Root phenotypic plasticity: agronomic, breeding and modelling implications

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Abstract

CONTEXT. Phenotypic plasticity is one of four strategies for coping with environmental heterogeneity, and can be valuable for crop adaptation.

OBJECTIVE. With a perspective of phenotypic plasticity, we focus on root traits associated to water uptake and yield formation in field-grown sorghum aiming to study: (1) How do genetic (G), environmental (E) and management (M) factors and their interactions, affect functional root traits? (2) How does plasticity in root traits affect crop yield and yield stability?; and (3) How can plasticity in root traits be introduced in functional crop models?

METHODS. A new high-throughput functional root phenotyping approach, that uses time-lapsed electromagnetic induction (EMI) surveys, was used in field G´E´M trials to quantify maximum rooting depth – RD, and a root activity index– RA. Phenotypic plasticity was determined using a reaction norm method.

RESULTS. The root phenotyping approach captured G´E´M effects on RA and RD. There was a hierarchy of plasticities for above and below ground traits, i.e., grain number traits > root traits > grain weight traits. The plasticity of root traits was associated to the stability in grain yield traits. Hybrids with high plasticity in root traits tended to stabilise grain numbers and grain weights. Useful diversity in the mean value and plasticity of root traits amongst commercial sorghum hybrids was found here, that could be used to match root phenotypes to target production environments.

CONCLUSIONS. The developed high-throughput root phenotyping approach can be a useful tool in breeding and agronomy to increase crop adaptation to drought stress.

Introduction

Plants have developed four main strategies to cope with environmental heterogeneity, (1) specialization, entailing the production of a phenotype tailored for a specific environment; (2) generalisation, where a phenotypic variant has broad adaptability across various environments; (3) bet-hedging, characterized by the organism's stochastic production of multiple phenotypes, either among units within a modular plant, or probabilistically as a single phenotype; and (4) phenotypic plasticity, whereby alternative phenotypes are produced in response to environmental cues (Dewitt and Langerhans 2004). Under the assumption of "perfect plasticity" and within a simplified spectrum of environmental scenarios, modelling of these four strategies, after four generations, yielded a fitness ratio of 1:1.6:1.5:25 (Dewitt and Langerhans 2004). This suggest that in the absence of constraints, plasticity is a superior strategy in variable environments. Though as plasticity is not perfect or infinite, costs and limits to plasticity will be present (Schneider 2022). The costs and limits of plasticity are usually observed in terms of trade-offs in fitness across environments (Clarke et al., 2019), though such information remains valuable to identify optimum crop designs (G×M) for specific environments (Hammer et al. 2009).

In ecology, the concept of phenotypic plasticity has been used in evolutionary and developmental studies for well over a century (Henslow 1894; Bradshaw 1965). More recently it was also used to complement conventional analyses of interactions between genotype (G), environment (E), and management (M) for grain yield and grain yield components (Sadras et al. 2009; Ruiz et al. 2019), tillering (Sadras and Rebetzke 2013), biomass allocation (Galizia et al. 2020), phenological development (Grogan et al. 2016), transpiration rate (Marguerit et al. 2012), stomatal conductance (Sadras et al. 2012), and grain protein (Giordano et al. 2024).

The plasticity of root traits, the focus of this study, has been previously documented in response to intraspecific competition (Wang et al. 2021), drought (Tran et al. 2015), elevated CO2 and high temperature (Benlloch-Gonzalez et al. 2014), and nutrient availability (Hodge 2004; Sandhu et al. 2016). Though, whether root plasticity should be a target in plant breeding programs might not have a straight answer (Schneider and Lynch 2020). Root trait phenotyping exercises have primarily focused on inferring on root function from costly and laborious 2D and 3D visualisations of the root system, usually from growing single plants under controlled conditions or on unrepresentative soils (Singh et al. 2010; Richard et al. 2015; Menamo et al. 2023). This is extrapolating root function from root form. Here we propose that there might larger opportunities from directly quantifying the influence of G×E×M effects on the mean value and plasticity of functional root traits in the field, under actual canopy structures, and in response to known environmental cues.

Recent progress in the development of functional high throughput phenotyping of root traits (Zhao et al., 2022), offer opportunity to overcome the present root phenotyping bottleneck for the quantification of valuable root traits in the field. These new tools appear to be sufficiently accurate, fast, and cost effective to enable the method to be scaled to levels relevant to breeding and agronomic applications. The approach combines the use of time-lapsed electromagnetic induction (EMI) surveys, drone imagery, crop-ecophysiology principles, and machine learning techniques, to build a 3D representations of root growth and function in the soil profile. Similar approaches were previously used to measure layered crop water in field trials across numerous genotypes and fertiliser treatments in wheat (Shanahan et al. 2015; Blanchy et al. 2020), and chickpea (Huang et al. 2018), and sorghum (Zhao et al. 2022). In Zhao et al. (2023) an EMI-derived root activity factor was shown to be closely related to the distribution of root length density of sorghum in the soil profile down to 1.5m irrespective of contrasting times of sowing, seasons, and irrigation levels. Advantages of the approach are that it is non-destructive, and overcomes typical artifacts of alternative methods, e.g., the preferential root pathways generated by roots growing against a glass-wall in a rhizo-box, or hard surfaces in pots or soil columns.

Since the pioneering work by de Wit (1959), process-based crop simulation models have been used as research tools to integrate knowledge, in data analysis and interpretation, for extrapolations across sites and seasons, and cropping system design (Yin et al. 2021). Particularly, functional modelling approaches that use simple, though robust assumptions from biology, ecology, soil, and environmental sciences, have seen applications in G×E×M studies (Hammer et al. 2014; Rodriguez et al. 2018), and genotype-to-phenotype studies (Cooper et al. 2023). As our understanding of crop physiology increases, modelling

assumptions need revisiting, while seeking to balance biological reality, simplicity, and elegance (Yin et al. 2021). An area of crop physiology where there is ample room for improvement is the simulation of root growth and function under stress. Common assumptions in most functional models include the uniform distribution of roots in homogenous soil layers, the lack of responses of roots to changes in the environment, e.g., water supply or inter-/intraspecific competition, and lack of intraspecific variability in root traits. For example, in APSIM, the simulation of root growth and water uptake includes crop-specific constants for root elongation rate (mm day^{-1}), and a fixed maximum rooting depth that is achieved at flowering. Other assumptions include a static relationship to describe the fraction of extractable water that can be taken up per day from a particular soil layer (Dardanelli et al. 2004). These assumptions overlook, genetic differences in the efficiency of the rooting system to capture water resources; the influence of intraspecific competition, environmental conditions, and hybrid in root activity and maximum rooting depth, and differences between cultivars in root architecture plasticity and effects on yield stability.

In this study we applied the high-throughput functional root phenotyping approach to characterise the mean value and plasticity of functional root traits, i.e., maximum root depth (RD), and an index of root activity in the soil profile (RA), on six sorghum commercial hybrids grown in contrasting environments and managements. We ask: How do G×E×M interactions affect functional root traits in the field? How does the plasticity of root traits affect crop yield and yield stability? and How can plasticity in root traits be introduced in functional simulation models?

