



Sowing summer grain crops early in late winter or spring: effects on root growth, water use, and yield

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Abstract

Context Drought and extreme heat at flowering are common stresses limiting the yield of summer crops. Adaptation to these stresses could be increased by sowing summer crops early in late winter or early spring, to avoid overlap of drought and heat with critical crop stages around flowering. Though little is known about the effects of cold weather on root growth, water use and final grain yield in sorghum.

Objective This study aims to explore the effects of cold conditions in early sowing sorghum on crop and

root growth and function (i.e., water use), and final grain yield.

Methods Two years of field experiments were conducted in the Darling and Eastern Downs region of Qld, Australia. Each trial consisted of three times of sowing (late winter, spring, and summer), two levels of irrigation (i.e., rainfed and supplementary irrigated), four plant population densities (3, 6, 9 and 12 pl m⁻²), and six commercial sorghum hybrids. Roots and shoots were sampled at the flag leaf stage on three times of sowing, two levels of irrigation, and three replications, for a single hybrid and a single plant population density (9 pl m⁻²). Crop water use and functional root traits were derived from consecutive electromagnetic induction (EMI) surveys around flowering. At maturity crop biomass, yield and yield components were determined across all treatments.

Results The combinations of seasons, times of sowing and levels of irrigation created large variations in growth conditions that affected the growth and production of the crops. Early sowing increased yield by transferring water use from vegetative to reproductive stages and increasing grain numbers in tillers. Cold temperatures in the early sowing times tended to produce smaller crops with smaller rooting systems, smaller root-to-shoot ratios, and larger average root diameters. Total root length and root length density increased with increasing pre-flowering mean air temperatures up to 20 °C. Linear relationships were observed between an EMI derived index of root

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activity and the empirically determined values of root length density (cm cm^{-3}) at flowering.

Conclusions Sowing sorghum, a summer crop, early in late winter or spring transferred water use from vegetative stages to flowering and post-flowering stages increasing crop water use later in the season. Root length and root length density were reduced by pre-flowering mean temperatures lower than 20 °C, indicating a need to increase cold tolerance for early sowing. The higher grain numbers in early sown crops were related to higher grain numbers in tillers. The EMI derived index of root activity has a potential in the development of high throughput root phenotyping applications.

Highlights

- Sorghum sown early into cooler than recommended soils will reduce root and vegetative growth and transfer water use from vegetative to reproductive stages mitigating terminal water stresses, and increasing water use efficiency.
- Electromagnetic induction technology has a great potential for high throughput root phenotyping applications.
- To adapt to warmer climates, there is a need for sorghum breeders to include cold tolerance as a target.

Keywords Climate adaption · Agronomy · Early sowing · Root morphology · Water use efficiency · Root phenotyping

Introduction

Sorghum (*Sorghum bicolor* (L.) Moench) is a major dryland crop across Australia's northern grains region, where droughts and extreme heat are common abiotic stresses that limit grain yield (Clarke et al. 2019; Rodriguez et al. 2024). Across the region, and for conventional sorghum sowing times i.e., spring and summer, there is a high likelihood of heat stress events at flowering (Singh et al. 2017). Even though heat stress affects multiple physiological processes e.g., photosynthesis, respiration, and transpiration, the most yield sensitive phase in sorghum is around a narrow window i.e., 10–15 days centred at flowering (Prasad et al.

2015; Singh et al. 2015). A short duration of high-temperature episodes coinciding with this window, will cause pollen damage (flattened and collapsed pollen) leading to reduced pollen viability and pollen germination on the stigmatic surface (Singh et al. 2015; Prasad et al. 2017). This causes fertilization failures and reduced seed set resulting in lower grain numbers and grain yield (Prasad et al. 2008; Nguyen et al. 2013; Singh et al. 2015). Terminal drought stresses after flowering may also affect grain filling by reducing grain weight and quality (Muchow et al. 1994; Barnabás et al. 2008; Impa et al. 2019).

Ongoing climate change is increasing global surface temperatures and the frequency and intensity of extreme heat and drought events (IPCC 2021). In addition to irrigation and conservation agriculture practices, pathways to increase adaptation to heat and drought stress include improved genetic tolerance and agronomic avoidance (Fitter and Hay 2012; Reynolds et al. 2016; Prasad et al. 2017; Jagadish 2020). Genetic tolerance to heat stress has been shown for both, the threshold at which pollen viability starts to be affected, and the response of pollen viability to increases in temperature above that threshold (Singh et al. 2015). In-silico assessments of the likely benefits of genetic tolerance to heat stress have shown yield gains between 5 and 8% and 13–17% under baseline and climate change projections, respectively (Singh et al. 2014). Clearly, in the long haul, plant breeding should be able to contribute to crop adaptation in warmer and drier environments (Nguyen et al. 2013), though in the meantime, agronomy might be used to avoid the likelihood of heat stress damage. Agronomy practices such as early sowing (in late winter or spring), could advance flowering dates so that the overlap between times of the year of a high likelihood of the stresses and sensitive crop stages are avoided (Chiluwal et al. 2018; Rodriguez et al. 2024). Early-sowing sorghum will develop during periods of the year of lower atmospheric demand, and flower before yield-limiting summer heat waves, reducing the impact of heat and terminal water stresses (Raymundo et al. 2021; Rodriguez et al. 2024). However, sowing sorghum into soil temperatures lower than 16 °C will slow the rate of metabolic activation enzymes in the seed (Patanè et al. 2021), leading to poor emergence and seedling establishment, and reduced plant stands and growth rate (Forbes et al. 1987; Yu et al. 2004; Kapanigowda et al. 2013;

Rutayisire et al. 2021). Chilling temperatures after crop emergence can also reduce rates of photosynthesis and shoot and root growth (Wang et al. 2008; Kapanigowda et al. 2013; Ortiz et al. 2017). A poorly developed root system might limit access to soil water and nutrients (Aroca et al. 2001), further reducing crop growth and production. Here we present results from a two-season field experiment in which we aim to i) answer whether sowing sorghum early i.e., in late winter or spring affects crop and root growth and function (i.e., water use), and final yield, and ii) study the relationships between ambient temperature, root traits, root function, shoot biomass, yield, and yield components.

Materials and methods

Field trials

Field trials were conducted at a commercial farm in Nangwee, Qld Australia (27°34'2.73" S, 151°18'34.36" E) during the 2019/20 and 2020/21 Southern Hemisphere summer growing seasons. The climate in the region is semi-arid subtropical with an average of 621 mm rainfall per annum and mean annual maximum and minimum temperatures of 27.0 °C and 12.0 °C, respectively (Bureau of Meteorology 2023). Each season the trial covered an area of ~3.2 ha (82 m × 384 m) of a uniform black, self-mulching cracking clay, characterized as a Vertosol soil (Isbell 2016), with a clay content larger than 60%.

