



Phosphorus management is key to effective deployment of root ideotypes in complex soil environments

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Abstract

Purpose We questioned how root ideotypes selected for deep or shallow root architecture function in complex environments with heterogeneous distributions of phosphorus (P), such as in many cropping systems in north-eastern Australia.

Methods We used the rhizobox method to evaluate how contrasting genotypes of durum wheat and sorghum (wide and narrow root angle) responded to combinations of starter-P and deep P bands.

Results Although we found evidence that root angle may influence spatio-temporal exploration for deep P bands, (early) plant access to P was the critical driver for plant growth. Without P, root system growth was

retarded such that genotypic differences were hardly observed. Access to P boosted root exploration at depth by virtue of greater root system size, such that wide-angle genotypes with P outperformed narrow-angle ones without P. Plastic root responses to P benefited the expression of the broader root system architecture. We observed variation between species and individual parameters, but overall Starter-P and deep P bands tended to deliver complementary benefits when considering plant growth, P uptake, and phenological development together.

Conclusion Our study highlights that nutritional constraints may limit the ability of root ideotypes to function in complex target environments. Development and deployment of root ideotypes should consider how local conditions (including soil nutrient distribution, physical and biological properties) influence crop phenotype and their ability to deliver the

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intended benefits. Within this, soil nutrient management is a critical determinant and an opportunity to influence the target environment.

Keywords Root distribution · Root angle · Crop nutrition · Phosphorus placement · Root proliferation · Soil heterogeneity

Abbreviations

RSA	Root system architecture
P	Phosphorus
MAP	Mono-ammonium phosphate
WHC	Water holding capacity
LM	Linear model
LMM	Linear mixed model

Introduction

Roots are of fundamental importance for plant growth because they control the capacity of plants to take up water and nutrients. It is increasingly advocated that breeding programmes should select root functional traits, such as root angle, with the idea that this will deliver root system architectures (RSAs, the spatial and temporal distribution of roots in the soil) that are better adapted to explore specific soil domains and acquire limiting soil resources. Notable examples of RSA targets are deeper rooting patterns for improved access to soil water at depth in drought conditions, and shallower rooting patterns for improved access to limiting nutrients that are often more concentrated in the top of the soil profile (Lynch 2019). However, it is not clear how ‘designer RSAs’ targeted by crop breeding programmes function in real-life production environments. A deeper RSA designed for a drought-prone target environment may not necessarily perform well if other constraints (e.g. nutrient deficits) limit the plant’s ability to develop a deep and vigorous root system. Therefore, it is important to understand the interactions between RSA and other factors that constrain plant growth in different agricultural contexts (van der Bom et al. 2020).

In north-east Australia, starter phosphorus (P) applications are the traditional method to apply P, with a small amount of P fertiliser (typically 5 to 6 kg P ha⁻¹) placed either beside or adjacent to the seed at time of sowing.

Starter-P applications supply readily available P in a location where it is rapidly accessible to the limited root systems of emerging seedlings, supporting the initiation of potential grain number in cereals, and improving early vigour and competitiveness in most species. However, in this region, crop access to P in the topsoil (including starter-P) is often constrained by rapid soil drying (Raymond et al. 2021; Strong et al. 1997). In addition, subsoil P reserves have been largely depleted in many soils (Dang et al. 2015). This can lead to spatial separation between two critical soil resources: water and P. One way to address this problem has been to place P deeper in the soil profile (15 to 30 cm) in the form of concentrated fertiliser bands, with the rationale that the subsoil is less likely to dry out as rapidly as the topsoil—and therefore P placed as a deep P band will remain available for longer periods (Ma et al. 2009; Singh et al. 2005). Further, the highly concentrated placement should reduce the contact between P and soil surfaces, allowing for P to remain available for longer than broadcasted applications (Meyer et al. 2020; Thomas and Rengel 2002).

Deep P bands are often observed to improve grain yields, but responses can be inconsistent among sites, seasons, crops, and crop varieties (Freiling et al. 2022). Seasonal rainfall patterns likely play a major role, but some of the variation has been ascribed to differences in RSA among crops and individual varieties, with the resulting soil foraging strategies affecting how plants react to deep P band placement (Chen et al. 2013; Schwab et al. 2006). However, quantitative information on the influence of RSA on the capture of heterogeneously distributed P in soil remains scarce. Conversely, the influence of P placement on the function of RSA ideotypes remains poorly understood. Roots that encounter a P-rich patch often respond plastically by increasing root mass (proliferate) in this zone (Drew 1975; Hodge 2004). This local response substantially increases root surface to soil contact and may enable plants to optimise use of sparsely distributed resources, such as P placed as a deep band in background soil environment with low P availability. Apart from this architectural plasticity, plants may also exhibit morphological plasticity, i.e. changes of characteristics of a single root axis, such as its diameter (Lynch 1995). However, plastic responses may also come at the expense of the intended RSA, e.g. by reducing growth outside the proliferation zone (Hodge 2004), which may reduce

the effectiveness of root ideotypes (Lynch 2013; Schneider and Lynch 2020).

The complex interactions between RSA, plastic root responses, and heterogeneous distributions of P in soil present a challenge for the deployment of novel ideotypes and to the further improvement of P fertiliser management. To improve understanding of these interactions, we conducted two experiments to evaluate the responses of contrasting sorghum (*Sorghum bicolor* (L.) Moench) and durum wheat (*Triticum durum* Desf.) genotypes (wide and narrow root angle) to combinations of starter-P and deep P bands. Previous studies on these crops have focused on genetic variability and control (Alahmad et al. 2019, 2022; Mace et al. 2012; Singh et al. 2010, 2011, 2012). Building on these, the aim of the current study was to understand how contrasting genotypes respond to complex target environments. Within this, our objectives were to i) evaluate how P availability affects plant growth and RSA of the contrasting genotypes, ii) assess how different P fertiliser placements affect crop growth and P uptake, iii) understand how differences in RSA affect plant responses to deep placed fertiliser P, and iv) assess if plastic root responses affect the broader RSA of contrasting ideotypes.

Materials and methods

Two experiments were conducted in which plants were grown in rhizoboxes (60 cm height, 40 cm width, and 4 cm depth/thickness) in a temperature-controlled glasshouse at The University of Queensland, Brisbane, Australia (27°23'S, 153°06'E). The first experiment included two durum wheat genotypes and the second experiment two sorghum genotypes. These experiments shared a common experimental design but were conducted in sequence because these winter and summer-grown species require different growth conditions: glasshouse temperatures were set to 22/17 °C day/night (12 h) for durum wheat and 28/23 °C day/night (12 h) for sorghum.

Plant materials

The two durum wheat lines, QAF0512 (Narrow) and QAF0411 (Wide) were selected from a set of F₆ generation durum lines from a nested association mapping population that were previously characterised by Alahmad et al. (2019), in which they were observed to express contrasting seminal root angles (QAF0512=41° and QAF0411=82). These lines have also been included in a series of further screenings and targeted studies that confirmed their contrasting seminal root angles and relationship with RSA, whilst also displaying similarities in root system biomass, tiller number, growth rate, and time to flowering (Alahmad et al. 2022; van der Bom et al. 2023). The two sorghum lines, B35 (narrow) and SC999-14E (wide) were selected from a previously characterised set of inbred lines (Mace et al. 2012) in which they were observed to express contrasting nodal root angles (B35=28° and SC999=46° for the first flush of nodal roots, relative to a vertical plane). Based on further screenings they were expected to differ in the way they explored the soil profile (unpublished data: personal communication Alan Cruickshank and David Jordan). However, these genotypes were not isogenic lines and thus characteristics other than root angle may affect their phenotype. Considering the original screening studies used different procedures for measuring root angle, direct comparison between the two crops would require the sorghum root angles to be doubled, or the durum wheat root angles to be halved.