Material and methods

Study site and experimental design

Two field trials were conducted in Queensland, Australia at a commercial farm in Nangwee, (27°3'2.73" S, 51°18'34.36" E) in 2020/21, and at Gatton Research Station (27°32'44.19" S, 52°19'50.72" E) in 2021/22. Climate in the region is sub-humid and sub-tropical with long, hot summers and short, mild-to-cold winters. At both sites, the trials covered an area of ~ 3.2 ha (82 m × 384 m), and the soils were uniform black, self-mulching cracking clay soils, characterised as a Vertosol soil (Isbell 2021)

The trials consisted of the factorial combination of three times of sowing (TOS, late winter, spring, and summer), two water regimes, i.e. rainfed and supplementary irrigation, four plant population densities (3, 6, 9 and 12 plants m^{-2}), and six commercial hybrids that are coded as A (A66), B (Agitator), C (Cracka), D (G33), E (HGS114) and F (MR Buster). Each season, there were 432, 4 m wide (4 rows) × 10 m long plots. In 2020/2021, the sowing dates were 11 September, 6 October, and 5 November, and in 2021/2022, 25 August, 27 October, and 17 January. The combination of TOS, season, and water regime was aimed at creating a wide range of environmental conditions for root growth. The irrigated treatment was imposed by laying drip irrigation tape along each row after sowing. Pests, diseases, and weeds were controlled, and an automatic weather station was installed before sowing at each site to monitor daily air temperature, relative humidity, solar radiation, soil temperature, and rainfall. The normalised photo-

thermal quotient (NPTq) was calculated for a window around flowering from 20 days before to 14 days after anthesis as in Rodriguez and Sadras (2007).

Dry matter production, yield, and yield components

Yield and shoot biomass were sampled at physiological maturity from eight plants in the central two rows from each plot. Each sample was oven dried to a constant weight at 80°C. Panicles were then separated and threshed to determine yield components including grain yield (t ha^{-1}), grain number (grains m^{-2}) and grain weight (g per 1000 grains). The harvest index was estimated as the ratio of grain yield to shoot biomass. Yield components were partitioned into main stems and tillers. Grain protein content was determined via combustion using a LECO FP-528 nitrogen determinator (LECO Corporation, St. Joseph, MI) using a nitrogen to protein conversion factor of 6.25.

Root phenotyping

The high-throughput root phenotyping approach in Zhao et al. (2022) for the characterisation of crop water use, and root activity in the field was used to derive the maximum rooting depth (RD) and a root activity index (RA) at flowering (Fig. 1). In this approach, EMI is used to determine a root activity factor (R) at each soil layer in a 10-day dry window around flowering in which there was no rainfall or irrigation. The approach assumes that R_i represents the presence of active roots in an i^{th} soil layer, which can be calculated as a ratio of crop water use from the i^{th} soil layer (mm) to plant-available water (PAW, mm) of that i^{th} soil layer, and a term representing crop demand, i.e. canopy size (unitless), that is derived from satellite or drone imagery (Eq. 1):

$$R_i = \frac{Cropwateruse_i}{Plantwateravailibility_i * Canopysize}$$

1

where *Crop water use*$_i$ is the change in water content (mm) in i^{th} soil layer derived from the two consecutive EMI surveys and a detailed description of the method used to convert EMI readings to crop water use at each soil depth can be found in Zhao et al. (2022); *Plant-available water*$_i$ is the PAW in i^{th} soil layer at the first EMI survey, which was calculated as the difference between crop lower limit and soil water content; and the Normalised Difference Vegetation Index (NDVI) which was derived from satellite (PlanetScope) images (Planet Labs Inc 2020), was used to represent crop water demand (i.e. canopy size).

RD was calculated as the deepest soil depth at which no crop water use was detected over the two consecutive EMI surveys (Fig. 1). The root activity index (RA) is a proxy for the proportion of root activity in the top 0.5 m soil profile ($R_{0-0.5m}$) relative to the total root activity in the whole soil profile down to RD

(R_{0-RD}). Larger values of RA indicate larger water use from the topsoil layers, and smaller values of RA indicate a larger proportion of water use from the deeper soil layers:

$$RA = \frac{R_{0-0.5m}}{R_{0-RD}}$$

2

Statistical analysis

Linear mixed models (LMM) were used to test the effect of season, time of sowing, water regime, plant population density, hybrid, and their interactions, on shoot biomass, grain yield, grain number and grain weight, RD, and RA. We used the ASReml-R package (Butler et al. 2023) in R (R Core Team 2022). Terms describing the experimental design were included as random effects. Predictions obtained from the models were empirical Best Linear Unbiased Estimators (eBLUEs). Conditional inference trees were used to untangle interactions and explore the effects of the factorial combinations of season, time of sowing, irrigation, plant population density and hybrid on RA and RD. The conditional inference trees were performed using the R package 'partykit'.

Phenotypic plasticity

Phenotypic plasticity for each trait was calculated as the slope of the reaction norm between the trait for each hybrid and the mean of the trait across hybrids for each environment. A slope ≅ 1 indicates average plasticity, > 1 indicates above-average plasticity, and < 1 indicates below-average plasticity (Sadras et al. 2009). The combination of two seasons, three sowing times and two water regimes returned a total of 12 environments. Associations between traits and trait plasticity were analysed using biplots, correlation analyses, and linear regression, using the 'stats', 'corrplot', and 'ggplot2' packages, respectively.

Modelling with APSIM

APSIM sorghum was modified to reproduce the observed increase in maximum rooting depth in response to stress, i.e. water deficit and plant population density (Fig. 2a). Two responses were programmed, an increase in root exploration in depth in response to increasing plant population density, e.g., intraspecific competition, and an increase in root exploration in depth in response to both, water availability and plant population density. These effects were implemented in APSIM by modifying rooting depth at flag-leaf stage which potentially increases plant-available water (mm, Fig. 2b) when water is present in depth. The density response was simulated by increasing rooting depth with higher plant population densities. To model the effect of increased rooting depth, the volumetric equivalent of that depth increase was achieved by reducing the crop lower limit (CLL) towards wilting point (LL15), thereby increasing plant-available water capacity in depth (PAWC).

APSIM simulations were run for five sites, in an East – West transect across the main sorghum growing region of Australia, i.e. Gatton (27° 32' 44.17" S, 152° 20' 17.55" E), Dalby (27° 34' 2.73" S, 151° 18' 34.36" E), Warra (26° 55' 56.90" S, 150° 55' 27.64" E), Roma (26° 34' 18.71" S, 148° 47' 23.24" E) and Surat (27° 9' 31.38" S, 149° 4' 12.94" E). Each simulation started with an exhausted water profile after the harvest of a winter crop (typically wheat) in the previous year (1st Nov), and modelling the fallow period leading up to a sorghum crop sown on the 15th Sep the following year. The crop was sown with 150 kg N/ha. Seventy simulations of this fallow - crop sequence (1950–2020) were run using SILO climate data (https://www.longpaddock.qld.gov.au/silo/), and representative soil data in APSoil (https://www.apsim.info/apsim-model/apsoil/). The combination of plant population density and soil water availability yielded 4200 individual simulations of which 163 failed to reach maturity.

Results

Yield and root traits

The first season of trials was drier and closer to the long-term average, compared to the exceptionally wet second season (Fig. 3). The contrasting seasons, the different times of sowing and the use of irrigation created highly contrasting growing conditions and grain yields, which varied between a few hundred kilograms to more than 10 t ha^{-1} (Fig. 4a). A significant five-way interaction was observed for crop yield i.e., hybrid × plant population density × season × time of sowing × water regime ($p < 0.05$, Table S1). In both seasons, the early or late winter and spring-sown crops had similar yields and grain numbers (Fig. 4b), and harvest index (Fig. S1), especially in the irrigated treatments. As expected, yield was closely related to grain numbers per m^{-2}, and unrelated to grain weight (Fig. S1).