The trials included the factorial combination of three times of sowing (TOS, referred to as late winter, spring and summer), two levels of irrigation i.e., rainfed and supplementary irrigated, four plant population densities (3, 6, 9 and 12 pl m⁻²) and six commercial hybrids coded as A (A66), B (Agitator), C (Cracka), D (HGS114), E (MR Buster) and F (Sentinel). Each season, there were 432 plots with each 4 m wide (4 rows) × 10 m long. The factorial combination of times of sowing, target plant populations and hybrids were randomised to each individual plots within each trial using a split-plot design, with time of sowing and irrigation as main plots. Further details of the experiment layout can be found elsewhere (Zhao et al. 2022). In 2019/20, crops were sown on 14 August, 11 September and 10 October.

In 2020/21, crops were sown on 11 September, 6 October, and 5 November, respectively. Even though sowing was targeted to take place on soil temperatures ranging between 13 °C (low) and above 16 °C (recommended) at sowing depth, this was not always possible due to wet weather conditions. The supplementary irrigation treatment was imposed by laying drip irrigation pipes along each row after sowing. The objective of the supplementary irrigation treatment was to create additional growing environments, though water availability was limiting during the first season. Crops were fertilised following commercial sorghum production practices of the region and were kept free of weeds, pests and diseases.

An automatic weather station and soil temperature probe were installed before sowing to monitor daily minimum and maximum temperature, soil temperature at seed depth, total radiation, and rainfall. The normalised photo-thermal quotient (NPTq) was calculated using daily climatic records during flowering period (Rodriguez and Sadras 2007). Initial plant available water (PAW) was measured gravimetrically at each time of sowing (one core per replicate down to 1.5 m).

Measures of root growth and function

Time-lapse EMI surveys were conducted to infer spatiotemporal variability of the plant available water (PAW, mm) and crop water use (mm) across all plots and throughout the growing season in both seasons. A DUALEM-21S (DuaLEM Inc., Milton, ON, Canada) instrument was used to collect soil apparent electrical conductivity (EC_a), which is a function of soil moisture content. The instrument was towed 3 m to the right of a four-wheel all-terrain vehicle that traversed the field along the transect in the middle of each plot. In the first season fewer EMI surveys were taken, though during the second season surveys were conducted at fortnightly intervals. A detailed description of the method used to calibrate EC_a to PAW in this study is in Zhao et al. (2022). The crop water use down to 1.5 m was determined between every two consecutive EMI surveys using Eq. 1:

$$\text{Crop water use} = \Delta S + P + I \quad (1)$$

where ΔS (mm) is the change of PAW in the 0–1.5 m soil profile between the two consecutive EMI surveys,

P is precipitation (mm) and I is irrigation (mm). Here runoff was ignored as the site was flat and in-season rainfall amount was less than the minimum required for runoff reported in the same area (Connolly et al. 2002). Deep drainage was not considered because the soil is black Vertosols with a soil profile deeper than 2 m and negligible in-season changes of soil water content at the depth below 1.5 m were observed in Zhao et al. (2022). Crop water use was divided into pre-flowering, post-flowering, and total crop water use. Water use efficiency (WUE, kg mm^{-1}) was calculated as the ratio between grain yield (kg ha^{-1}) and total crop water use (mm). The approach for calculating WUE is simple (de Wit 1958; Passioura 1983; Passioura and Angus 2010), but it helps us focus on a wide range of physiological and morphological attributes of possible significance to this research.

In addition, in the 2020/21 growing season, a root activity factor was calculated at around flowering to represent the presence and activity in each studied soil depth as in Zhao et al. (2022) (Eq. 2). Briefly, Eq. 2 assumes that water use from an i^{th} soil layer can be represented by the plant available water (mm) of that i^{th} soil layer, a term representing the size of the canopy, and a factor termed as *root activity factor* (R_i) (Eq. 2). Another assumption is that given the large volume of soil surveyed, all treatments were affected by the same environmental conditions, and as all plots are measured within a small-time window (~2hs), therefore, changes in atmospheric demand can be expected to be small. The root activity factor was then calculated for the 0.3–0.5 m, 0.5–0.8 m, 0.8–1 m, 1–1.3 m, and 1.3–1.5 m soil layers.

$$\text{Root activity factor}_{\text{ph}} = \frac{\text{Crop water use}_{\text{ph}}}{\text{Plant water availability}_{\text{ph}} \times \text{Canopy size}} \quad (2)$$

In Eq. 2, the *Root activity factor* i^{th} can be considered as a functional proxy for root presence and activity in the i^{th} layer; *Water use* is the change in water content (mm) in the i^{th} soil layer between the two consecutive EMI surveys around flowering and permanent crop wilting point; *Plant water availability* is the plant available water (mm) in the i^{th} layer at the start of the measurement period; and canopy size as main determinant of crop water demand. The Normalized Difference Vegetation Index (NDVI) was used as a proxy of canopy size. In this study, NDVI around

flowering for each plot was derived from satellite images from PlanetScope (Planet Labs Inc 2020).

Root and shoot growth

The industry standard genotype (i.e., E, MR Buster) at one plant population density (9 pl m^{-2}) was selected to conduct roots and shoots sampling. The sampling was conducted at the flag-leaf stage for three times of sowing, the two irrigation levels and three replications, resulting in 18 plots sampled at each season. The shoots of twelve plants per plot were sampled and oven-dried at $65 \text{ }^\circ\text{C}$ until constant weight. After sampling the shoots, the root system was sampled using a narrow tubular soil auger (44 mm diameter) down to a soil depth of 2.1 m. At each sampled plot, six cores were taken, two taken in the row and four in the interrow (Fig. S1). Each core was cut into eight depths of 0–0.3, 0.3–0.5, 0.5–0.8, 0.8–1, 1–1.3, 1.3–1.5, 1.5–1.8 and 1.8–2.1 m. Corresponding depths of the six cores from each plot were bulked to give eight composite samples per plot, one from each depth. The samples were then soaked in water with a softening agent. The solution was then rinsed over a sieve in a root washing facility and the roots were collected with tweezers and stored in a 60–70% ethanol solution at $5 \text{ }^\circ\text{C}$. The root samples were then scanned using a digital scanner (Epson Expression XL 10000) with a resolution of 400 dpi. The scanned root images were analysed using the WinRHIZO[®] software, Regent Instruments Inc., Quebec, Canada (Trachsel et al. 2011). The root length (cm), average root diameter (cm), root surface area (cm^2), and root volume (cm^3) at each depth were calculated from WinRHIZO as in Rose (2017) and converted to per core basis. The root length density (cm cm^{-3}) and specific root length (cm g^{-1}) at each depth were calculated by considering the sample soil volume and root dry weights.

The total root length, total root surface area, total root dry weight, and total root volume at plot level were then calculated by summing the corresponding root traits across the soil profile (0–2.1 m). The average root diameter at plot level was determined from the total root length and total root volume. Similarly, a plot level average root length density (cm cm^{-3}), average specific root length (cm g^{-1}), and the root length to shoot dry weight ratio (cm g^{-1}) were calculated.

