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Agronomic adaptations to heat stress: Sowing summer crops earlier

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ABSTRACT

Context: Summer crops are exposed to heat and drought stresses at critical stages during and after flowering, and their intensity and frequency are likely to increase with climate change. Agronomic stress avoidance offers the opportunity to temporally separate critical crop stages from heat and drought events. However, it might require sowing cold-sensitive summer crops earlier into colder than recommended soil temperatures. There is a need to understand how cold is too cold to sow summer crops early in late winter as well as what are the yield benefits and risks.

Objective: Here, we quantify the likely benefits and trade-offs of sowing sorghum, a summer cereal, earlier to adapt to the increased frequency and intensity of heat and water stresses during flowering and grain filling.

Methods: Two years of multi-environment (n=32) genotype by management trials were conducted across the main sorghum growing regions of Australia. Environments (E) consisted of the combination of years, sites, three times of sowing (early, spring, and summer), and the use of supplementary irrigation. At each E a factorial combination of four plant populations (M) and eight commercial sorghum hybrids (G) were sown with three replications. Crop growth and yield components were measured, and the APSIM model was used to simulate all trials and treatments to quantify risks and derive insights into functional relationships between simulated and measured environmental covariates, and measured crop traits.

Results: The tested hybrids showed small differences in cold tolerance during crop establishment. Across the tested environments, the G×M combinations produced up to 60 % variation in treatment yields across environment yields, which varied between <0.5 to about 10 t ha^{-1}; this translated into a ~5.5-fold variation in water use efficiency. Significant G×E and M×E interactions were observed for grain yield components. No G×M or G×E×M interactions were observed on yield or yield components. Early sowing was associated with a reduced risk of heat stress and water use transfer from vegetative to reproductive stages. Early sowing in late winter or early spring resulted in no significant yield gain or loss when all sites and years were included in the analysis. However, early sowing yielded between 1 and 2 t ha^{-1} more when the hottest sites and years were considered separately. This resulted from both the avoidance of heat stresses and milder or no terminal drought stresses.

Conclusions: Early sowing of sorghum can reduce the likelihood of heat stresses around flowering as well as the likelihood of terminal drought stresses. Advantages include reduced yield losses in the hottest years and a transfer of water use to grain filling stages, resulting in increased grain yield and improved grain quality parameters.

Implications: Early sowing, an agronomic adaptation, offers the opportunity to quickly adapt to the increase in the frequency and intensity of extreme hot events during critical crop stages. However, for the practice to be de-risked, there is a need to increase cold and chilling tolerance in sorghum and/or identify interventions that enhance seed germination and seedling vigour when the crop is sown early into cold soils.

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1. Introduction

Heat and water stresses around flowering are critical factors affecting the productivity of summer crops around the globe (Lobell et al., 2015). Climate change is expected to increase the frequency, intensity, and persistence of extreme events, particularly at mid-latitudes (Pfleiderer et al., 2019; IPCC, 2021). Since 1910, the Australian climate has warmed by 1.4°C (CSIRO and BOM, 2022), reducing the profitability of cropping farms by 35 % relative to pre-2000 conditions (Gupta and Hughes, 2018). It is important to note that by the end of the century, increases of up to 3.3–5.7°C (scenario SSP5–8.5) can be expected (IPCC, 2021).