Figure 4d and 5a show smaller values of RA at flowering (i.e., deeper soil water extraction) during the first, drier season, particularly in the rainfed treatments, and with higher plant population densities ($p < 0.05$). During the second, wetter season, larger RA values indicate shallower water use, particularly in the summer and spring sowings and for the supplementary irrigated crops. Figure 5b shows that differences in RD at flowering were mainly driven by the time of sowing, with summer-sown crops generally having a deeper RD at flowering (1.27–1.45 m) than crops sown in late winter or spring (1.18–1.36 m). RD at flowering tended to be deeper (1.45 m) during the first drier season, and with high plant population densities (i.e. 9, 12 plants m^{-2}). For crops sown in late winter and spring, water regime was the main driver of differences in RD (Fig. 4e and 5b), with the rainfed plots having larger values of RD (1.36 m) than the irrigated plots (1.18 m in 2020/21 and 1.32 m in 2021/22).

The first two dimensions of a biplot including shoot biomass, grain yield, yield components, root traits, and pre-flowering plant-available water, explained 58% of the total variance in the dataset (Table 1). RA was positively associated to grain number and pre-flowering plant-available water, and negatively associated to grain protein and grain weight.

Trait plasticity

Median values of phenotypic plasticity were > 1 for traits related to grain number, RD, grain yield, and RA, and < 1 for traits related to grain weight (Fig. 6a).

The variation in yield plasticity between hybrids was larger in the first, drier season (0.42–1.53) than in the second, wetter season (0.65–1.19) (Fig. 7a, b). Four of the six hybrids (B, C, D and E) performed consistently across seasons. In general, hybrid B had lower yield plasticity and C, D and E were consistently more plastic in both seasons. Yield plasticity was associated to the plasticity of grain number (Fig. 6b).

Similarly, variation in grain number plasticity between hybrids was larger in the first, drier season (0.23–1.43) than in the second, wetter season (0.59–1.25) (Fig. 7c and d). Hybrid rankings for plasticity of grain number were consistent with the ranking for yield plasticity. Grain weight had lower plasticity in both seasons for hybrid A and B and higher plasticity for hybrids E and F (> 1.3) (Fig. 7e and f).

In contrast, variation of root trait plasticity was smaller in the first than in the second season (Fig. 7g-j). For example, RA plasticity ranged from 0.87 for hybrid C to 1.14 for hybrid B in the first season, and from 0.63 for hybrid D to 1.23 for hybrid F in the second season. Hybrids A and B showed consistently large plasticity values for RA and RD across both seasons, while hybrids E and D showed lower plasticity values. A larger root plasticity was associated with a deeper rooting depth (RD) and a larger root activity in the deeper soil layers in the drier environments, and a shallower rooting depth and a larger superficial root activity in the shallower soil layers in the wetter environments (Table 1, Figs. 5 and 7). There was a weak negative association between the plasticity of grain number and plasticity of RA, and a strong negative correlation between the plasticity of grain weight and the plasticity of RD (Fig. 8f).

Sensitivity analysis with APSIM

Dynamically simulating the effects of both increasing plant population density and water deficit on root growth after flag leaf emergence, produced similar or higher yield stability for the different plant populations, i.e. smaller slope of the relationship between simulated grain yield and environmental yield (Fig. 9a), particularly due to an increased stability in grain weights (Fig. 9c) rather than grain numbers (Fig. 9b), particularly for the lowest plant population densities (3 and 6 pl m^{-2}).

Discussion

We applied the high-throughput root phenotyping approach developed by Zhao et al. (2022) to characterise two functional root traits, their phenotypic plasticity, and their association with yield traits on six commercial sorghum hybrids growing in the field. We showed that (i) G×E×M interactions affected the studied traits as well as their plasticity, and (ii) that the plasticity of grain number and grain weight were inversely related to the plasticity of root activity, and rooting depth, respectively, suggesting that the plasticity of root traits can be associated to the stability of yield components.

High-throughput functional root phenotyping

So far, the lack of high-throughput functional root phenotyping tools in the field has limited the capacity of breeders and agronomists to select for valuable root traits or inform optimum combinations of genotypes and agronomic practices to fit specific environments (Lynch 2013; Lobet et al. 2019). Root phenotyping approaches on seminal or nodal roots of young individual plants grown under controlled conditions have so far been difficult to relate to the same traits during reproductive stages on crops growing in the field (Hassouni et al. 2018; Rich et al. 2020). Reasons for this may include the use of artificial substrates, e.g., lack of soil structure in pots and root chambers, the lack of intraspecific competition effects when single plants are grown in pots or root chambers, the presence of complex stress dynamics during the season and their effect in root growth and distributions in the soil profile later in the season at flowering or maturity. Other field approaches, e.g., “shovelomics” or soil coring, will only sample a small proportion of the rooting system, have large errors, and can be laborious and time consuming (Atkinson et al. 2019). Our approach overcomes these limitations and is focused on quantifying root function, rather than root form (Zhao et al., 2022). Here we have shown that multidisciplinary approaches that combines geophysical techniques to measure soil moisture profiles rapidly and accurately, in combination with drone or satellite imagery, and the use of crop eco-physiology principles, can help to characterise the functionaing of rooting systems across hundreds of plots in the field as required by breeding programs or precision agriculture applications.

Phenotypic plasticity of yield and root traits

Here, hybrid-dependent variations in the plasticity of yield, yield components and root traits were observed in response to the wide range of growing conditions the crops were exposed. A hierarchy of plasticities was established with the largest plasticity values observed for grain number traits, and the smallest for grain weight traits, and intermediate plasticity values for root traits (Fig. 6a). Even though the hierarchy of plasticities for grain yield components has been reported earlier (Bradshaw, 1965), this is the first time that the plasticity of below and above ground traits, and their relationships is presented. Hierarchies and trade-offs between grain number and grain weights, were previously explained in terms of sink source relationships (Gambín and Borrás 2007), and evolutionary and crop improvement aspects (Sadras 2007). Here, we found that plasticity of grain numbers was negatively associated to the plasticity of root activity, and that the plasticity of grain weight was negatively associated with the plasticity of rooting depth (Fig. 8). The weaker association between grain number and RA plasticity could be explained by the fact that in our trial RA was determined around flowering when final grain numbers were already defined. However, the stronger relationship between the plasticity in grain weight and that of RD might be related to the fact that grain weights are defined later in the season during grain filling. In general, hybrids showing plastic root phenotypes were able to explore deeper soil layers and access water from deeper soil layers at anthesis, which resulted in more stable grain weight (Fig. 8). This indicates that breeding for phenotypic plasticity in traits other than yield could potentially increase crop adaptation in highly variable environment. Plasticities in root architecture, root anatomy and root length density, lateral root length and/or branching, rooting depth and root growth angle, have been reported and related to more stable yield or plant performance across varying environments in various species (Ehdaie et al. 2012; Sandhu et al. 2016).

Here, the hybrids that showed the most stable yields (and plastic root traits), were outperformed by plastic yield hybrids in high yielding environments. So, plastic root traits showed a cost, expressed as a trade-off in fitness between low and high yielding environments. For example, the higher average yield of hybrids A and B in low-yielding environments was linked to lower yields in the more productive environments (Fig. 7). For the main sorghum-growing environments in eastern Australia, crops are typically grown on relatively deep soils, rely primarily on stored soil moisture complemented by large and infrequent summer rainfall events, and usually under terminal drought stress (Clarke et al. 2019). This means that phenotypes that invest resources in deeper roots are likely to profit from accessing deeper soil water at critical stages around flowering and grain filling. We do not know whether the lower yield of hybrid A and B in the higher-yielding environment might be related to the cost of deep roots (Wegner 2022). Root respiration can consume up to 30% of the total plant sugars allocated to the roots (Lambers et al. 2003), and faster respiration rates are associated with traits such as high specific root length, high root nitrogen concentration and fine roots, compared to roots that have high tissue density (Han and Zhu 2021). Indeed, selection for yield and agronomic adaptation of wheat in Australia, Europe and China might have favoured the production of smaller root systems (Aziz et al. 2017; Feng et al. 2023).