Dry matter production, yield, and yield components

Yield and biomass data were measured on samples taken at physiological maturity from eight plants in the central rows of each plot; areas showing uniform plant density were selected. Each sample was oven dried to a constant weight at 65 °C to determine the above-ground biomass. Panicles were then separated and threshed to determine yield components including grain number (grains m⁻²), grain weight (g per 1000 grains), and grain yield (t ha⁻¹). Seed set (%) was calculated for a period of 10–15 days around anthesis as in Singh et al. (2017). Yield components were partitioned into main stems and tillers. The harvest index was estimated as the ratio of grain yield to total biomass.

Statistical analysis

Root traits were analysed using a linear mixed model (LMM) framework for each season at both plot and across depths levels. At the plot level, the LMMs included fixed effects for TOS, irrigation, and the interaction between TOS and irrigation. Replicate was included as random effects.

Across depths, the LMMs were used to test the effects of TOS, irrigation, depth, and their interactions on root traits. The residual variance model was upgraded in stages, to test for heterogeneity of residual variance between depth intervals, as well as residual correlation models across depth intervals. The most parsimonious model for each measure was selected using the Akaike Information Criterion (Akaike 1998). Moreover, the values of root traits (i.e., root length, root surface area, root dry weight and root volume) were weighted on a “per 10 cm” basis to account for the differing widths of the depths.

Grain yield and its components (i.e., grain number and grain weight) and water use (i.e., pre-flowering, post-flowering, total crop water use and WUE) were also tested with LMMs. The season, TOS, irrigation, plant population density, and genotype levels and their interactions were used as fixed factors and season×replication interactions were taken as random. Separate residual variances were fitted for each season by a separate scaled column×row variance structure.

All LMMs were fitted using the ‘ASReml-R’ statistical package (Butler et al. 2017), whereby variance components were estimated using residual maximum likelihood (Patterson and Thompson 1971) in R (R Core Team 2022). The fixed effects were tested using Wald tests (Kenward and Roger 1997), and Empirical Best Linear Unbiased Estimates (eBLUEs) were generated from the models for significant effects. Significant differences between pairs of treatments were determined using Fisher’s least significant difference (LSD) (Welham et al. 2014), and all significances were assessed at the 5% level. The estimated means of each studied root and shoot traits were presented at the significant interaction levels.

To explore the environmental effects of TOS on root growth, root function (i.e., crop water use), yield components and harvest index, a principal component analysis (PCA) was performed including environmental covariates (Table 1) based on the ‘stats’ package in R. Conditional inference trees and random forest models were performed to untangle the G×E×M effects on yield in R using ‘partykit’ (Hothorn and Zeileis 2015) and ‘randomForest’ (Breiman 2001) packages. In addition, the relationships between plot level root traits and pre-flowering mean air temperature and between WUE and yield components were also fitted with JMP®, Version 17 software (SAS Institute Inc., Cary, NC, 1989–2023), based on the least squares function.

Results

The effects of early sowing on the avoidance of heat stresses around flowering are described in full in our previous articles that used results from a multi-environment (n=33) network of G×E×M trials and includes the sites in this manuscript (Rodriguez et al. 2024; Mumford et al. 2023). In this manuscript we focus on the effects of early sowing of sorghum on crop and root growth and function (i.e., water use), and final grain yield.

Environments, yield, and yield components

The combination of season, TOS and supplementary irrigation exposed the crop to a highly diverse range of growing conditions (Table 1). In the first season,

Table 1 Environmental conditions for the late winter, spring, and summer sown sorghum in the 2019/20 and 2020/21 growing seasons at Nangwee, Queensland, Australia

Environmental variables	2019/20			2020/21		
	Late winter	Spring	Summer	Late winter	Spring	Summer
Sowing-emergence average soil min T (°C)	10	12.8	15.4	15.7	18.9	20
Emergence-flag leaf average soil min T (°C)	15.1	17.8	19.6	18.6	20.4	22.3
Mean T (°C)	17.4	19.5	22.5	20.7	21.7	22.8
Pre-flowering average min T (°C)	7	8.2	11.3	12.7	14.8	16.8
Post-flowering average min T (°C)	12.5	14.6	17.3	17.7	17	15.9
Pre-flowering average max T (°C)	25.4	27.5	30.4	26.7	28.1	29
Post-flowering average max T (°C)	31.2	33	36	28.4	27.6	29.4
NPTq (MJ m ⁻² °C ⁻¹ kPa)	0.96	0.79	0.55	0.90	1.38	1.40
Pre-flowering rainfall (mm)	16	10	28	60	83	111
Post-flowering rainfall (mm)	19	30	37	85	82	107
Initial PAW (mm)	105	102	104	145	171	228
Pre-flowering irrigation (mm)	102	119	94	136	137	160
Post-flowering irrigation (mm)	28	28	0	52	25	0
Total plant available water (mm)	271	289	263	478	496	603
Seed set (%)	91.5	95.7	91	89	92	87.6

T, NPTq and PAW indicate temperature, normalised photo-thermal quotient and plant available water, respectively

soil temperatures for the late winter sown crop were well below the recommended 16 °C at sowing depth, though in the second season they were close to 16 °C. The early sown crops were also exposed to chilling ambient temperatures (<15 °C) between emergence to flowering.

There was a significant ($p < 0.002$) five-way interaction on grain yield between season, time of sowing, irrigation, plant population density and hybrid (Table S1). We used conditional inference trees and random forests on G, E and M variables, to further untangle these interactions. Figure 1a and b show that total plant available water, a measure of heat stress around flowering i.e., Seed set (%), and hybrid were the most important variables yields classifying grain yields within the whole data set (both seasons together). The highest yields were obtained with values of total plant available water higher than 340 mm, and values of seed set higher than 88%. Higher yields were also associated to hybrids A, B and D, while plant population was the least important variable (Fig. 1b).

In both seasons, spring sown sorghum had larger or similar yields than the late winter sown crop, and the summer sown crop always had the lowest yields (Fig. 2a). Grain yields were associated to grain

numbers, with the late winter and spring sown crops having a larger contribution of grain numbers from tillers (Fig. 2b and Fig. S2).

