soil (Figure 1), suggesting a limit or maximum level of P fertilizer application for optimum shoot biomass production. In barley, shoot biomass increased exponentially with an increasing P supply (George et al., 2011), but in Lantana, the response was linear (Kim & Li, 2016). Here, the response trend of root biomass was inconsistent between the two experiments, being linear at the five-leaf growth stage and exponential quadratic at the GPD growth stage. This suggests that early root biomass production might be proportionate to soil P supply, but demand increases substantially beyond the 14 days after planting. The relationship at the GPD growth stage could be due to greater demand for rapid root and canopy expansion. In Lantana, Kim and Li (2016) reported that root biomass production was logarithmically related to P but added that the plant growth phase influenced biomass accumulation.

Similar to the response of young barley plants (George et al., 2011), the shoot P concentration of the sorghum increased linearly with the addition of P in 14-day-old plants. In 28-day-old plants, the increasing trend in shoot P was quadratic. It is apparent that in older plants, the magnitude of shoot P at high P supply levels is smaller than that of younger plants. Thus, under high P supply levels, tissue P concentration in sorghum decreases as the plant ages, possibly due to increased biomass. The present results might exemplify the dilution effect in mineral nutrition (Fageria et al., 2013), but we draw this conclusion cautiously. The dilution principle may be applied to the P maxima in biomass response curves. Still, it is clear that yield did not increase beyond 200 mg P kg^{-1} for both shoot and root, but tissue P concentration increased beyond the 200 mg P kg^{-1} point strongly in roots than in shoots (Figure 1). The possible explanation for this phenomenon, whether due to physiological expenditure, limited uptake, or poor assimilation, is not immediately apparent and will require further investigation. Still, the stressor is removed in older plants and when the P supply exceeds 200 mg P kg^{-1}. There could also be a deregulation mechanism in older plants in particular concentrations of external P. In field crops, including rice, maize, and bean, shoot P decreased exponentially as the plants aged (Fageria et al., 2013). Therefore, physiological processes associated with plant aging and

vagaries of experimental conditions might be implicated in the observed pattern of biomass and tissue P concentration responses to P supply in the current study. Even so, interspecific variability cannot be ruled out in accounting for different response trends between sorghum and other crops.

4.3 | P supply and macroscale root architecture traits

Plants frequently alter their roots' morphology to improve their roots' capacity to absorb P from the soil (Kumar et al., 2019). Increased lateral root proliferation typically compensates for reduced primary root growth and increases root length under low P conditions (Shen et al., 2018). This study observed variation in specific RSA traits in response to P availability. However, the typical modification of root length under deficit P conditions was only evident when plants were grown for 28 days. Here, plants under high P conditions had close to 2-fold less TRL than those in low P conditions (Figure 2). At the five-leaf growth stage, root length increased with increasing P supply with up to a 2.5-fold difference in root length between low and high P conditions (Figure 2a).

Similarly, Shen et al. (2018) reported that wheat root length was reduced with increasing P deficiency. In the present study, increased TRL at the five-leaf growth stage in response to P was caused by increased LRL and SRL (Figure 2a,c). Decreased TRL at 28 days in response to P was caused by decreased LRL and SRL (Figure 2b,d). The result at the GPD growth stage was consistent with (Yuan et al., 2016), who reported that P deficiency increased root length. From our results, root length response to P deficiency in sorghum shows plant age or growth stage variations. The relative plasticity indices confirmed length-related traits as the most plastic in the present study. Compared to the other root features, data for both growth stages consistently found high plasticity in lateral root-related traits (i.e., LRL and LRD) (Figure 6). This observation suggests that juvenile sorghum's lateral roots might be more dynamic and responsive to P fertilization than other traits. Optimization of lateral root proliferation and elongation in sorghum might be necessary under conditions of low availability of soil P. Still, this result has to be verified in mature plants under field conditions.

The type of plasticity reported in this paper, where the trait responds only to a specific environmental cue, may not benefit low-input agriculture. Ideally, phenotypic plasticity that expresses the desired trait value regardless of the environment is preferable, as it would facilitate the design of a single genotype that could be grown anywhere. This is, however, challenging and perhaps impractical. Since there cannot be a "perfect plasticity," Schneider and Lynch (2020) suggested that in low-input systems, highly plastic root phenotypes with variable values of various traits may be beneficial for acquiring heterogeneous soil resources in environments with significant root loss. It is also important to note that root plasticity can be defined at various spatial scales (Grossman & Rice, 2012). The plasticity reported here may correspond to global plasticity in which respective rates of nutrients were uniformly supplied to the root system to assess plasticity among plants. On the other hand, local root plasticity, where nutrients are provided locally to sections of the soil's volume, has shown that local root proliferation could be helpful in response to higher concentrations. The distinction of global versus local plasticity is beneficial in establishing whether the observed responses show among- or within-plant plasticity. Between- and within-plant root plasticity could offer insights into plants' foraging capacity in heterogeneous soil conditions. However, root plasticity may be maladaptive due to plant maintenance costs occasioned by root growth (Grossman & Rice, 2012).