After about 130 years since first published by Henslow (1894), phenotypic plasticity in field crops and rooting systems shows opportunity to increase adaptation to drought stress. Most sorghum-breeding programs breed for yield and yield stability, so whether breeding for an indirect root trait such as root plasticity has value, remains open to research (Schneider 2022). For a trait to be incorporated into breeding programs to improve drought adaptation, it must satisfy a number of criteria: (i) it must be genetically correlated with yield in the target environments, where the patterns of stress need to be quantified in terms of timing, duration, and intensity, (ii) it should have higher heritability than yield, (iii) it should not be associated with low yield in favourable conditions, though this might depend on the company commercial strategy, (iv) it must show genetic variability, (v) it must be genetically stable, persistent across generations, and relevant in different genetic backgrounds, and (vi) it must lend itself to rapid, cost-effective, and reliable quantification (Sadras and Richards 2014). Our method meets criterion vi. In our small sample of hybrids, diversity is apparent (criterion iv). Root traits did not relate to yield but showed physiological and agronomically meaningful associations with yield components (criterion i). Probing for diversity and quantifying heritability of root traits requires a focus on material representing wider variation.

Simulating growth and function in variable environments

Modelling applications in crop improvement and agronomy need to balance biological reality and parsimony (Hammer et al. 2019). As our understanding of biological processes improves, model assumptions need revisiting. Highly mechanistic 2D and even 3D modelling approaches of root growth and function are available (Schnepf et al. 2018; Sidhu et al. 2023). However, their application is usually limited to studies of root resource acquisition, due to “computation hungry” for GxExM studies (Rodriguez et al. 2018), or genotype-to-phenotype modelling (Cooper et al. 2023). Typical assumptions in functional crop models include that plant roots are uniformly distributed in homogeneous soil layers

(Wang and Smith 2002); that the advancing front (in depth) of the root system is constant e.g., un-affected by plant competition or crop stress; that maximum rooting depth is a crop or soil attribute and reached before flowering (Holzworth et al. 2014); and that the capacity of the rooting system to extract water (KL) is a crop attribute and declines with soil depth (Dardanelli et al. 2004). Our experimental and modelling results indicate that some of these assumptions need revisiting. We showed that the intensity of water stress, as the result of the growing environment or intra-specific plant competition, can affect both the maximum rooting depth and the depth at which crops will use water, indicating changes in resource allocation between above- and below-ground growth (Schneider 2022; Wegner 2022). By modifying the soil volume explorable by the rooting system in response to water stress, i.e. dry conditions and or increased plant population density around flowering, introduced different degrees of yield and yield components plasticity, showing a possible pathway to improve the biological realism in functional simulation models like APSIM.

Conclusions

We found useful diversity in root traits and their plasticity in a small set of six commercial sorghum hybrids, which could be used to match root phenotypes to target production environments. There was a hierarchy of plasticity for yield, yield components and root traits, so that the stability of some traits was related to the plasticity of other traits. Hybrids with high root phenotypic plasticity had more stable yields and yield components. Hybrids showing plastic root activity and rooting depth produced the highest yields in the driest environments, though were outyielded in higher-yielding environments which indicate a cost in phenotypic plasticity. The approach needs to be scaled to a population of materials as used in pre-breeding trials, and the use of genomic tools. We conclude that high-throughput functional root phenotyping approaches as the one used here can be useful to increase crop adaptation in breeding and agronomic research.

Declarations

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CRediT author statement

Dongxue Zhao: Performance of the research method, data analysis, R programming, data collection and curation, writing the manuscript; **Daniel Rodriguez**: Design of the research, method, data analysis, data collection, R programming, Writing - first draft; **Peter deVoil**: APSIM modelling and software programming, R programming, editing; **Victor O Sadras**: Writing and editing; **Jairo Palta**: Writing and editing.

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Table

Table 1 is available in the Supplementary Files section.

Figures

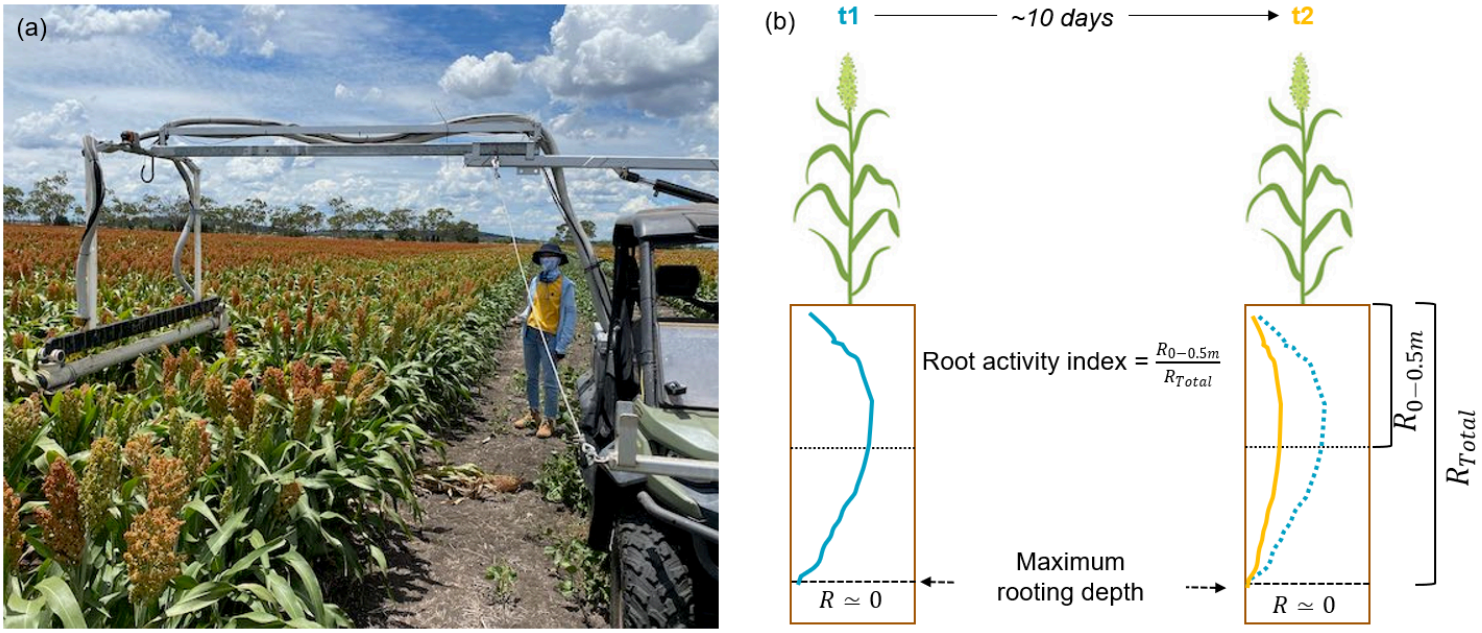

Figure 1

(a) Soil water surveying using an electromagnetic induction (EMI) instrument - DUALEM-21S (Dualem Inc., Milton, ON, Canada) shown over the crop canopy though the sensor is traversed on the soil surface in between the crop rows, and (b) calculation of root activity index (RA) and maximum rooting depth (RD, m) during a 10-day window around flowering, see eq. 1 and 2 in the text. RA is the ratio of a root activity factor (R) characterized from EMI (Zhao et al., 2022) for shallow soil layers (0-0.5 m, $R_{0\text{-}0.5m}$) relative to R for the 0-RD (R_{Total}). The blue and yellow curves represent the soil water profiles sensed from the EMI survey at t_1 and t_2, respectively and the difference between these two curves define the profile of crop water use.