Root traits

Differences between treatments on root traits were affected by the contrasting environmental conditions between both seasons of trials (Table S2). However, from the collective analysis, the wide range of environmental conditions across seasons and times of sowing, allowed to develop functional relationships between environmental co-variables (Table 1) and the studied traits (Fig. 3). In the drier and cooler 2019/20 season, the late winter sown crop had a significantly smaller rooting system, i.e., smaller total root length ($P < 0.001$), total root surface area ($P = 0.014$), root length density ($P < 0.001$) and shoot dry weight ($P = 0.03$) (Fig. 3). Conversely, the roots of the late winter sown crop were significantly thicker ($P < 0.001$, Fig. 3d). Compared to spring and summer sown crops, late winter crops were smaller (Fig. 3f), particularly under dryland conditions. Similarly, late winter crops had a smaller total root length to shoot dry weight ratio ($P < 0.001$, Fig. 3e). In the wetter and warmer 2020/21 season, the value of the root traits

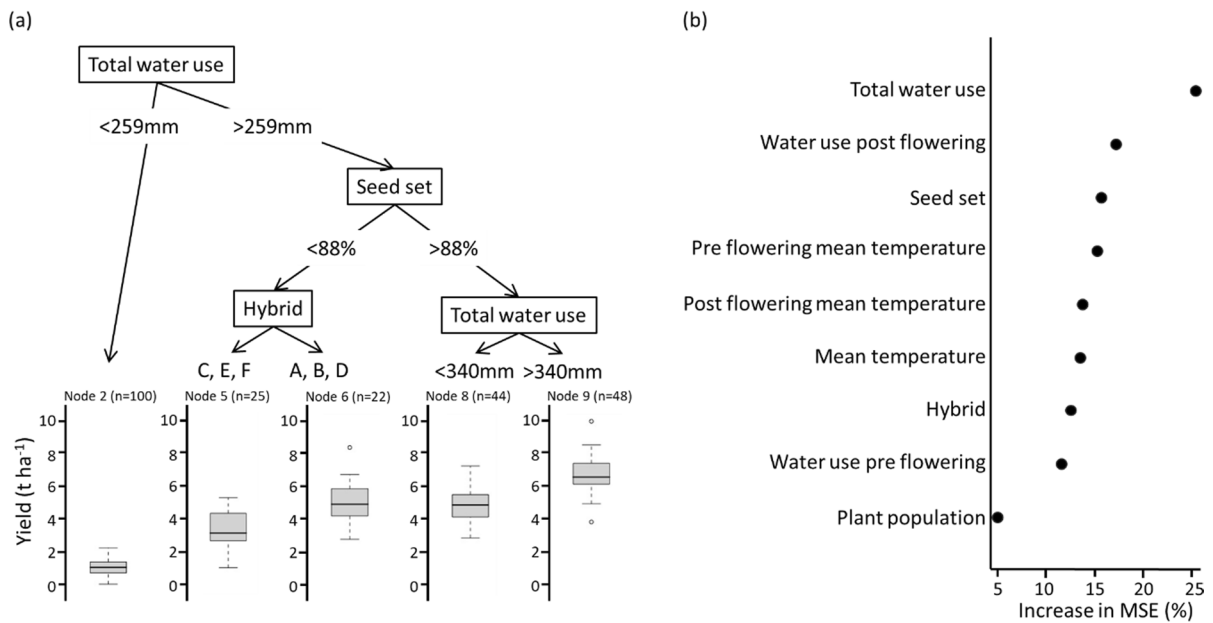


Fig. 1 Conditional inference tree explaining the interaction terms of environmental (i.e., time of sowing, irrigation, and season), genotype and management factors on grain yield in Table S1 (a), and (b) variable importance represent the increase in MSE (%) of yield predictions when the variable

is permuted from the random forest model. The most relevant descriptors either relate to the total plant available water, water use after flowering and a measure of heat stress around flowering (Seed set, %) calculated as in Singh et al. (2012)

was generally larger than in 2019/20, although there were no significant differences between treatments (Table S2).

Figure 4 and 5, and Tables S2 and S3, show root traits (eBLUEs) from the LMM for the Depth×TOS or Depth×TOS×Irrigation interactions. In 2019/20, the cold conditions of the winter sown crop led to a significantly smaller root length ($P=0.002$, Fig. 4a) and root length density ($P=0.009$, Fig. 4b) at each soil depth. Whereas the opposite was true for the average diameter ($P=0.047$, Fig. 4c) in which late winter sown sorghum significantly increased the average root diameter in the 0–0.8 m soil profile. This was also the case for the root volume ($P=0.026$, Fig. 4d), especially in dryland treatments. In contrast, late winter sowing reduced the surface area (Fig. 5a), root dry weight (Fig. 5b), and specific root length (Fig. 5c) across the soil profile, though differences between TOS were not significant.

The warmer and wetter conditions during the second season of trials, reduced the differences between sowing times, though as in the first season summer sown sorghum had a significantly larger root

dry weights in the topsoil ($P<0.001$, Fig. 5e, and Table S3). In the second season, there were no significant effects of TOS, irrigation, or their interactions with depth observed for the other root traits (Fig. 4e–h, Fig. 5d and f, and Table S3).

Irrespective of the contrasting time of sowing, the root activity factor (R) calculated using eq. 2 was linearly related to the measured root length density (RLD) (Fig. 6), this is, the larger the root length density the larger the root activity factor. Figure 6 also shows that for similar values of root length density, the dryland plots had a larger values root activity than the supplementary irrigated plots. In the dryland plots, the relationship did not hold for the topsoil layer (0.3–0.5 m) as in the top layers the main limiting factor to water uptake was plant available water.

Plant available water (PAW) and water use

Plant available water was highly contrasting between the two seasons and three times of sowing. (Table 1). Across both seasons winter and spring sown crops

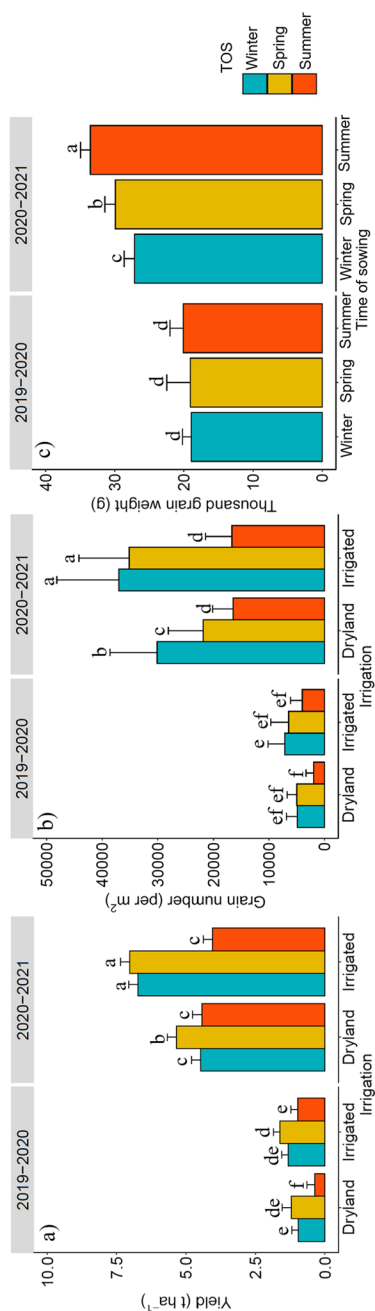


Fig. 2 Effects of time of sowing (TOS, i.e., late winter, spring, and summer) or TOS by irrigation (i.e., dryland and irrigation) on the (a) grain yield, (b) grain number, and (c) grain weight across the 2019/20 and 2020/21 seasons. Different lowercase letters indicate a significant difference at $P \leq 0.05$. Error bars represent standard errors of the estimations

tended to have less pre-flowering water use and larger post-flowering water use than the summer sown crops (Figs. 7 and 8). Even though similar values of total plant available water across times of sowing i.e., within the dryland and irrigated treatments in the first season (Fig. 7c), during both seasons the values of water use efficiency were larger for the winter and spring sown crops comparing to the corresponding summer sown crops (Fig. 7d and h).