Soil

A grey vertosol soil (Isbell 2016), was collected from the 10 to 30 cm soil layer of a field cropped to grains and cotton near Hopelands, in the Western Downs Region, Queensland, Australia (26°49' S, 150°37' E). In the FAO classification system this soil is referred to as a Vertisol (FAO 2015). This soil had concentrations of 7 mg kg⁻¹ Colwell-P and 44 mg kg⁻¹ BSES-P (Table 1) and had previously been observed to elicit strong crop responses to P fertiliser applications. After collection it was air-dried and crushed

Table 1 Selected soil properties

Clay (g kg ⁻¹)	Silt (g kg ⁻¹)	Sand (g kg ⁻¹)	Total C (g kg ⁻¹)	Colwell P (mg kg ⁻¹)	BSES P (mg kg ⁻¹)	PBI	pH H ₂ O
354	154	491	0.5	7	44	101	8.7

with a jaw crusher to obtain a maximum particle size of approximately 8 mm.

Experimental setup

The experimental design was a completely randomised block design with full factorials (genotype×P placement), replicated in five blocks. For each rhizobox, 10.0 kg of air-dry soil was weighed into a bag and basal nutrients were carefully mixed in at the following levels (mg kg⁻¹ soil) for each element: 100.0 N, 166.2 K, 123.7 S, 20.4 Ca, 40.0 Mg, 2.0 Zn, 36.2 Cl, 3.4 Mn, 0.5 Cu, 0.1 Mo (similar to Raymond et al. 2018 but with additional Zn). These nutrient additions ensured that all nutrients except P were in adequate supply. The rhizoboxes were then packed with the fertilised soil, leaving 5 cm of head space for watering.

Four P treatments were established by placing P fertiliser in specific locations in each rhizobox during filling (Fig. 1):

1. No-P, control from which P fertiliser was completely withheld
2. Starter-P, placed ~2 cm below the seed
3. Deep P band, placed at ~30 cm depth and ~10 cm off-centre to the left of the seeding row
4. Starter-P + Deep P band, combined as above

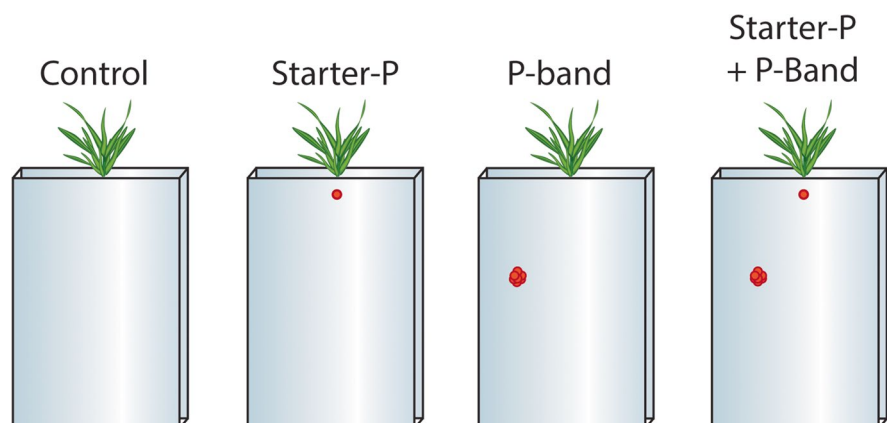
The P fertiliser was applied as mono-ammonium P (MAP), which is the preferred product by farmers in north-east Australia. The MAP contained 100 mg N g⁻¹ and 219 mg P g⁻¹ according to the fertiliser manufacturers' specifications; hence,

apart from the P, additional N was also added on top of the initial basal application. Starter-P was applied as a single medium-sized granule of MAP (44 ± 1 mg P box⁻¹) and the deep P band was applied as a row of granules across the 4 cm depth/thickness of the rhizobox (455 mg P box⁻¹). When considering a rhizobox as a 'slice' taken from the field directly below the plant, these applications correspond to 6 kg P ha⁻¹ of Starter-P, and 50 kg P ha⁻¹ of deep banded P.

All rhizoboxes were wrapped with reflective foil as a barrier to incoming light and radiant heat. They were then gradually wet up over the course of five days, allowing soil water to equilibrate between waterings. The gravimetric soil water content was 90% of water holding capacity (WHC, determined using pressure plates (Dane and Hopmans 2002)) when the wetting front visibly reached the bottom of the rhizoboxes.

To minimize any potential effects of differences in speed of germination, a batch of seeds of each genotype was allowed to imbibe from distilled water-saturated filter paper in petri-dishes for 24 h in the dark at room temperature (20 °C). From each batch, seeds of similar size were selected that had a visible coleorhiza. Three seeds were placed in the centre of each rhizobox, spaced one cm apart, oriented such that the radicle faced downwards. The seeds were covered with 250 mg of additional soil (basal fertilized) and once emerged, plants were thinned to one similarly sized plant per rhizobox. Throughout the growth period, soil water content was maintained between 80 and 90%

Fig. 1 Schematic overview of the phosphorus placements. Coloured dots illustrate the placement of phosphorus fertiliser in each treatment. Note that the Starter-P applications were substantially smaller than the P-band applications (corresponding to farmer practices of 6 kg P ha⁻¹ of Starter-P vs 50 kg P ha⁻¹ in deep P bands)



of WHC by intermittent watering, depending on plant water use.

Harvest and measurements

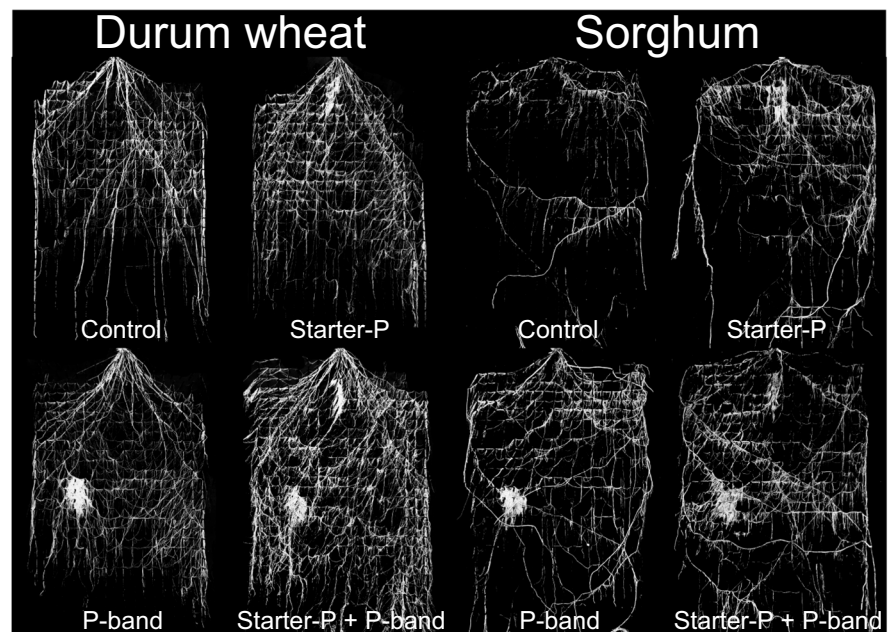
Plants were grown until the largest root systems visibly reached the bottom of the rhizobox, which was 39 days for durum wheat (corresponding to the late tillering stage) and 31 days for sorghum (corresponding to the six-leaf stage). The number of tillers was recorded, and all aboveground biomass was cut off at the soil surface. The front of each rhizobox was then removed and a pinboard with dimensions similar to those of the root chamber was pushed into the soil, allowing the soil to be carefully washed away to expose the intact root system (Singh et al. 2010). Root systems were photographed with a digital camera. Photo quality was optimised in Adobe Photoshop to ensure high-quality analyses (i.e. rotation, contrast, black and white, and touch-up of scratches and nails on the pinboard).