Seed P reserves and exogenous P status in the initial growth stage might affect the modification of RSA and P uptake. In this study, the soil was incubated once at the beginning of both experiments. Phosphorus reserves in seeds and soil in the 14-day trial were possibly higher than in the 28-day trial, where the P reserves might have been depleted. Seed P was maize's primary source during its early growth (Nadeem et al., 2011). Wheat plants grown from seeds with high P reserves developed better root systems and accumulated more P from soil (Zhu & Smith, 2001). In the 14-day-old sorghum, seed P reserves might have interacted synergistically with exogenous P to increase root length with increasing P. Still, when seed P reserves could have been depleted in the 28-day-old plants, there might have been more partitioning to roots under deficit P conditions to enhance soil exploration for the resource. The seed and exogenous P phenomenon might have also been reflected in root diameters. A smaller root diameter enhances root adsorption surface per unit of root biomass (Atkinson, 1990). Sometimes, P deficiency leads to fine root production (Shen et al., 2018). Still, in this study, the response of root diameters to P supply was inconsistent between root types and experiments. Although the diameters of lateral roots generally tended to increase to an asymptote with increasing P in younger plants, that of seminal roots decreased with increasing P (Figure 2) in 28-day-old plants. The present results might also disagree with the results in other crops because it has been confirmed that the root growth response to low P is genotype dependent and contradictory results could be obtained when different growing conditions are employed (Liu, 2021).

The MFA showed that plant biomass consistently contributed to variation in the first two dimensions at both growth stages. Still, root hair and rhizosheath traits contribute more to variation at early development stages, whereas root length traits become essential later (Figures 6 and 7). Selection based on fine root development might be advantageous at the early seedling stage. Other critical root system traits for anchorage and soil penetration would become necessary at later growth stages. RV coefficient is a multivariate generalization of the squared Pearson correlation coefficient that quantifies the similarity between two matrices of quantitative variables (Abdi, 2007). The RV coefficients from the MFA in the present study were lesser than those reported for field-grown sorghum root traits (Adu et al., 2022), suggesting plant age-dependent influence on root trait associations. Even so, there were moderate associations between various trait groups and tissue P, including associations with RHD (RV = .44), root

diameters (RV = .51), shoot biomass (RV = .55), and root biomass (RV = .53), suggesting linear dependence, albeit moderately, between each the two respective multivariate data vectors.

4.4 | RHD was more sensitive to P supply than RHL

RHDs and RHLs vary widely between species and cultivars and are among the attractive targets for crop breeding programs for soil resource acquisition (Parra-Londono et al., 2018). There have been many studies on sorghum root hair production of sorgoleone. There is a considerable lack of data on variations in root hair densities and lengths about soil resource acquisition. The pot-grown sorghum genotypes in the present study produced many root hairs of average size (∼200 μm), slightly higher than the ∼150 μm reported for 3-week-old sorghum grown in soil-filled rhizotrones (Wojciechowski & Kant, 2021). Compared to other crops, the RHL recorded here appears shorter. In field-grown barley, for example, 400–700 μm root hairs have been documented (Haling et al., 2014; Marin et al., 2020). In maize, Adu et al. (2017) noted that RHD might compensate for RHL, whereas genotypes with shorter RHLs produced denser root hairs. Contrarily, in 3-week-old sorghum, positive correlations between RHL and RHD were reported, where cultivars with more root hairs also had longer root hairs (Wojciechowski & Kant, 2021). Neither of these phenomena was evident here. Moreover, there was no significant distinction in the length of the root hairs measured between the two genotypes, which might be due to previously discussed reasons.