Particularly during the second, wetter season, larger PAW values were observed for the early sowing crops at flowering stage (Fig. S3). For example, in 2020/21 the irrigated late winter sowing had 272 mm PAW at flowering compared to the summer sown crop (211 mm). During the second season lower plant populations (3 and 6 pl m⁻²) showed larger values of plant available water at flowering displaying a difference of up to 61 mm compared to higher populations and left more water in the soil profile by maturity, particularly in the early sown crops.

Relationships between root traits, water use, yield components, and environments

In both seasons (Fig. 8), PC1 explained ~45% of variations in the dataset, which was largely attributed to differences in root traits and environmental conditions, while PC2 was primarily associated to yield and yield components, shoot biomass, and crop water use. In general, the larger yield and harvest index values of the early sown crops were associated to a higher value of post-flowering water use resulting in higher water use efficiency values (WUE). Figure 8 also shows an association between the root length, root weight, root surface area, root length density, and specific root length, in the summer sown crop with mean temperature and solar radiation.

Irrespective of the season, there were positive linear relationships between WUE and the total grain number (Fig. 9a). As expected, different relationships were observed between the irrigated and dryland treatments. The larger values of WUE in the early sown crops were also associated to a larger grain number contribution from tillers (Fig. 9b), and a larger fraction of water use after flowering (Fig. 9c).

As shown in Fig. 8, root traits were related to the temperature environment. Figure 9d and e, show that root length and root length density responded positively to increasing pre-flowering mean air temperatures ranging between 16 and 20 °C, but there was

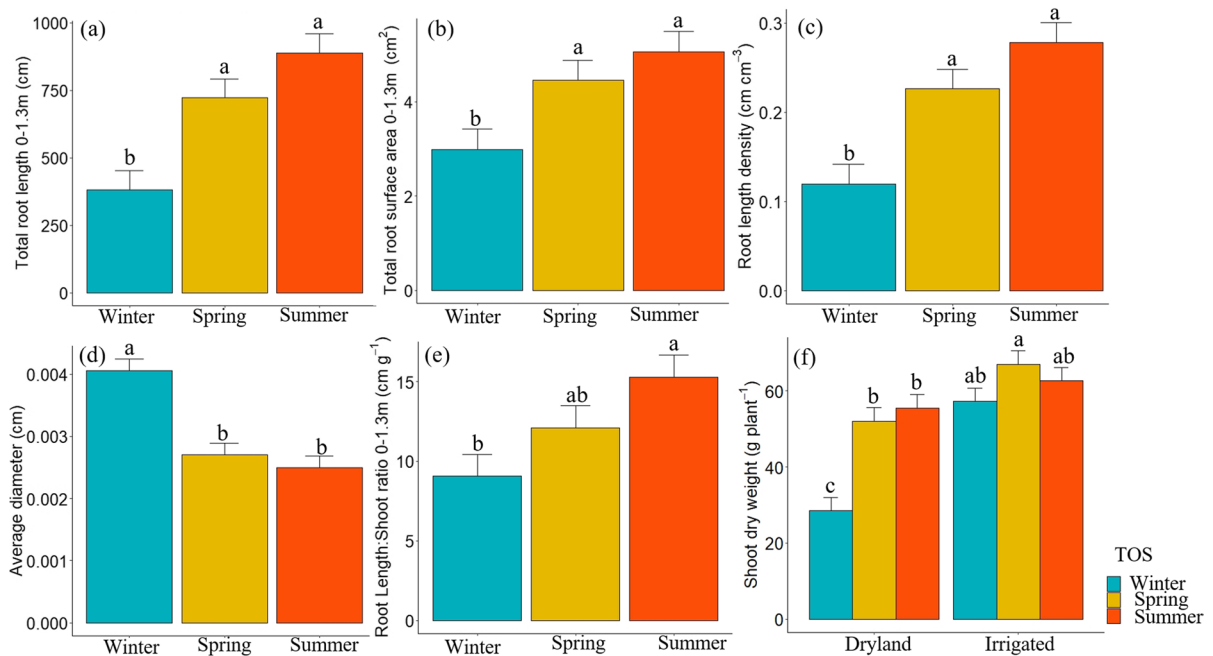


Fig. 3 Effect of time of sowing (TOS) including late winter, spring, and summer on (a) total root length, (b) total root surface area, (c) root length density, (d) average root diameter, (e) total root length to shoot dry weight ratio and the effects

of TOS by irrigation on (f) shoot dry weight at plot level at the flag leaf stage in the season 2019/20. Different lowercase letters indicate a significant difference at $P \leq 0.05$. Error bars represent standard errors of the estimations

little further response above 20 °C. In addition, in the first cooler season, the late winter sown sorghum crops had thicker roots. Irrespective of the season or irrigation treatment, the mean root diameter fitted quadratic relationships with pre-flowering mean air temperatures, with the smallest values observed at around 20 °C (Fig. 9f).

Discussion

Common strategies for adapting summer crops to heat stress during flowering include: (i) genetically improving the tolerance to high temperatures, and/or modifying flowering dynamics so that pollination can take place at cooler times of the day, and (ii) using agronomic practices to avoid the overlap between heat stresses and the flowering by simply advancing sowing dates (Jagadish 2020; Prasad et al. 2017; Reynolds et al. 2016). Though this requires sowing sorghum, a summer crop, early during late winter or early spring, at soil and air temperatures lower than optimum.

In this study we explored the effects of cold weather in early sowing sorghum, on crop and root growth and function i.e., water use, and final grain yield. We showed that sowing early in late winter or spring, increased yield and water use efficiency through an increase in harvest index as a result of larger grain numbers, primarily in tillers. In general terms, root length and root length density responded positively to increasing pre-flowering mean air temperatures ranging between 16 and 20 °C, but there was little further response above 20 °C.

The linear relationships observed between an EMI derived index of root activity and the empirically determined values of root length density (cm cm⁻³) show potential to be used in the development of high throughput functional root phenotyping applications.