Root angles were measured from the photographs using Fiji (Schindelin et al. 2012). For durum wheat, root angle was measured as the angle between the seminal roots. For sorghum, root angle of the nodal roots was measured relative to a vertical plane, on

both sides, and then averaged. This approach follows the common procedures used for each of the crops (Alahmad et al. 2019; Mace et al. 2012) and means that for a direct comparison with sorghum, the measured root angle of durum wheat would have to be divided in half. All other root data including root length and area were obtained using WinRHIZO Pro 2019a (Regent Instruments, Inc., Quebec City, QC). The root data were collected separately for 10 cm intervals (i.e. soil layers) starting from the location of the seed down to 50 cm depth. We report the projected root area (cm^2), defined as the total visible root area on each photo (analysed by WinRHIZO) because we observed that the software tended to underestimate root length (cm) and overestimate root diameter in zones with substantial root overlap (Fig. 2). Specifically, the algorithm identified (segments of) parallel roots and root clusters as a single root with a large diameter. Subsequently, the relationship between root length and projected root area was mostly linear but tended to level off at high root intensities in which the projected area provided better relative comparisons than the calculated root lengths (van der Bom et al. 2023).

For both experiments, shoot and root biomass were oven-dried at 65 °C until stable weight, after

Fig. 2 Examples of clear root architectural responses of durum wheat and sorghum plants to placement of phosphorus fertiliser in different locations of the soil profile



which biomass dry matter was determined. Shoot biomass samples were finely ground and a 0.5 g subsample was digested in nitric acid and hydrogen peroxide using microwave-assisted closed vessel digestion, after which the P concentrations were analysed using inductively coupled plasma-optical emission spectroscopy. Total P uptake was calculated by multiplying the measured P concentrations with the shoot biomass dry matter.

Statistical analyses

Treatment effects were analysed separately for each crop. In the durum wheat experiment, seeds in one rhizobox (Wide, Starter-P + deep P band) did not germinate so this replicate was excluded in all analyses.

Treatment effects on biomass, tiller number and P uptake were analysed using linear models (LMs), with Genotype, P placement, and Block as the explanatory variables. Effects on root distribution were analysed using linear mixed models (LMMs), with Genotype, P placement, and Soil layer as fixed effects, and a random effect structure to account for the nesting of the soil layers in each rhizobox and the replication across blocks. In all cases, we started with a full interaction model and used backwards selection to test the interactions between the fixed effects, using an *F*-test for the LMs, and a likelihood ratio test for the LMMs. For the LMMs, the full model was fitted using Maximum Likelihood, and the final model was refitted using Restricted Maximum Likelihood before pairwise comparisons were made. Anova tables are provided in the supplementary materials.

Pairwise comparisons were made using Estimated Marginal Means, using Tukey's method to adjust for multiplicity. For projected root area, family-wise error rates were calculated by soil layer.

All statistical analyses were conducted using R version 4.2.1 (R Core Team 2020) making extensive use of the *tidyverse* family of packages (Wickham et al. 2019), *nlme* (Pinheiro et al. 2020), and *emmeans* (Lenth 2021). All models were checked for normality of residuals and homogeneity of variance using a combination of diagnostic plots and formal tests (Levene's test for homogeneity of variance, Shapiro–Wilk test for normality). Where required, analyses have been performed on log or square root-transformed data to meet the assumption of homogeneity of variance.

Results

Biomass responses of durum wheat genotypes to phosphorus placement

The P fertiliser placements increased plant biomass of both durum wheat genotypes, but genotypic differences were generally small (Fig. 3). An exception was the combined Starter+Band application in which the Narrow genotype tended to be larger, but this response was variable and not significant.

Across the genotypes, the Starter-P ($P < 0.001$) and deep P band ($P < 0.05$) placements both increased shoot and total biomass. Their joint application (i.e. Starter+Band) showed an additive effect on shoot biomass ($P < 0.05$), with this clearly being driven by the response of the Narrow genotype. The total amount of P that was applied in starter-P was much smaller than that applied in a deep P-band, but the increases in shoot, root and total biomass tended to rank in the order of Control < P-band < Starter-P < Starter+Band. The proportion of dry matter biomass in roots varied from 34 to 39% but effects of genotype or P placement were not significant (Table 2.).

Increasing amounts of applied P tended to progressively increase P uptake and the number of tillers per plant (Fig. 4A), which led to the greatest P uptake and tiller number for the combined Starter+Band application (both $P < 0.05$). Further, P uptake was linearly related to shoot biomass (Fig. 5, $P < 0.001$). However, Starter-P did not increase plant tissue P concentrations, whereas the Band applications did ($P < 0.001$, Fig. 4B).

Root angle and projected root area of durum wheat genotypes in response to phosphorus placement

The measured root angles for durum wheat varied from 74° to 89° (Table 2.) and were significantly influenced by P placement. On average, plants growing in the low-P control soil had a greater root angle than any of the other treatments ($P < 0.05$). This effect was greatest for the Narrow genotype, such that under control conditions its root angle was in fact wider than that of the Wide genotype (89° vs 81°). However, these differences between the genotypes were not significant.