Root hairs and rhizosheath are two different root traits whose developments are occasionally linked in some crops, and they may play similar roles in soil resource acquisition. RHL and RHD are two features of root hairs often associated with P acquisition. Root hairs grow longer and denser in many crops under low P (Ma et al., 2001). Here, sorghum plants grown in low P soil produced nearly 35% greater RHD than in high P soil, and the response was more extensive in the red than the white sorghum genotype (Figure 3b). Consistent with our results, RHD decreased linearly as P with increasing P supply in *Arabidopsis thaliana* (Ma et al., 2001). Under P deprivation, RHD may increase to compensate for reduced trichoblast length by initiating more trichoblast files, some of which may have multiple root hairs. These occurrences may not be mutually exclusive (Ma et al., 2001). Contrarily, [P]$_{ext}$ did not significantly affect RHL. Although the insignificant response of RHL is not immediately apparent, it might suggest that root hair proliferation (RHD) is more sensitive to exogenous P supply than root hair elongation (RHL) in sorghum or the varieties used herein.

Interestingly the plasticity of RHL and RHD were comparable, but the ranking for the two experiments conflicted. The plastic indices for RHL, RHD, and total rhizosheath weight were moderate at the five-leaf growth stage but low at the GPD growth stage. The low plasticity index of root hair-related traits at the GPD growth stage was unexpected. Under P deprivation, plasticity typically manifests as increased

RHL or density to improve P uptake (Zhu et al., 2010). It appears, however, that the root hair traits are more sensitive to external P in the younger (five-leaf growth stage) than older plants, having obtained the least RDPIs at the GPD growth stage (Figure 6b). Thus, root hair traits may adapt to enhance P uptake and plant performance under P deficiency in sorghum, but the magnitude of adaptation might differ depending on the age of the plant. This observation has to be determined in field-grown plants. The results of the present study suggest that sorghum has a genetic disposition to rhizosheath formation (Figure 3c,d). Even so, the extent to which rhizosheaths develop could respond to soil P, where sorghum establishes and enhances rhizosheath size under deficit P conditions as an adaptive trait. Rhizosheath adaptation under deficit P conditions to improve P uptake has been reported in other crops, including barley (George et al., 2014) and white lupin (Aslam et al., 2021).

4.5 | Relationships between traits

Positive correlations were established in several pairs of traits, which were unsurprising, given that they were natural relationships where an increase in one feature could automatically increase the other attribute. Interestingly, there was a considerable reduction in significant correlations at the GPD growth stage (Figure 5a,b). We are not immediately sure why many of the correlations were transient. By day 28, the root system might have been thigmotropic due to the size of the pot, effectively impacting the expected allometric relationships of the parts of the root system. Root hairs have been implicated in the formation of rhizosheath in several, but not all, crop plants (Pang et al., 2017). When the root hair traits and rhizosheath size were correlated, we found an insignificant relationship between measures of rhizosheath and root hair traits at the five-leaf growth stage (Figure 3e) and a positive albeit weak relationship (Figure 3f) at the GPD growth stage. Although inconsistencies in the relationships between root hair and rhizosheath traits may be attributable to variations in rhizosphere properties, root morphology between crop species, or the contribution of other factors other than root hairs to the formation of rhizosheath, our results also illustrate that plants' developmental stage may confound the relationship. Here, the relationship between root hair and rhizosheath traits became somewhat evident in a later growth stage, possibly due to the influence of seed P reserves at the early growth stage. If root hair development is endogenously triggered by tissue P status, then at the early developmental stage, when the starting seed P concentration may be high, the formation of root hair and rhizosheath traits may be delayed or proceed allometrically. Indeed, reports on the crosstalk between rhizosheath formation and root hair development have conflicted. A robust relationship between RHL and rhizosheath weight per unit root length was reported for wheat (Delhaize et al., 2012). A weak but positive correlation between rhizosheath weight and RHL was found for maize and barley (Adu et al., 2017; George et al., 2014). Pang et al. (2017) observed no significant relationship between rhizosheath weight and RHL in chickpeas.

Total root length and tissue P concentration were positively correlated (Figure 5e). Therefore, P acquisition might be limited in plants with reduced root system length. Adu et al. (2015) reported similarly in *Brassica rapa*. They argued that roots' ability to explore the soil volume was of greater importance for P acquisition than the rate of P uptake per unit root length. Here, we found that RHD was negatively correlated with the tissue P concentration of shoot and root biomass (Figure 5d,e); therefore, the rate of P uptake per unit root length might also be crucial. Specific rhizosheath weight (mg cm^{-1}) was positively correlated with shoot P concentration in the early developmental stage (Figure 5c), which is consistent with the results of Aslam et al. (2021) and George et al. (2014). Rhizosheath is thus a vital root trait to enhance sorghum's P status. It is noteworthy that RHD displayed a higher and more consistent correlation with tissue P than RHL at the two growth stages, possibly pointing to a more significant advantage of RHD than RHL in facilitating P acquisition in sorghum. An increase in RHL, however, presented more considerable importance for nutrient uptake than an increase in RHD in dry soils (Zygalakis et al., 2011). Perhaps, RHD is critical in replete soil moisture conditions and at the early development stages of sorghum, when root systems' capacity to explore new soil volumes is crucial for nutrient intake before root overlap and competition occur at later growth stages.