Soil water dynamics and crop yield

Crop production in terminal water stress and hot environments is primarily determined by the interactions between crop phenology, seed set, and water use dynamics before and after flowering

Fig. 4 Effects of depth by the time of sowing (TOS) or depth by TOS by irrigation on root length, root length density, average root diameter, and root volume in 2019/20 (a, b, c, and d, respectively) and 2020/21 season (e, f, g and h, respectively). Values were the means for the three replicates. Error bars represent standard errors of the estimations

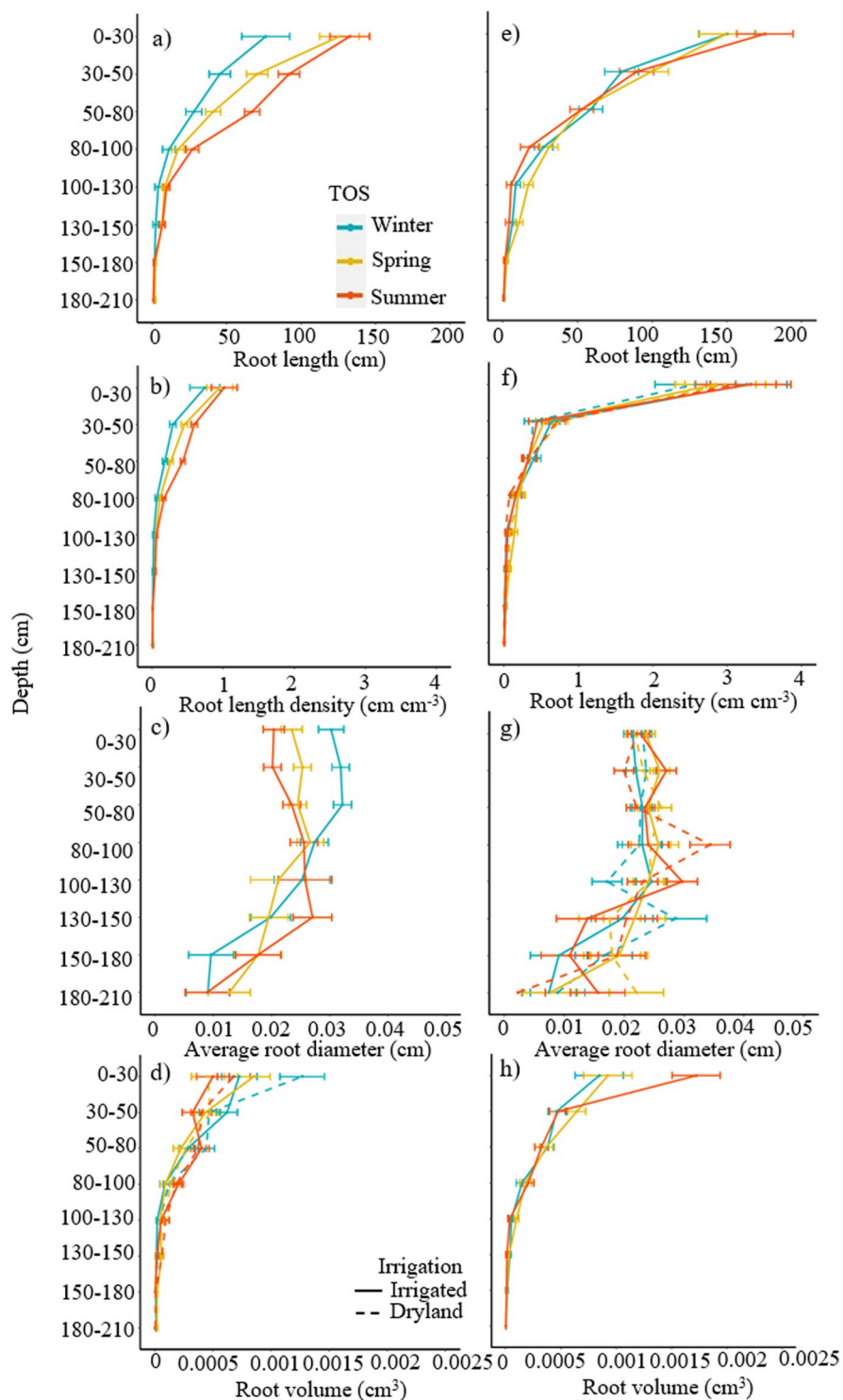
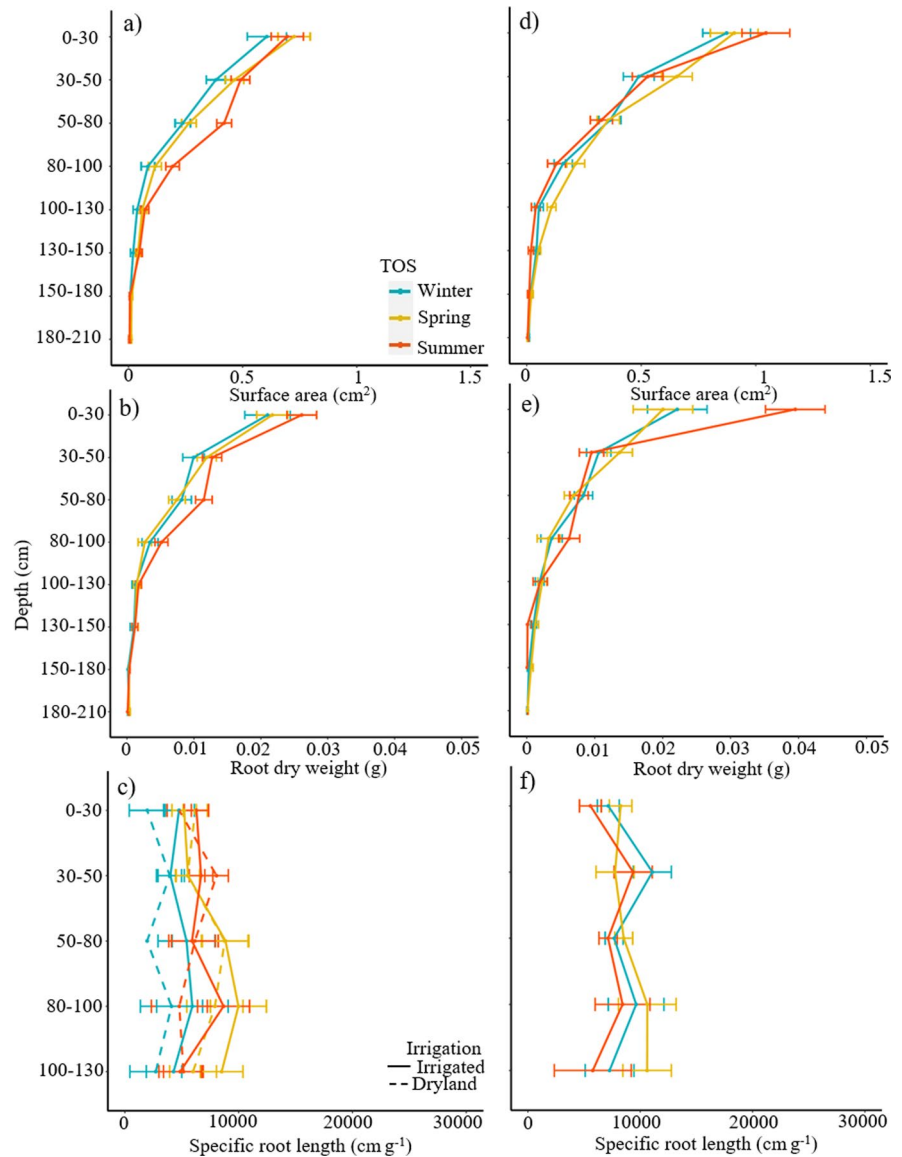