On average, the total projected root area (i.e. the sum of all layers) was not significantly different between the two genotypes, but the genotypes

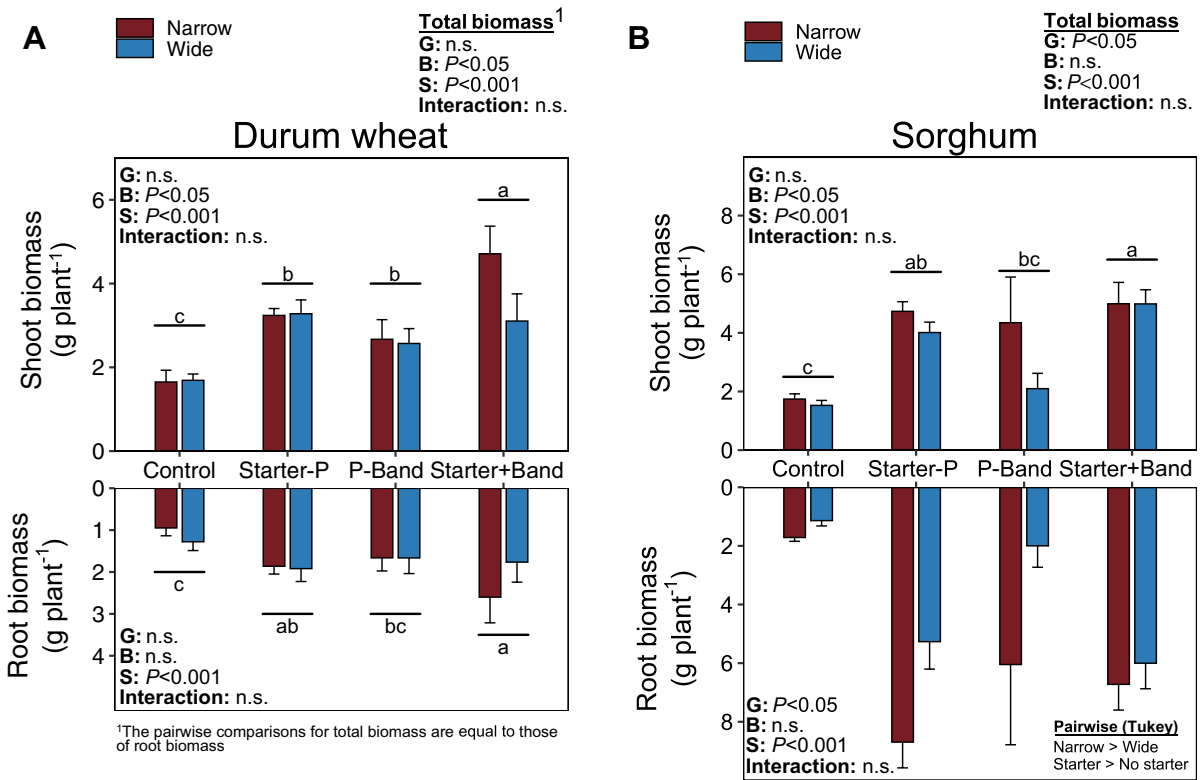


Fig. 3 Contrasting root angle (narrow/wide) and placement of phosphorus fertiliser interactively affected plant biomass responses. **A:** durum wheat genotypes, **B:** sorghum. Error bars

indicate the standard error of the mean. Treatments sharing a common letter are not significantly different ($\alpha < 0.05$)

showed differences in root distribution down the soil profile (Fig. 6, Table 3). The projected root area generally peaked in the 10 to 20 cm layer, after which it tended to decline with greater depth. Under the same treatment conditions, the Wide genotype typically had a greater root area in the 0 to 10 cm ($P < 0.05$) and 10 to 20 cm ($P < 0.01$) soil layers, but in the layers below its root area declined rapidly. Conversely, on average the Narrow genotype had a greater projected root area (relative to the Wide genotype) in the 40 to 50 cm layer ($P < 0.05$). The application of Starter-P led to an increase in root area in all soil layers ($P < 0.01$), reflecting the production of larger root systems whilst the overall distribution pattern resembled that observed under the control treatment.

Root responses to a deep P band were characterized by a peak of root area in the 30 to 40 cm layer for the Narrow genotype (relative to its root distribution in the control and Starter-P treatments).

This depth corresponds to the location of the deep band (30 cm depth) and the peak will to a great extent have been determined by the local proliferation of roots in or around the band, according to visual observations (Fig. 2). However, visually, the Wide genotypes also showed a local response to the deep P placement, but it was very small such that no similar peak was observed in the measurement of projected root area. Further, the peak in projected root area of the Narrow genotype was particularly clear when Starter-P and the deep P band were applied together (30–40 cm layer, Fig. 6). On average, a deep P band tended to increase root area in the subsoil (30 cm onwards) relative to the low-P control treatment, which was significant for the 30 to 40 cm layer ($P < 0.01$). In contrast, the presence of deep P resulted in a reduction in root area in the 10 to 20 cm layer ($P < 0.05$), with this effect being driven by the combined Starter+ Band *versus* Starter-P.

Table 2. Root angle (°) and the proportion of plant dry weight in roots (%) of the durum wheat and sorghum lines under the influence of phosphorus fertiliser placement

Phosphorus placement	Genotype	Durum wheat				Sorghum			
		Root angle ¹ (°)	std. err.	Root biomass proportion (%)	std. err.	Root angle ² (°)	std. err.	Root biomass proportion (%)	std. err.
Control	Narrow	89	2.0	36	1	47	4.4	50	2
Control	Wide	81	0.7	38	2	62	5.6	42	2
Starter	Narrow	77	2.1	36	2	41	1.4	64	1
Starter	Wide	80	4.7	37	4	52	4.6	56	3
Band	Narrow	74	1.7	39	3	37	2.7	52	5
Band	Wide	77	2.3	38	2	51	6.6	46	2
Starter + Band	Narrow	75	1.6	34	3	38	2.9	58	1
Starter + Band	Wide	80	2.7	35	4	53	4.1	54	2
Significance (Anova results for linear mixed models)									
Genotype		n.s		n.s		<0.001		<0.001	
Starter-P		<0.05		n.s		n.s		<0.001	
Band		<0.001		n.s		<0.05		n.s	
Starter × Band		<0.05		n.s		n.s		<0.05	
Block		<0.05		n.s		n.s		n.s	

¹angle between seminal roots

²angle of nodal roots relative to a vertical plane

Biomass responses of sorghum genotypes to phosphorus placement

The two sorghum genotypes differed in their responses to P placement, with the Narrow genotype showing greater root biomass and greater total biomass, when averaged across all treatments (Fig. 3, $P < 0.05$). There were no significant interactions, indicating that the P placements did not moderate the genotypic differences more than what could be expected by chance. However, the Narrow genotype tended to show a stronger response to Starter-P and the deep P band; but this was paired with considerable above and belowground variability, especially for the response to the deep P band. Broadly speaking, the biomass responses to P placement tended to show a pattern similar to that observed for the durum wheat genotypes, increasing in the order of Control < P-band < Starter-P < Starter + Band in which Starter-P significantly increased the biomass of both genotypes compared with the control treatment or the deep P band (both $P < 0.001$, Table 2.). The proportion of dry matter biomass in roots ranged from 46 to 64% and on average the biomass allocation

to the roots was greater for the Narrow sorghum genotype ($P < 0.01$), as well as when Starter-P was applied ($P < 0.01$).

The genotypes showed differential responses to P placement in terms of tissue P concentrations (Fig. 4A). For the Narrow genotype, the P concentrations decreased relative to the control when P was applied in a single spot (Starter-P or P-Band), which was significant for the Starter-P application ($P < 0.01$). However, the co-application of Starter-P with a deep P band improved P concentrations compared with the single applications ($P < 0.05$). For the Wide genotype, the inclusion of a deep P band improved P concentration compared with the control ($P < 0.001$), which was not the case for Starter-P. Both Starter-P and a deep P band increased total P uptake in similar manner, but co-application of Starter-P and a P-band had a clear additive effect (Fig. 4E). Similar to the observed plant biomass response, P uptake in response to the deep P band tended to be greater for the Narrow genotype, but this response was variable. Phosphorus uptake was linearly related to shoot biomass (Fig. 5, $P < 0.001$).