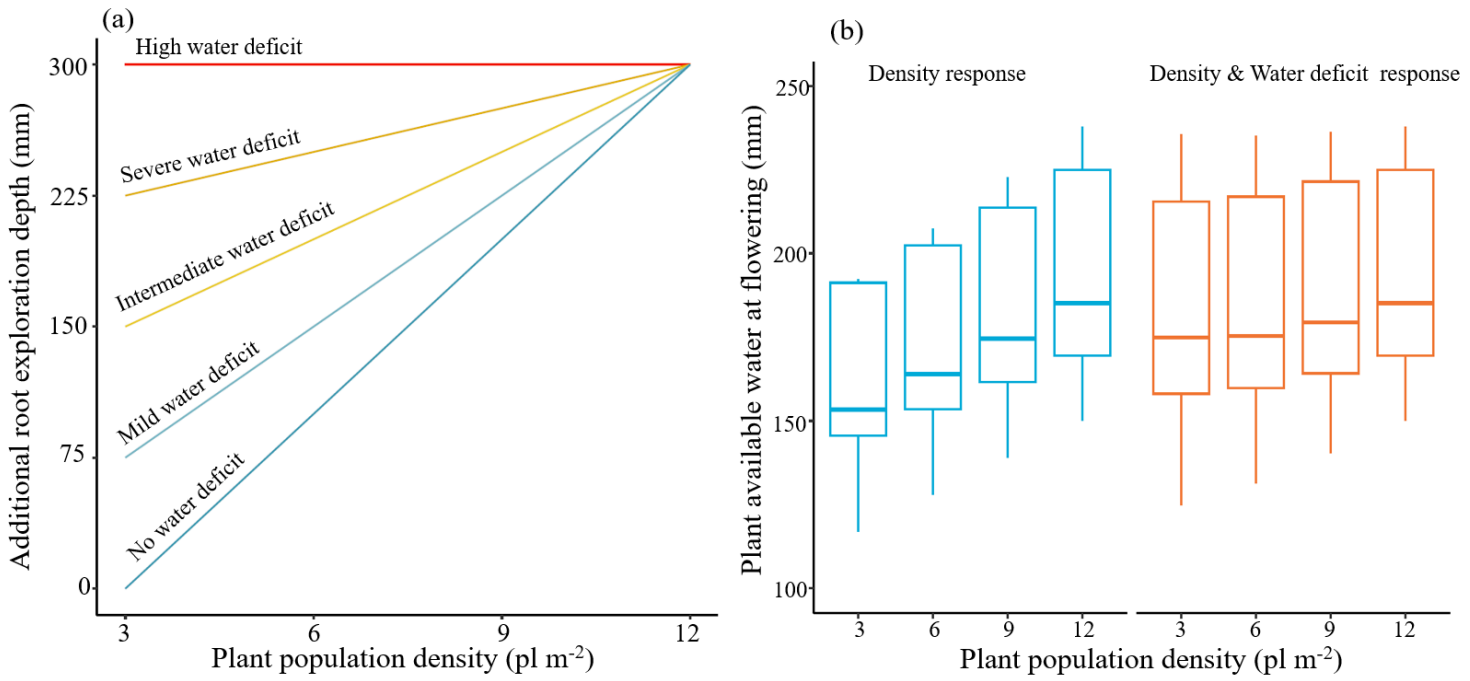

Figure 2

Assumptions in the parameterisation of APSIM to dynamically simulate root growth as driven by plant population density and water deficit. Water deficit was simulated assuming a continuous measure calculated as 1 – the fraction of plant-available water capacity (PAWC) in the active root zone at flag leaf emergence. The hypothesis assumes that root soil exploration in depth will increase by up to 300 mm, i.e. PAWC factor = 1, with increasing plant population density and with both increasing plant population density and water deficit (a); and simulated plant-available water at flowering assuming only plant population density effects or plant population density and water stress effects (b).

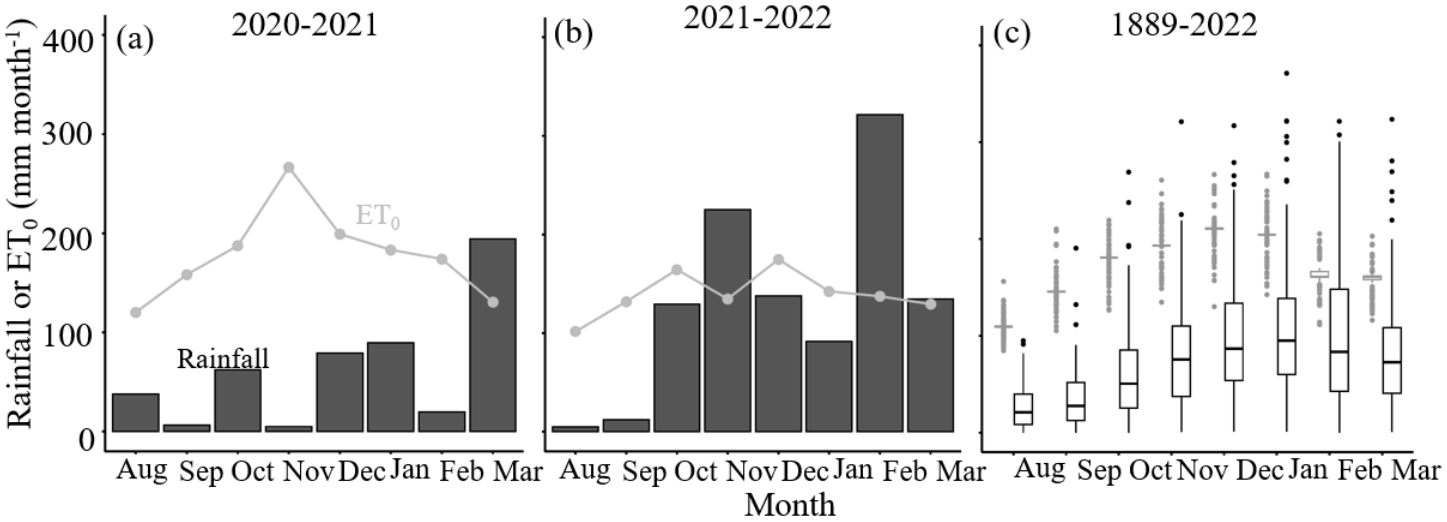

Figure 3

Rainfall and reference evapotranspiration (ET_0) per month during 2020/2021 (a), 2021/2022 (b) sorghum growing seasons and the period between 1889 and 2022 (c). In (c), boxplots indicate percentiles 0.25 (box), 0.75 (box), 0.50 (central line), 0.1 (whisker) and 0.9 (whisker), and points represent outliers. Weather data were obtained from https://www.longpaddock.qld.gov.au/silo/ for the region of Darling Downs, Qld, Australia.