Fig. 5 Effects of depth by the time of sowing (TOS) or depth by TOS by irrigation on the surface area, root dry weight, and specific root length in the 2019/20 season (a, b and c, respectively) and 2020/21 season (d, e, and f, respectively). Values were the estimated means. Error bars represent standard errors of the estimations



(Siddique et al. 2001; Nguyen et al. 2013). In these environments, using genotypes that show stay-green phenotypes (Borrell et al. 2000), wide or skip row configurations and low plant populations (Whish et al. 2005), can transfer water use from vegetative to reproductive stages stabilising grain yields (Clarke et al. 2019; Carcedo et al. 2021). While avoiding air temperatures higher than 33 °C during a 10–15-day window around flowering (Singh et al. 2017) will reduce seed set losses due to pollen sterility (Prasad et al. 2017). Most of these principles are relevant when summer

grain crops are sown early in late winter or in early spring. Our results agree with these results to show that earlier sowing tended to reduce pre-flowering water use, particularly in the dryland treatments (Figs. 7 and 8). The relatively larger availability of soil water during reproductive stages (Fig. S3), the lower total water use (Fig. 7), the larger grain yield contribution from tillers (Fig. S2i), and larger grain yields (Fig. 2), resulted in higher values of water-use efficiency for the early sown crops (Fig. 7d, h). Higher values of seed set (%) i.e., cooler temperatures around flowering, were also associated to

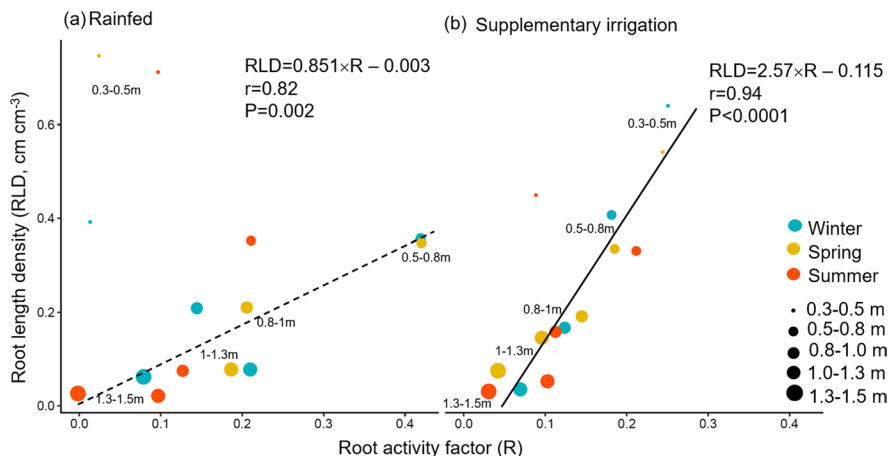


Fig. 6 Relationship between the root length density (RLD, $\text{cm}^3 \text{cm}^{-3}$) and root activity factor (R) at flowering for the rainfed/dryland (a) and irrigated (b) plots. The data is for genotype E, sown at 9 pl m^{-2} in the 2020/21 season. Blue, orange, and red dots indicate the late winter, spring, and summer sown

crops, respectively, and the size of the points indicate the soil layer. The linear relationships were not fitted to the data from the 0–0.3 m and 0.3–0.5 m depths, as those layers were close to wilting point, particularly in the rainfed treatment

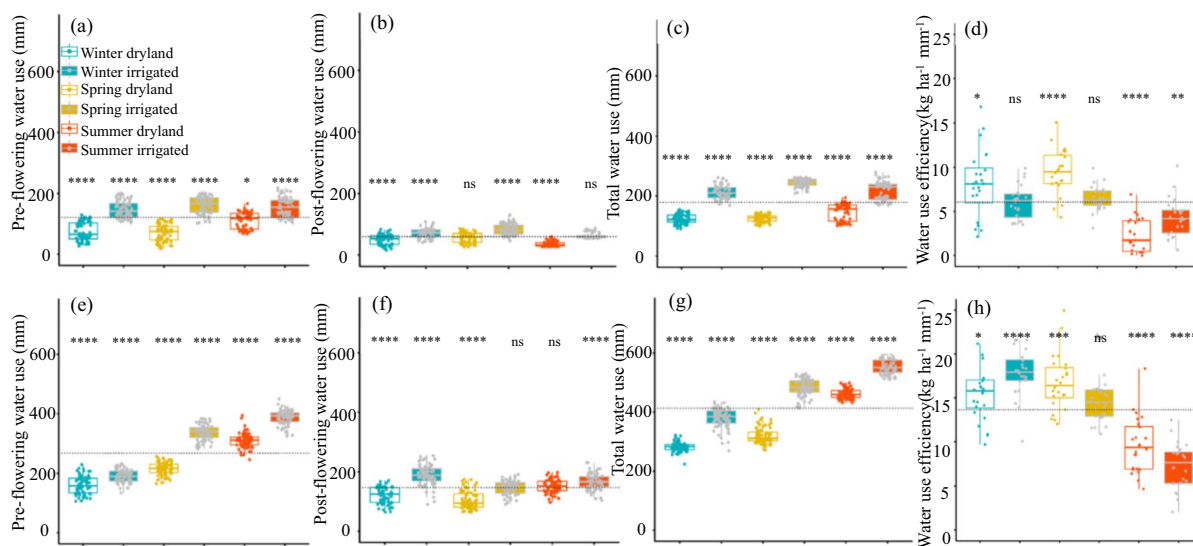


Fig. 7 Cumulative crop water use (mm) derived from the electromagnetic induction surveys during (a) pre-flowering, (b) post-flowering, and (c) the whole crop cycle during 2019/20 (a, b, c, d, respectively), and 2020/21 (e, f, g, h, respectively).