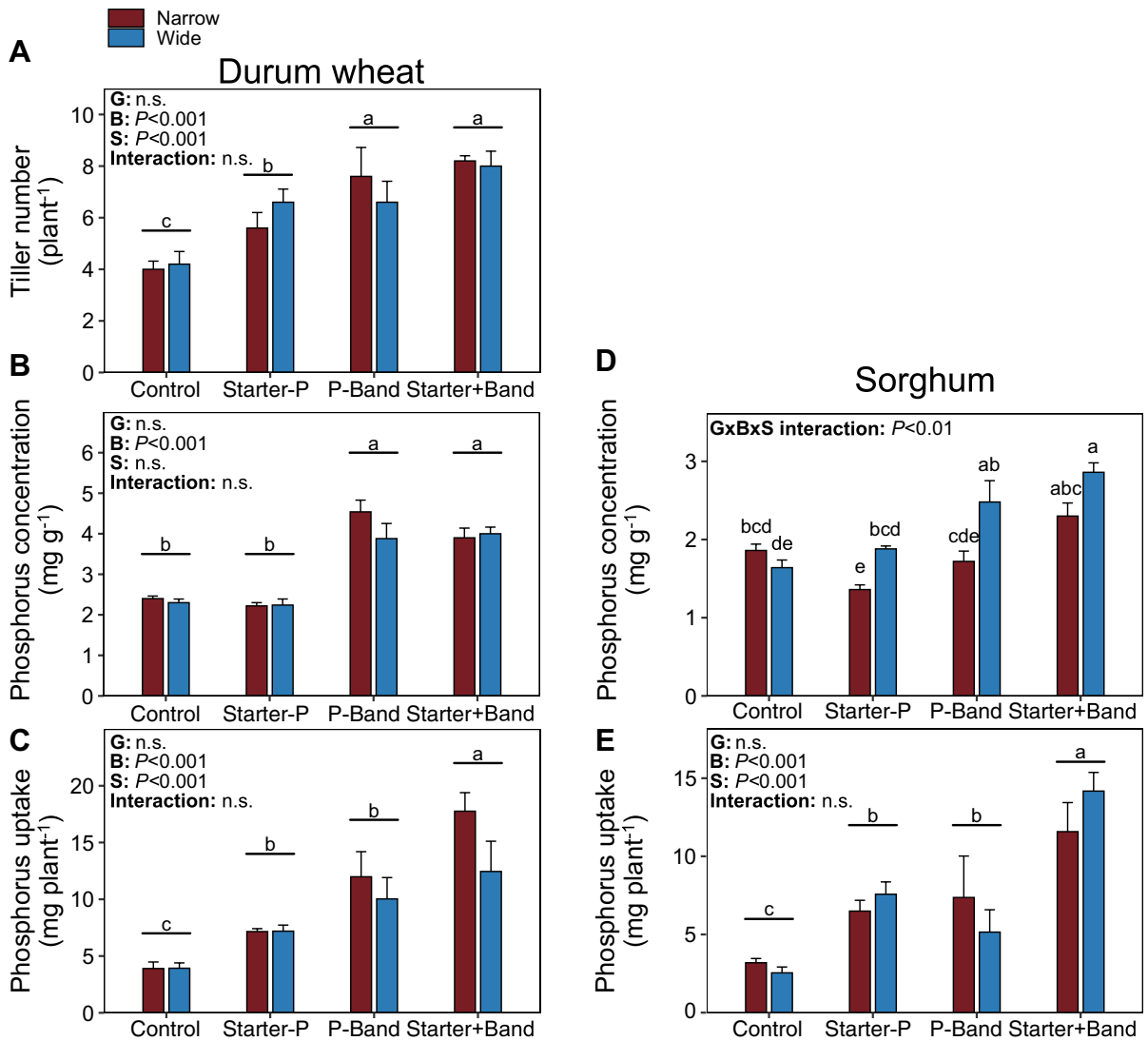


Fig. 4 Growth responses of two durum wheat genotypes (A-C) and two sorghum genotypes (D-E) with contrasting root angle to placement of phosphorus fertiliser. Error bars indicate

the standard error of the mean. Treatments sharing a common letter are not significantly different ($\alpha < 0.05$)

Root angle and projected root area of sorghum genotypes in response to phosphorus placement

Nodal root angles of the sorghum plants ranged from 38° to 62° (Table 2.) and the Narrow genotype consistently had a smaller root angle than the Wide genotype ($P < 0.05$). The addition of P fertiliser as a deep P band led to a narrower nodal root angle, when averaged across the genotypes and starter-P placements ($P < 0.05$).

The projected root area was generally low for both genotypes when P was not applied, and it tended to decrease with increasing depth (Fig. 6). On average, the Narrow genotype had a greater projected root area when summed across all soil layers ($P < 0.01$). Both genotypes had a similar root area in the 0 to 10 cm layer, but the Wide genotype showed a slightly more distinct decline of root area with depth, which resulted in significantly greater

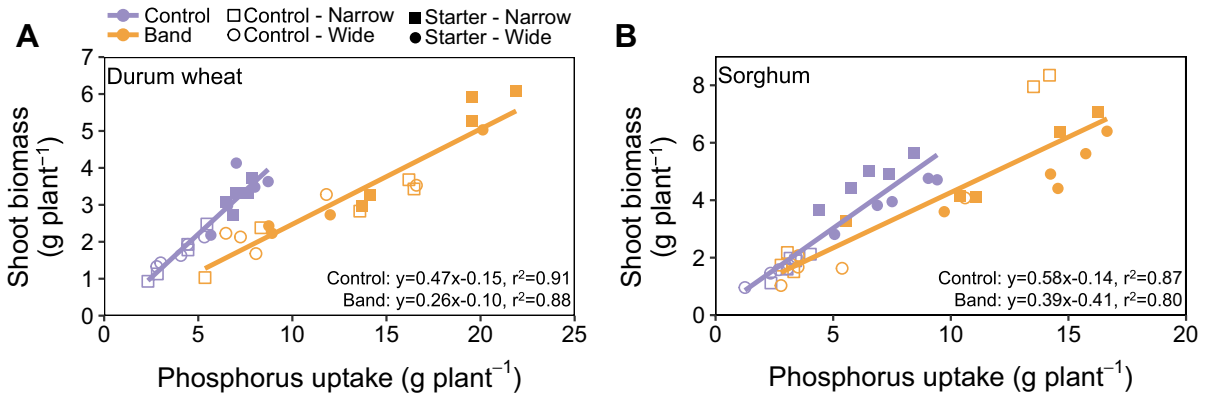


Fig. 5 Phosphorus uptake was linearly correlated with total shoot biomass. **A:** durum wheat, **B:** sorghum

Fig. 6 Projected root area (cm^2) of two durum wheat genotypes (**A**) and two sorghum genotypes (**B**) with contrasting root angle changed under the influence of phosphorus fertiliser placement. Note different scales on the x-axes between the two crops. Error bars indicate the standard error of the mean. Pairwise comparisons are provided in Table 3