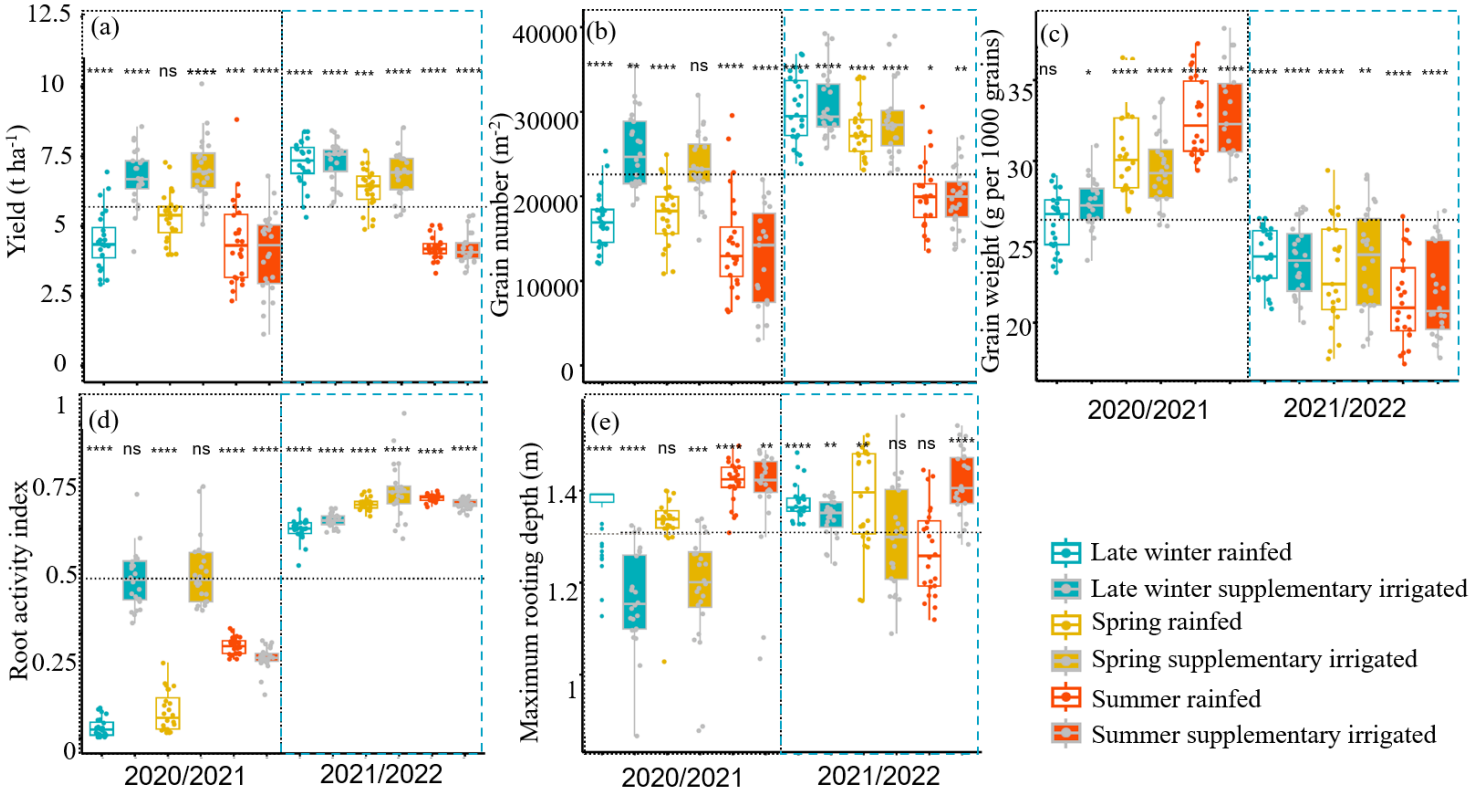

Figure 4

Variation of (a) grain yield, (b) grain number, (c) grain weight, (d) root activity index, and maximum rooting depth of six sorghum hybrids sown in late winter, spring and summer, under two water regimes (i.e. rainfed and supplementary irrigation) in 2020/2021 and 2021/2022. Box and whisker plots show the median (central line), 25th and 75th percentiles (box), and 10th and 90th percentiles (whisker) of the trait. Dots are means for the three replicates from the linear mixed model as indicated in Table S1. Significance tests (t-test) are for the environmental mean versus the overall mean with stars corresponding to *p* values < 0.05 (* < 0.05, ** < 0.01, *** < 0.001, **** < 0.0001) and those with *p* values > 0.05 as not significant "ns" using 'stat_compare_means' function in R.

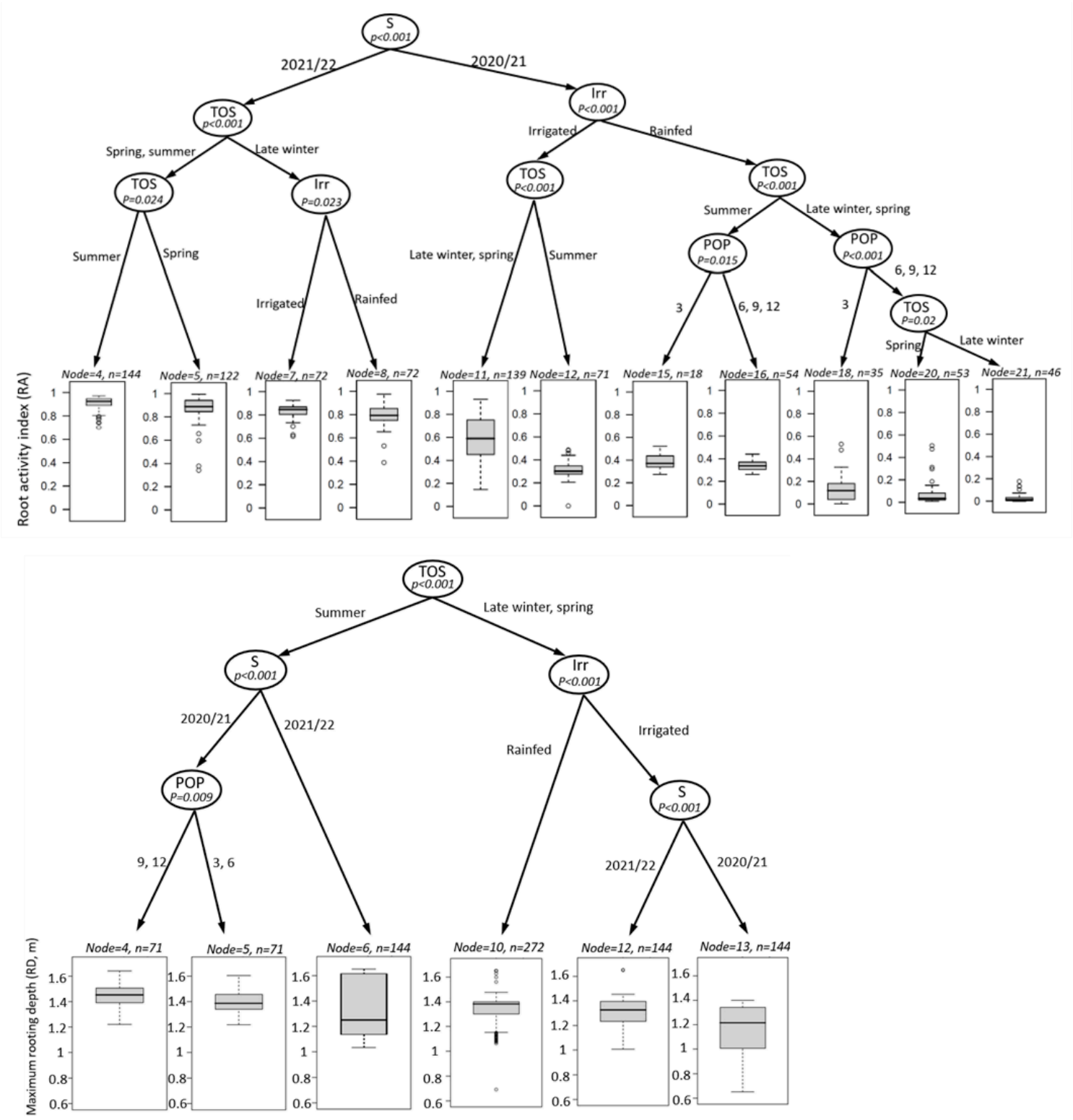

Figure 5

Conditional inference trees explaining the variations in (a) root activity index (RA) and (b) maximum rooting depth (RD, m) for the two seasons (S, 2020/2021 and 2021/2022), times of sowing (TOS, late winter, spring and summer), irrigation (Irr, rainfed and supplementary irrigated), and plant population densities (POP, 3, 6, 9 and 12 pl m^{-2}). In each boxplot, the central rectangle spans the first and the third

quartiles. The solid line inside the rectangle shows the mean. The upper and lower whiskers are the maximum and minimum values.