The weak relationship between RHD and rhizosheath traits made it unsurprising that tissue P concentration correlated negatively with some rhizosheath features (Figure 6c–f). The slopes of the present study's regression lines are less steep than those reported for spinach, tomato, and rape by Foehse and Jungk (1983). The linear model to predict tissue P concentration found that variation in RHD and specific rhizosheath weight explained up to 59% of the variation in tissue P. Our result is comparable to other crop plants, including Brachypodium, tomatoes, and rape, where root hairs have been reported to explain 50%–86% of the variation in P uptake (Jungk, 2001; Zhang et al., 2018), providing circumstantial evidence that root hair and rhizosheath traits contribute significantly to P acquisition. Although tissue P concentration was influenced by [P]$_{ext}$, the results indicate that the concentration of P in the plant tissue could be implicated in the proliferation of root hairs. Thus, tissue P status systemically regulates root hair proliferation in sorghum, impacting rhizosheath formation. Indeed, Jungk (2001) suggested that the signal for root hair development originates from the plant tissue's limiting P. However, we agree with Jungk (2001) and Foehse and Jungk (1983) that the present results do not fully clarify the factor that regulates the development of sorghum root hairs under deficit P conditions. The contribution of the balance of P concentration at the epidermal surface of roots versus the concentration of P within root tissues in regulating root hair and rhizosheath formation and growth in sorghum has to be determined.

5 | CONCLUSIONS

Despite sorghum's importance as a climate-resilient and food security crop, little is known about the genotypic variations of its root systems concerning soil resource dynamics. This study explored the responses of plasticity and trait relationships of the root systems of two prevalent sorghum genotypes (red and white) grown in Ghana to variable external P supply. The study comprised an experiment in which the sorghum genotypes were harvested for analysis at the five-leaf and GDP growth stages. The results showed that the measured root traits were more variable at the GDP growth stage than at the five-leaf growth stage. The two genotypes significantly differed, mainly in TRL and LRL, in favor of the red genotype. As reported by farmers, this might support better soil exploration and contribute to the slightly better yield performance of the red over the white genotype. Most root traits of juvenile sorghum can be responsive to external P supply. Still, the responses are more significant and more predictable in the early days of growth (14 days after sowing) compared to the subsequent days. Further investigation is needed to investigate whether additional P supply after the 14 days would make the responses persistent and predictable in the subsequent growth stages. Also, sorghum shows a genetic disposition to rhizosheath formation. Specific rhizosheath weight correlates with RHD, albeit weakly, and also with shoot P concentration. RHD displayed a higher and more consistent correlation with tissue P than RHL, possibly pointing to a more significant advantage of RHD than RHL in facilitating P acquisition in sorghum. RHD and specific rhizosheath weight explained up to 59% of the variation in tissue P. Under conditions of high external P supply, TRL and LRL and RHD can significantly increase at the early growth stages. Still, the subsequent rate of growth declines or becomes variable. Similar observations apply to the relationships between rhizosheath and root traits. Plastic responses of root system traits to external P supply might be higher in much younger sorghum genotypes than older plants. Application rates from 200 to 300 mg P kg^{-1} soil might produce optimal responses of root system traits. Between the two growth stages, the transient nature of the plasticity and responses of the characteristics to external P supply does not support the criterion of persistence as a basis for targeted root trait selection for crop improvement. This non-persistence requires further investigation.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest regarding the publication of this article.

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The peer review history for this article is available in the Supporting Information for this article.

DATA AVAILABILITY STATEMENT

Data are available upon request.

ORCID

Michael O. Adu https://orcid.org/0000-0001-5243-7472
Nathaniel Zigah https://orcid.org/0009-0004-2647-4551
David O. Yawson https://orcid.org/0000-0002-5771-4042
Kwadwo K. Amoah https://orcid.org/0000-0002-2122-624X
Emmanuel Afutu https://orcid.org/0000-0002-9182-3939
Kofi Atiah https://orcid.org/0000-0002-5061-4364
Alfred A. Darkwa https://orcid.org/0000-0002-2074-9102
Paul A. Asare https://orcid.org/0000-0003-3047-0428

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SUPPORTING INFORMATION

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