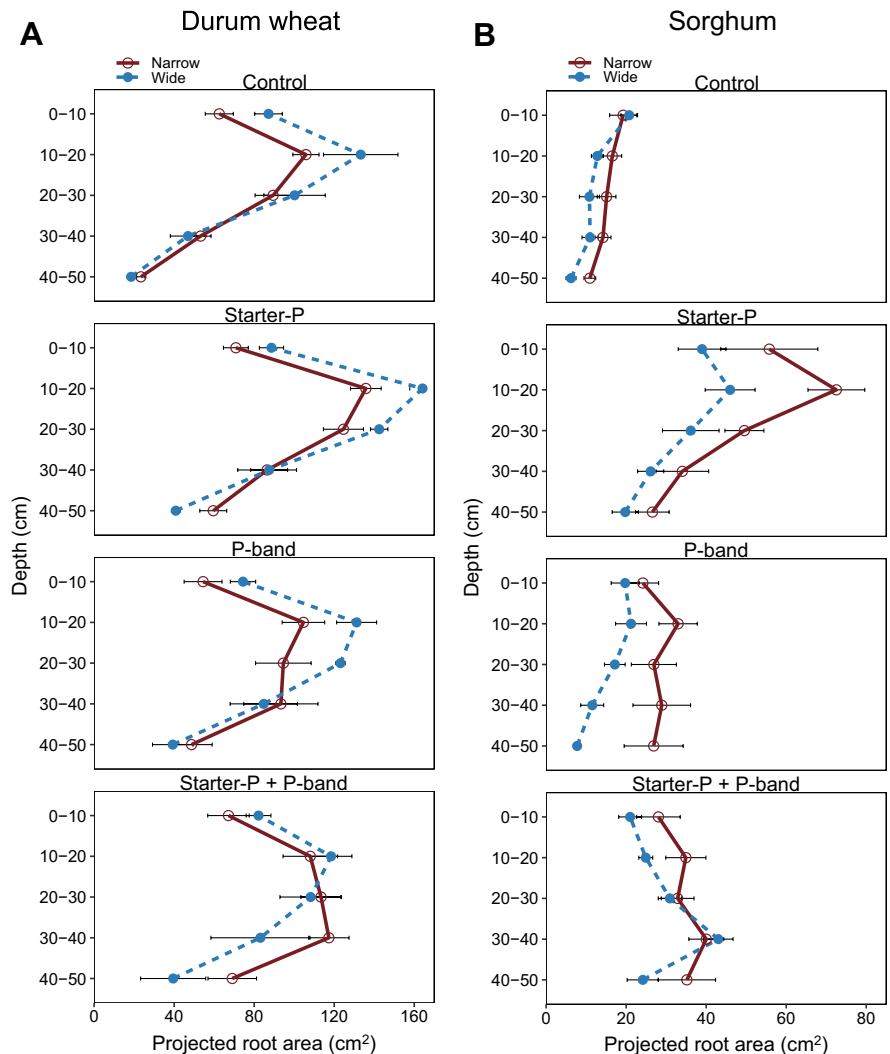


Table 3 Pairwise comparisons for projected root area within each 10 cm sampling layer. Stars indicate significance levels for treatment differences (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, n.s. = not significant)

Depth (cm)	Durum wheat			Sorghum	
	Genotype	Starter-P	P-band	Genotype \times Starter-P	P-Band \times Starter-P
0–10	W > N*	starter > no starter**	n.s.	n.s.	starter > control, Band, Starter + Band***
10–20	W > N**	starter > no starter**	Band > no band*	1. N starter > N control, W control*** 2. W starter > W control***	starter > control, Band, Starter + Band***
20–30	n.s.	starter > no starter**	n.s.	1. N starter > N control, W control*** 2. W starter > W control***	starter > Band, control***
30–40	n.s.	starter > no starter**	Band > no band**	N starter & W starter > N control & W control***	starter > no starter***
40–50	N > W*	starter > no starter**	n.s.	1. N starter > N control, W control*** 2. N control > W control*** 3. W starter > W control***	starter > control***

N Narrow, W Wide

projected root area in the deepest 40 to 50 cm layer for the Narrow genotype (Fig. 6 & Table 3, $P < 0.05$).

Starter-P markedly increased the projected root area in the top 0 to 20 cm soil layers, where its application resulted in the greatest root area amongst all the treatments (Fig. 6, $P < 0.01$). Both genotypes growing with Starter-P reached their maximum projected root area in the 10 to 20 cm layer, after which it progressively decreased with increasing depths, but a clear effect remained relative to the control.

Visually, both genotypes showed root proliferation in the vicinity of the deep P band, but local proliferation responses were variable among the treatment replicates. On average, deep P band placement did not increase the projected root area in the 0 to 10 cm layer but it had a positive effect in the soil layer immediately below (10 to 20 cm, Fig. 6 & Table 3, $P < 0.05$). Subsequently, root area tended to decline for the Wide genotype such that from 30 cm onward it reached a projected root area that was similar to that of the control. In contrast, the Narrow genotype showed a small peak in the 30 to 40 cm layer and maintained a greater projected root area in the 40 to 50 cm layer, but this response was highly variable.

The application of starter-P and a deep P-bands together resulted in a strong local response to the P-band, which was visually confirmed to be consistent among the replicates (Fig. 2). Subsequently, the

distribution of root area down the soil profile differed between the Starter+Band-P application and all other treatments, with both genotypes showing a pronounced peak in the 30–40 cm layer rather than in the topsoil layers (Fig. 6). Further, the combined Starter+Band-P application increased the projected root area in the 40 to 50 cm layer compared with the band alone ($P < 0.05$) and tended to lead to the overall largest projected root area at depth. In contrast, Starter-P in addition to a deep P band only had a marginal effect in the 0 to 20 cm layers, with the combined placement resulting in a smaller projected root area than Starter-P alone ($P < 0.001$).

Discussion

The overall objective of this study was to evaluate how P fertiliser placement and RSA interact to determine performance of ‘designer’ ideotypes. We adapted the rhizobox method previously used to investigate genotypic variation in seminal or nodal root characteristics among wheat and sorghum genotypes (Manschadi et al. 2008; Singh et al. 2010) by use of strategic placement of P fertiliser in a low-P soil. This approach allowed us to explore how contrasting genotypes respond to conditions that more closely resemble target environments and their fertiliser management. Our results illustrate how complex

interactions and feedbacks between RSA and heterogeneous distributions of P in soil jointly determine genotype functioning, and they support the view that complex soil environments are likely to modify the impact of proposed root ideotypes on overall crop performance (van der Bom et al. 2020).

Phosphorus access is critical for plant growth and the expression of root system architecture

Our first objective was to evaluate how P availability affects growth of the contrasting genotypes. In the absence of P fertiliser, all plants showed clear symptoms of P deficiency, including low biomass and overall low root intensities throughout the soil profile, with lower projected root areas in sorghum than wheat. Limited P also reduced tiller numbers in the durum experiment (Fig. 4A), which can irreversibly affect yield potential by reducing the number of grain-bearing panicles (Carstensen et al. 2018; Elliott et al. 1997). Further, under these low-P conditions, genotype-specific variations in root distribution were minor.