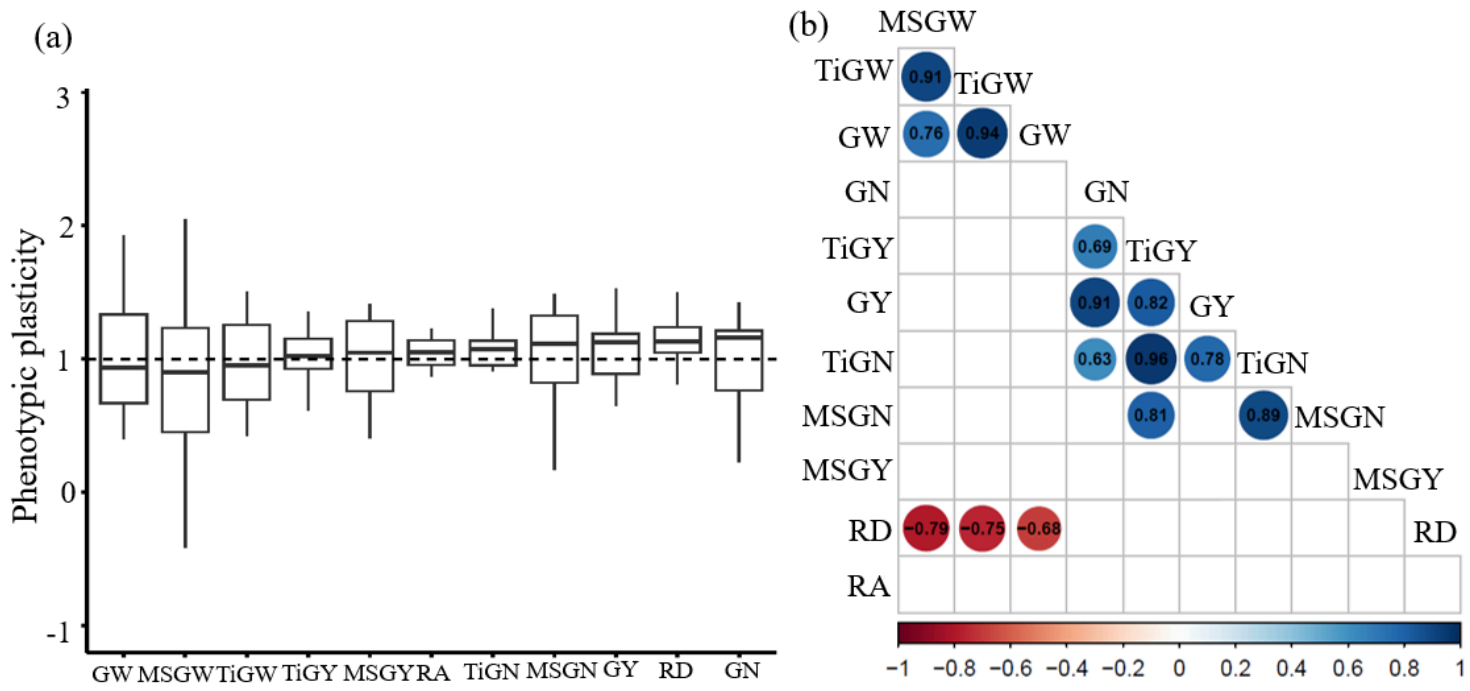

Figure 6

Hierarchy of phenotypic plasticity for yield and yield components, and root traits (a); and (b) correlation matrix for the phenotypic plasticity traits in (a), where GW = Grain weight; MSGW = Grain weight on main stem panicles; TiGW = Grain weight on tiller panicles; RD = Maximum rooting depth; tiller grain yield (TiGY) = Grain yield on tillers; RA = Root activity index; main stem grain yield (MSGY) = Grain yield on main stem panicles; TiGN = Grain number on tiller panicles; GY = Total grain yield; MSGN = Grain number on main stem panicles; GN = Total grain number. The dashed line in (a) is plasticity =1 to aid the comparison between traits that are ranked from low to high values.

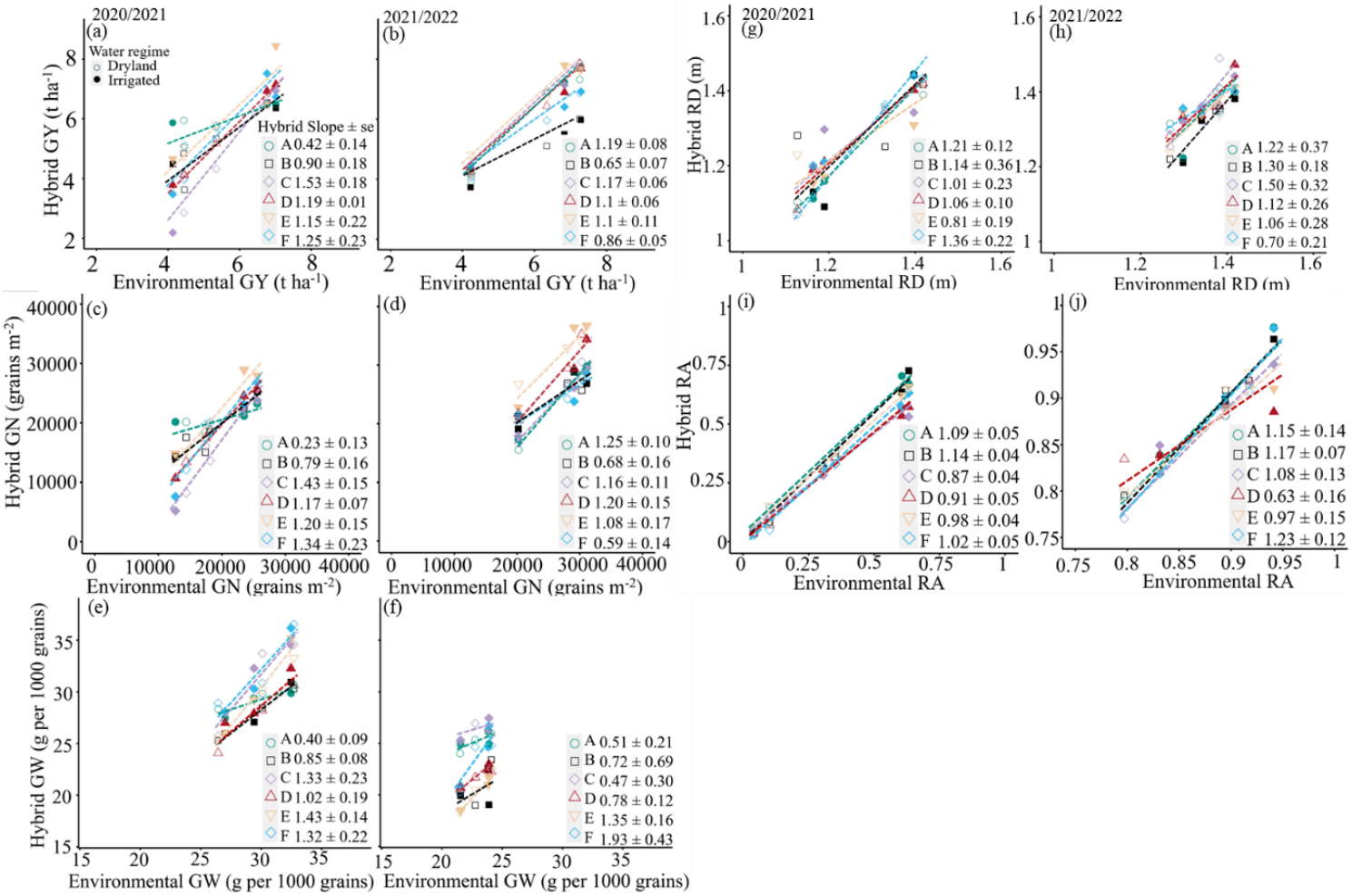

Figure 7

Relationships between hybrid traits and trait environmental means for grain yield (GY), root activity index (RA) and maximum rooting depth (RD) for six sorghum hybrids (A to F) sown in late winter, spring and summer, under two water regimes (rainfed and supplementary irrigation), and four plant population densities (3, 6, 9 and 12 pl m^{-2}) in 2020/2021 and 2021/2022. Numbers next to symbols are slopes ± s.e., r^2 and *p* values are shown in Table S2.