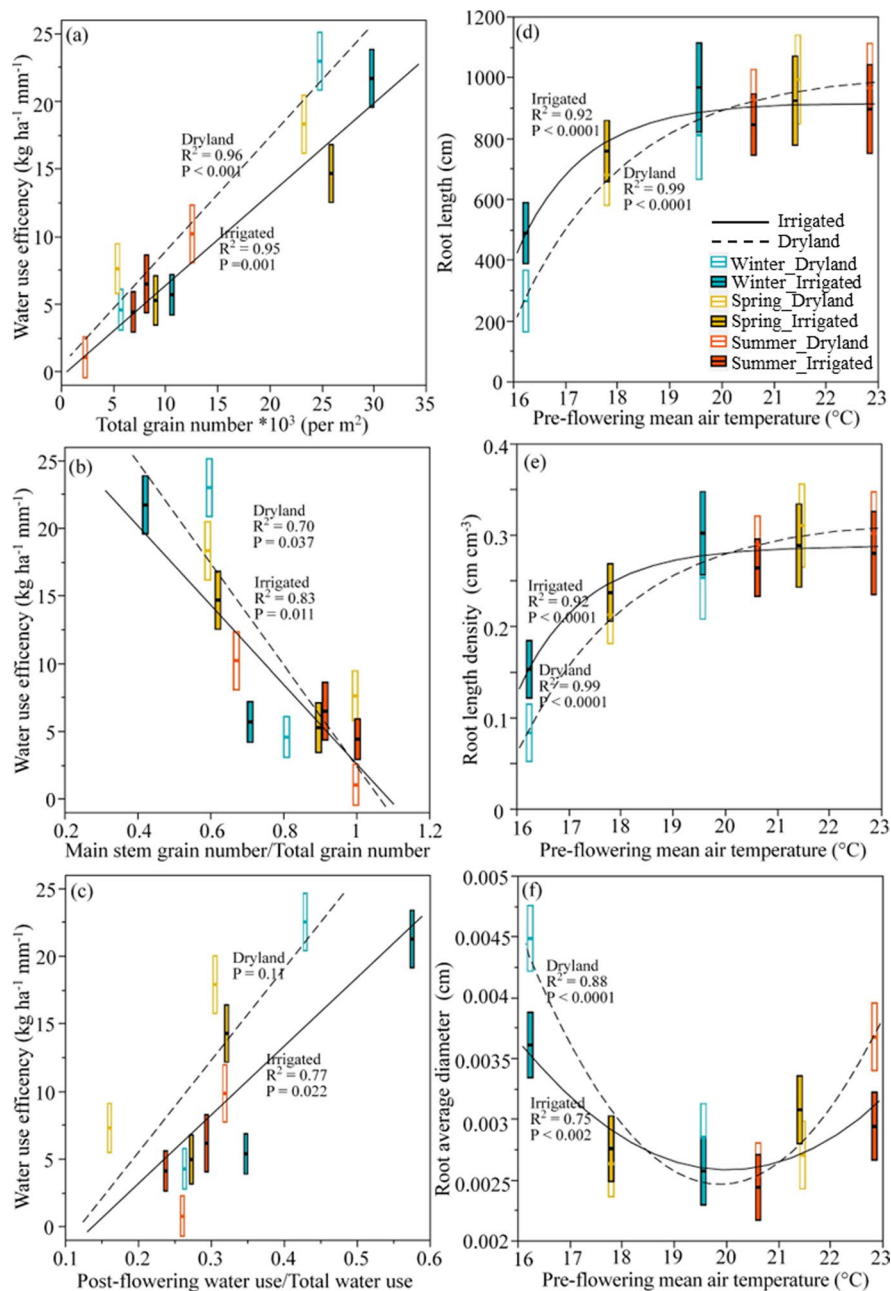
Significance tests are for the treatment mean versus the overall mean with ns, *, **, *** and **** representing the significant level > 0.05 , ≤ 0.05 , ≤ 0.01 , ≤ 0.001 and ≤ 0.0001 , respectively

higher yields (Fig. 1a), seed set was also an important variable associated to grain yield in the random forest analysis (Fig. 1b).

In the long term, breeding can be expected to contribute to improving genetic tolerance to heat stresses

(Singh et al. 2014), though in the meantime, early sowing can play an important role in improving crop adaptation to present and future climates before well-adapted cultivars are available (Munaro et al. 2020). However, sorghum is sensitive to cold temperatures

Fig. 9 Relationships between water use efficiency ($\text{kg ha}^{-1} \text{mm}^{-1}$) and (a) total grain number (per m^2); (b) the ratio of main stem grain number to total grain number; and (c) the ratio of post-flowering water use to total water use and between plot-level. Figures d, e, and f show the relationships between root length (cm), root average diameter (cm) and root length density (cm cm^{-3}) and pre-flowering mean air temperature ($^{\circ}\text{C}$), respectively, across both seasons for the three times of sowing (i.e., late winter, spring and summer), and two water levels (i.e., dryland and irrigated). The horizontal line in each boxplot is the mean with upper and lower bounds for standard errors of the estimation



calculated root activity factor was closely related to root length density (RLD) across most of the soil profiles, for the three times of sowing and two soil water treatments. The decline in RLD with soil depth was previously related to a lack of time for the rooting system to explore deeper soil layers (Robertson et al. 1993). Irrespective of the time of sowing, the larger the RLD the larger the values of the root

activity factor (Fig. 6). Figure 6 shows that different linear relationships were evident for the irrigated and dryland treatments. For the same value of RLD, dryland plots had larger values of the root activity factor than the irrigated plots, while in the top layer of the dryland plots root activity was limited by water supply irrespective of the presence of roots. The differences in slope between the dryland and irrigated

treatments might be related to a stress adaptation e.g., an increase in root hair and length, or in root hydraulic conductivity in water-limited environment (Calleja-Cabrera et al. 2020; Schneider 2022). The linear relationship between RLD, and its consistency between times of sowing highlight the opportunity to use EMI techniques to develop high throughput functional root phenotyping tools for breeding and agronomy. So far, high throughput phenotyping of rooting systems in the field has been a bottleneck for breeding to select for root traits that increase crop fitness to specific environments (Atkinson et al. 2019; Tracy et al. 2020). Presently most of the root phenotyping approaches are conducted under costly and laborious trials run under controlled conditions (Atkinson et al. 2019). These may involve growing plants in pots, tubes, root chambers or lysimeters on artificial media (Clark et al. 2011; Singh et al. 2012; van Dusschoten et al. 2016; Menamo et al. 2023). These approaches ignore the presence of intraspecific competition, plant density and the dynamics of water supply and demand on root structure and root function (Tracy et al. 2020). Many of these studies have been used to characterise the rooting system during seedling or early vegetative stages (Watt et al. 2013; Joshi et al. 2017; Menamo et al. 2023) and have related poorly to the same root traits latter in the season around flowering or during grain filling in the field (Watt et al. 2013; Tracy et al. 2020). This mismatch can be explained by the presence of plasticities in root traits (Schneider and Lynch 2020; Zhao et al. 2024). This is the capacity of a single genotype to express alternative phenotypes when grown in different environments (Schneider 2022). The EMI approach (Zhao et al. 2022), and the results in this manuscript, present a functional, quick, and affordable approach for field root phenotyping that is likely to overcome most of the limitations mentioned above.

Conclusion

Sowing sorghum, a summer crop, early in late winter or spring transferred water use from vegetative to reproductive stages mitigating terminal water stresses, and increasing water use efficiency. The higher grain numbers in early sown crops were related to higher

grain numbers in tillers. Root length and root length density were reduced by pre-flowering mean temperatures lower than 20 °C. The relationship between the root activity factor and root length density highlights an opportunity to develop high-throughput functional root phenotyping tools for breeding and agronomy.

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Data availability The data is available upon request to the corresponding author and approval from the funding body (GRDC).

Declarations

Competing interests The authors declare that they have no known competing interests or personal relationships that could have appeared to influence the work reported in this paper.

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