The P applications generally increased plant biomass and root intensities such that RSA patterns were more clearly expressed in accordance with their selection, i.e. root angle is presumed to shift the distribution of roots in the soil profile and deliver a more vertical (Narrow) or horizontal (Wide) RSA (Manschadi et al. 2008; Singh et al. 2012). Accordingly, the treatment combinations with the greatest projected root area in the deepest soil layer (40 to 50 cm) were all Narrow genotypes that received P. However, in both crops P also substantially increased the root system size of the Wide genotypes, such that projected root area at depth was considerably greater than that of the Narrow types without P fertiliser. The only exception to this was the deep P band placement in sorghum, in which the Wide genotype had only a limited improvement of P uptake and biomass. The important role of P in increasing root size and exploration has also been observed in crops such as winter wheat (Liu et al. 2022), rice (De Bauw et al. 2019), and common bean (Ho et al. 2005). Further, a common bean genotype with an overall larger root system performed best in a variety of soil environments and explored soil horizons in a manner comparable to that of 'specialist' root systems (Ho et al. 2005). These observations highlight the importance of P access 1) to improve

plant growth and root size regardless of RSA, and in so doing increase (shallow and deep) soil exploration, and 2) as a facilitator of genetic trait expression, i.e. to ensure that desired RSA patterns are reliably expressed. Within this, the current rhizobox setup had a relatively limited available depth and only a short experimental growth period; there is merit for further studies that address these effects in a deeper soil environments and across longer growth periods.

Starter phosphorus and deep phosphorus bands can deliver complementary benefits

Our second objective was to assess how different P fertiliser placements affect crop growth and P uptake. The starter-P application alone improved plant biomass more than the deep P band applied alone, even though its application rate was relatively small (6 kg P ha^{-1}). Phosphorus has a low mobility in soil, so placing it where plant roots can contact it early should allow crops to make a more vigorous early start (Grant et al. 2001). This is particularly important in conditions in which very low soil P concentrations rapidly limit early crop P uptake (Lauzon and Miller 1997; Richards et al. 1985), where it is desirable to ensure plant P access before seed reserves run out. However, starter-P did not affect tissue P concentrations for durum wheat, and for the Narrow sorghum genotype P concentrations even decreased (Fig. 4B and E).

Whole shoot tissue P concentrations can be considered marginal if they are equal to or smaller than 3 mg g^{-1} for wheat and $2.2\text{--}2.6 \text{ mg g}^{-1}$ for sorghum (Reuter and Robinson 1997); hence, the plants growing under Starter-P in our experiments would have been P limited. This is indicative of a nutrient dilution effect, in which starter-P maximized early shoot growth whilst only having a limited effect on total P uptake. This may be attributed to the limited soil volume that was enriched with fertiliser P, whilst new roots that grew away from the starter-P application could scavenge little additional P. Further, the capacity to extract P from the starter-P may have reached a limit if proliferating roots started to compete for P within the small enriched soil volume (see Fig. 2). Irrespective of the mechanism involved, our results show the major effect of starter-P was to advance early growth, but that it was not an effective solution

to meeting seasonal crop P demand in a soil with an overall poor P status.

The deep P band placement generally supported greater tissue P concentrations than Starter-P. This greater ability to support P uptake would be expected given the greater application rate (45 kg ha⁻¹). Further, the 4 cm concentrated band would have enriched a larger soil volume than the Starter-P application, thus providing more space for roots to proliferate (Fig. 2). On the other hand, early plant P uptake would have been limited due to the relatively large distance of the P band from the seed (Eghball and Sander 1989), which may explain why plants growing under the deep P band treatment tended to lag in terms of their biomass response (as well as in total P uptake for the sorghum genotypes). Without co-application of starter-P, young plants would have relied on seed P reserves and minimal amounts of scavenged P until their roots had grown through the upper soil layers and intercepted the deep P band.

A potential limitation to the study is that the P fertiliser was applied as MAP. This mimics farmers' practices in North-East Australia, but MAP also contains N. However, the basal fertilisation in the experimental setup was designed with the goal to isolate the response to P, and a previous comparison of MAP and monocalcium P (also referred to as triple superphosphate) in an otherwise similar rhizobox setup indicated that responses to P bands could be attributed to the fertiliser P content {van der Bom et al. 2023 #2072}.

Taking everything together, the combination of Starter-P and a deep P band resulted in the most consistent responses across the crops and P placements, including improved shoot and root biomass, tiller numbers, P concentrations, and P uptake. This was associated with more pronounced proliferation responses in and around the deep P band, which we interpret as Starter-P enhancing early root size, early subsoil exploration, and the probability of a young root system encountering a deep P band. An exception to this was projected root area of the Wide durum wheat genotype, presumably reflecting limited time to develop a large root mass, but the combined observations of tiller number, P uptake and biomass suggest similar improvements were still achieved. These observations further agree with field observations that deep P bands and starter-P can have additive effects, although responses can be variable among sites and

crops (Lester et al. 2019). In part, this would reflect the variation in seasonal rainfall that would result in differential drying of the topsoil layer and limiting crop access to starter-P.

Does root architecture influence spatio-temporal exploration for deep phosphorus bands?

Our third objective was to understand if differences in RSA affect plant capacity to access deep P bands. The longer it takes for roots to reach a fertiliser band, the less effective root proliferation in the band area will be (Eghball and Sander 1989). Therefore, any RSA that improves timely root-to-fertiliser contact should be advantageous. In this context, a deep, narrow root system may improve this and increase the likelihood of rapidly encountering a deep fertiliser band. However, a too narrow root system may limit the horizontal reach of the root system causing it to 'miss' a narrow fertiliser band (van der Bom et al. 2020). In the current experiment, we considered two separate factors: a) the distinct root systems of each of the two crops, and b) the contrasting narrow and wide root angles. For durum wheat, the observations support the hypothesis that root angle changes soil exploration (Lynch 2019) with the Wide genotype delivering greater projected root area in the 0–20 cm topsoil and the Narrow genotype delivering greater root area at depth (40–50 cm). For sorghum this contrast was less obvious, possibly owing to differences in genetic potential between the two genotypes, therefore, we focus our interpretation on the relative treatment effects.

For both crops, roots of Narrow genotypes grew more in the 30–40 cm layer when a deep P band was applied, compared with the patterns observed for the control treatment. This increase in projected root area corresponded to visual observations of local proliferation (Fig. 2) and improved P uptake, indicating that these root systems had responded to the deep P band by constructing new root mass after taking up additional P. However, the response of the Narrow sorghum genotype to the deep P-Band treatment was highly variable. Sorghum has a coarser root system than durum wheat (Himmelbauer et al. 2004; Singh et al. 2010), which would have led to an overall less comprehensive soil exploration – as demonstrated by its overall smaller projected root areas whilst its root biomass was typically greater than that of durum

wheat. Further, sorghum had not produced any tillers, which can have a strong effect on root growth and development (Hendriks et al. 2016; O'Brien 1979). Therefore, we interpret the variable response in sorghum as a reflection of the smaller odds of growing roots of this crop to rapidly encounter the placed fertiliser band.