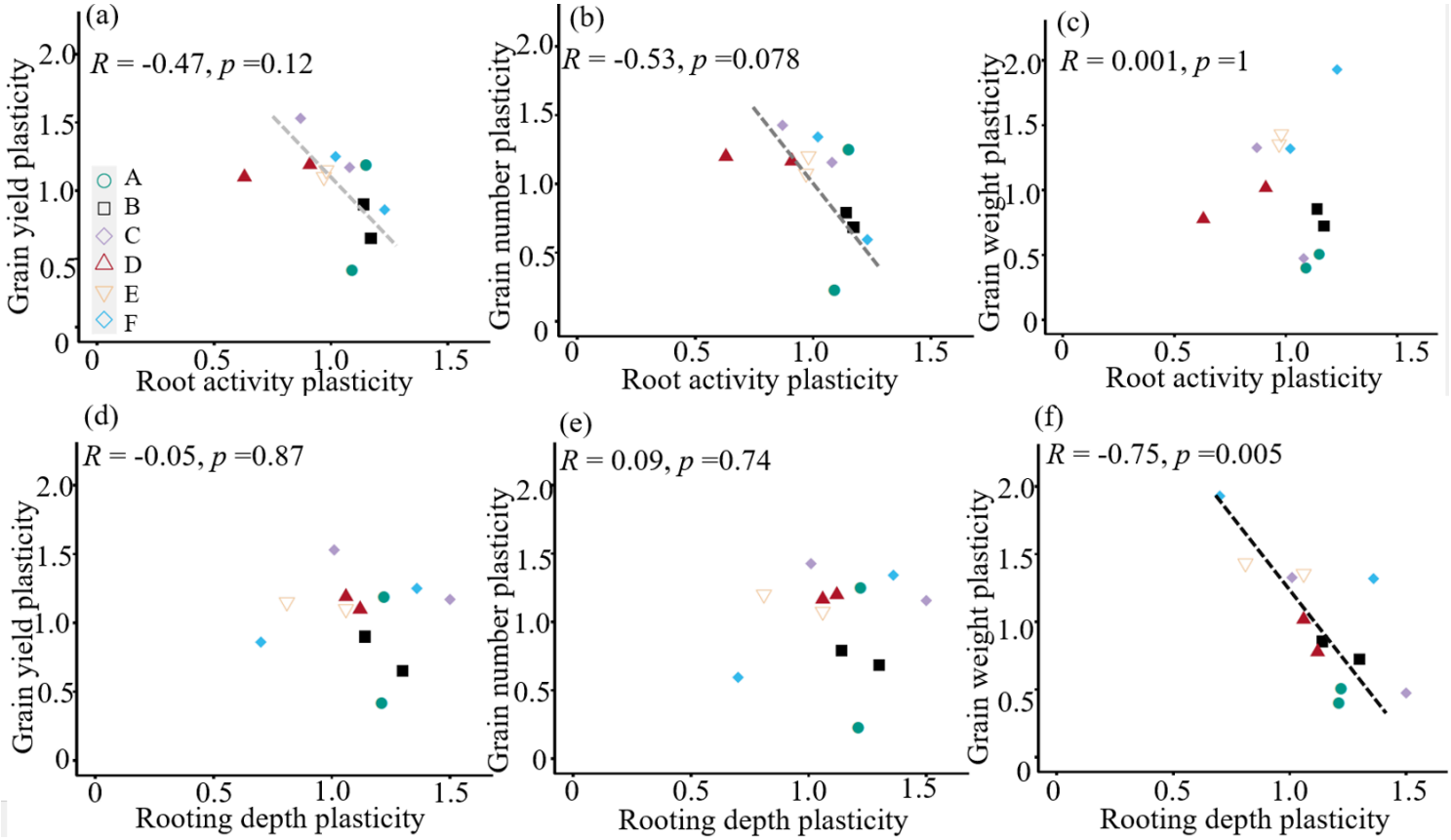

Figure 8

Relationships between the plasticity of grain yield (a and d), grain number (b and e) and grain weight (c and f) and that of root activity index (RA) (a, b and c) and maximum rooting depth (RD) (d, e, and f) for six sorghum hybrids, A to F over two seasons of trials. Dashed lines are the reduced major axis (RMA) regressions.

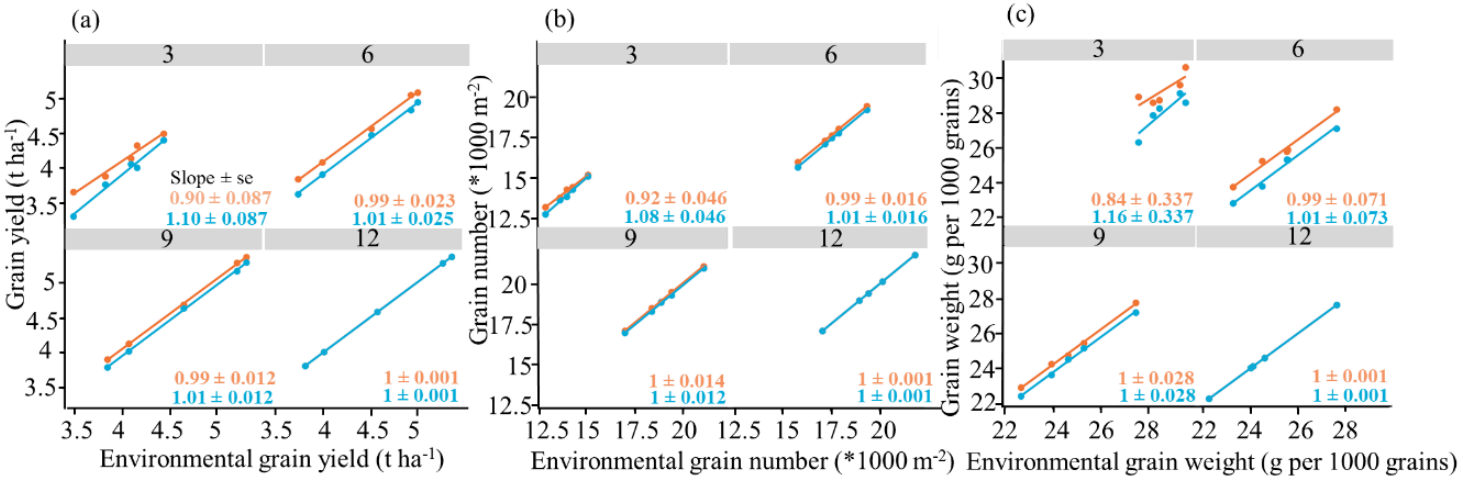

Figure 9

Simulated relationship between yield and mean environmental yield for grain yield (a), grain number (b), and grain weight (c), assuming only plant population density effects (3, 6, 9 and 12 pl m^{-2}) on root growth (blue lines), and both plant population density and water deficit effects (orange lines). Each dot is the mean trait value simulated from APSIM at each environment i.e., Gatton, Dalby, Warra, Roma and Surat, from 1950 to 2020.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Table1.png