The local root responses of the Wide genotypes tended to be less obvious, with the exception of the Wide sorghum genotype growing under the combined P-Band and Starter-P treatment. Presumably, the more horizontal root orientation of the Wide genotype reduced the capacity of its young root system to reach down into the subsoil layer and encounter the deep P band. The Starter-P application allowed the sorghum genotype to overcome this limitation, by virtue of boosting the size of its root system. However, the visual observations for durum wheat differed from the root area measure in this respect, with the Wide genotype showing signs of early root proliferation at the location of the deep P band, in conjunction with greater P concentrations, P uptake, biomass and tiller number (as well as greater P concentrations and P uptake in sorghum). These observations suggest that the Wide genotypes had still been able to respond to the deep P band by improving their P status, despite an absence of a clear proliferation response.

The improved P uptake in absence of substantial proliferation suggests that roots of the Wide genotypes may have taken longer to encounter the deep P band, but that the genotypes were able to rapidly respond to the newly discovered P source. This fits with the understanding that root tips play a particularly important role for total P uptake (Smith 2002). It has often been observed that physiological responses (e.g. improved P uptake) can occur before morphological ones (e.g. the initiation of new roots) (Drew and Saker 1978; van Vuuren et al. 1996) and it has been suggested that root physiological changes are likely important in the short term *versus* morphological responses being required for the longer-term exploitation of nutrient-rich patches (Hodge 2004). Altogether, these data suggest that RSA may deliver benefits by altering early soil exploration and in that manner the probability of encountering scarce resources located in specific soil layers *in time*. However, considering the increases in P uptake by the Wide genotype may be a precursor to root proliferation, this spatio-temporal effect of RSA may be

limited to a relatively short timeframe; it remains necessary to validate these effects as the crop develops over a growing season, and how they relate to crop resource uptake and crop yields.

Plastic responses influence the broader root system architecture

Our fourth objective was to assess if plastic root responses affect the broader RSA of contrasting ideotypes. The most marked plastic responses were those of localised root proliferation at the sites of Starter-P and deep P band placement (Fig. 2). We had questioned whether these responses would limit the ability of a genotype to express the intended RSA phenotype. In an evolutionary context, proliferation may allow an individual plant to better tolerate soil environments with a limited nutrient supply, but the same response may limit crop productivity if the resulting phenotype is not well adapted to the agronomic context (Correa et al. 2019), such as one in which terminal drought is likely. However, in the current P-limited soil system, the proliferation responses allowed plants to improve their growth rates and nutritional status, such that root size and the projected root area throughout the soil profile were greater, and expression of RSA was improved. This supports the hypothesis that adaptive root systems may be beneficial in complex environments with multiple constraints, in which the root system must be able to cope with temporal and spatial variability (Correa et al. 2019; van der Bom et al. 2020).

For both crops, the projected root area in the upper soil layer was greatest when starter-P was applied, and in the case of sorghum, this was significantly greater than for the joint application of Starter-P and a deep P band. It has previously been observed that allocation of dry matter into root growth corresponded with the level of nutrients applied i.e. that roots preferentially grew in a zone with greater nutrients at the expense of root growth elsewhere (Gersani and Sachs 1992) - although this response is not always observed (Robinson 1994). The responses in the current experiment seem to be in agreement, with plants able to respond to both P hotspots simultaneously but reducing root proliferation in and around the less concentrated Starter-P patch. Another possibility is that root turnover increased in the (original) Starter-P patch when the root system located the deep

P band with sufficient P to divert resources away from the Starter-P (Hodge 2004), but given the relatively short experimental timeframe this seems less likely.

A second plastic response was a tendency for root angle to become wider under the control treatment, albeit variable (or *vice-versa*, for root angle to become narrower when P was supplied). Similar observations have been made before in common bean, in which root angle and basal root growth were shallower when P was limited (Bonser et al. 1996; Liao et al. 2001). In many ecosystems, soil P concentrations are greater in topsoil layers, therefore this plastic change of root angle is thought to be an evolutionary adaptation to increase the plant's ability to grow roots in these shallow soil horizons (Lynch and Brown 2001). However, all the observed angles in our experiment were substantially greater (wider) than those reported in the original phenotype screenings (Alahmad et al. 2019; Mace et al. 2012). Considering the overall low P status of the soil, this may reflect plastic responses to sub-optimal P conditions in all treatments, which would cast some doubt about the ability to deploy ideotypes with very narrow root angles in low P fertility environments. Other possible factors include the experimental soil (*vs* potting mix and a fine sandy soil in the original screenings) and the time of measurement being substantially later in the current experiment. The latter was also proposed by van der Bom et al. (2023), who observed that the same durum genotypes had contrasting root angles as 5 d seedlings but not in a later growth stage. This may be a reflection of how plant development affects root growth, for instance, the manner in which later axes arise from the embryo (or tiller) may affect root angle (O'Brien 1979). Indeed, root phenotypes of young plants in controlled environments are often inconsistent with those at a later stage (Rich et al. 2020; Watt et al. 2013).

A third plastic response was observed in sorghum, in which biomass allocation to the roots was greater for the Narrow genotype as well as when Starter-P was applied. Firstly, the sorghum genotypes in this experiment were not near-isogenic lines, so the difference in partitioning may, in part, be attributed to a presence of adaptive genes. Secondly, nutrient stress generally causes plant resources to be refocused towards the root system to address the shortfall in nutrient uptake, and the greater biomass allocation to roots under Starter-P is consistent with the low tissue P concentration under

this treatment. The increased root biomass proportion prioritizes nutrient acquisition so plant growth may be optimized (Bloom et al. 1985; Poorter and Nagel 2000). Furthermore, no clear differences were observed for durum wheat, but the biomass allocation to the roots was relatively high in all treatments (34 to 39%). For comparison, Elliott et al. (1997) observed values between 21 and 29% for wheat grown for 35 d under high-P applications. Hence, the relatively high biomass allocation towards the roots may reflect various degrees of P limitation during the duration of the experiment, in agreement with the overall low background P status and generally wide root angles.

Conclusions and perspectives

Previous discussions about root architectural trade-offs have mostly considered deep and shallow soil foraging i.e. the capture of water and mobile nutrients in deep soil domains *vs* capture of immobile resources in the topsoil (Lynch 2019; Schneider et al. 2017). Our study highlights the importance of considering how crop system nutrient management may alter the environments in which root ideotypes are expected to function.

We conclude that P access improves plant growth and root size regardless of RSA, and in so doing increases (deep) soil exploration. The data suggest that P nutrition can function as a facilitator of genetic traits i.e. to ensure that desired RSA patterns are reliably expressed. Within this, plastic root proliferation responses helped deliver benefits to crop growth and the expression of RSA by improving P uptake. The responses of RSA to P access are relevant for the deployment of ideotypes with root traits selected to enhance drought resilience e.g. (Lynch 2013; Wasson et al. 2012), suggesting that although specialised ideotypes may deliver benefits in systems in which water is the fundamental limitation, severe P deprivation (or that of other nutrients) would likely limit their ability to function. Under such conditions, soil nutrient management would be a priority. This requires recognition of how management practices affect soil nutrient distribution and physical and biological properties that can influence the availability of P to crops and individual species with different P requirements.

Placement of P fertiliser as Starter-P and deep P bands are among the management practices that can

be adopted to improve crop P access. Within this context, root angle can change early exploration patterns; a narrow root angle may allow plants to ‘find’ a deep P band sooner, although this effect was variable. Starter-P seemed to deliver more consistent improvements irrespective of RSA, by virtue of greater overall root size.

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Data availability The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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