Even though sorghum is considered well-adapted to hot and dry environments, terminal drought and heat stresses remain the most critical abiotic constraint to crop production (Ciampitti et al., 2020; Craufurd and Peacock, 1993; Prasad et al., 2021). The impact of heat stress on sorghum yield depends on the stress's timing, intensity, and duration. It is primarily reflected in lower grain yields through reductions in grain number that, in most cases, are not compensated by larger grain weights (Prasad et al., 2019). However, heat stresses often occur in combination with water stresses (Iizumi and Ramankuty, 2016), so optimum flowering windows must be defined based on the likelihood of extreme temperatures and water stresses (Flohr et al., 2017). Options to increase crop adaptation to abiotic stresses have been proposed, including genetic and agronomic options involving tolerance, avoidance, and escape mechanisms (Jagadish, 2020). For example, tolerance to heat stress can be expressed in cultivars showing higher temperature thresholds at which the grain set starts to be reduced and/or grain set responses as temperature increases over such a threshold (Singh et al., 2017). Variability in cultivar tolerance has been identified for heat stresses during sporogenesis and anthesis (Nguyen et al., 2013) and functionally described in the form of contrasting higher air temperature thresholds at which pollen and pistil viability start to be damaged (Djanaguiraman et al., 2018). Variability in damage responses as temperature increases above such a threshold has also been quantified (Singh et al., 2015). The impact of high air temperature on seed set stress in sorghum has also been included in functional crop simulation models (Singh et al., 2017, 2015). The observation that the variability in heat tolerance amongst the current availability of germplasm might not be enough to avoid significant yield losses (Nguyen et al., 2013; Singh et al., 2015; Tack et al., 2017) calls for alternative approaches to be explored. Avoidance refers to the overlap between sensitive crop stages with times of the year or time of the day with a high probability of heat stress events (Flohr et al., 2017). For example, agronomic adaptations to heat stress may include sowing sorghum, a summer crop, earlier in late winter or early spring, into colder than recommended soil temperatures (<16°C) so that the critical stages around flowering avoid high temperatures. In overhead irrigated systems, evaporative cooling could also be added to the range of agronomic mitigation options available to reduce canopy temperature during critical stages around flowering (Liu et al., 2021). Both adaptation pathways, avoidance and tolerance, need to be seen as complementary. In one case, agronomic solutions could, in the short term, be identified and adopted, while over time, it can be expected that breeding will improve stress tolerance in commercial germplasm (Jagadish, 2020). Instead, crop adaptation to drought stresses is based on resource accumulation and translocation of resources from the vegetative to the reproductive stages (Sinclair and Jamieson, 2006). For sorghum, the translocation of water resources from the vegetative to reproductive stages is an important pathway to minimise the likelihood and intensity of drought stresses around flowering and during grain filling (Borrell et al., 2000). Here, we explore the more immediate agronomic options farmers might have to increase adaptation to heat and terminal water stresses associated with sowing sorghum, a summer crop, early in late winter or early spring, and discuss the cascade of implications at the crop level. We hypothesise that sorghum crops sown into cooler environments during late winter (i) are likely to avoid the overlap between the crop critical stages and heat stresses and that (ii) the reduction of vigorous crop growth under low ambient temperatures and the lower atmospheric demand is likely to transfer water use from vegetative to reproductive stages, reducing the likelihood of terminal drought stresses. These ideas are tested and discussed by summarising the learnings from two years of on-farm multi-environment experimentation across eastern Australia. These trials aimed to create contrasting thermal environments around flowering, to assess the feasibility of sowing sorghum early to avoid heat and terminal water stresses, and to answer the question: 'How cold is too cold to sow sorghum?

2. Material and methods

Two years of multi-environment trial (MET) data was collected across the main sorghum growing regions in Australia, i.e., Liverpool Plains and Moree (New South Wales), Darling Downs (South-East Queensland), and Central Queensland in Australia in the 2018–2019 and 2019–2020 years. Across the two years, 32 environments resulted from the combination of sites, three times of sowing (referred to as "early", "spring", and "summer"), and the use of supplementary irrigation (Table 1 and S1).

Most trials were conducted on farmers' fields using researcher equipment and sown in solid configurations. At each site, initial soil moisture was measured at sowing, and an automatic weather station was installed to record daily values of maximum and minimum temperatures, rainfall, soil temperature at sowing depth, solar radiation, and relative humidity. Plot sizes were 10 m long by four 1 m rows, and samples were taken at maturity from uniform areas of the middle two rows. Each environment had four target plant populations (3, 6, 9, 12 pl m-2) in factorial combination with eight commercial sorghum hybrids and three replications. For simplicity, hybrid names were coded as commercial hybrids, which are coded as A (A66), B (Agitator), C (Apollo), D (MR Buster), E (Cracka), F (G33), G (HGS114), and F (MR Taurus). The factorial combination of times of sowing, target plant populations and hybrids were randomised to each plot within each trial using a split-plot or split-split plot design. Most hybrids were represented in all environments and included the most common commercial hybrids recommended across the region. Phenology differences between these hybrids were small. Hybrids varied between 55 and 62 days to flowering and from 106 to 113 days to maturity.

Crop establishment was determined at the 3–4 leaves stage. Yield and biomass data were determined on samples taken at crop maturity from eight plants in each plot's central rows in areas with uniform plant density. Samples were dried to constant weight at 65 °C. Panicles from the main stem and tillers were separated and threshed to determine yield components, grain yield, and a measure of yield quality, i.e., the per cent weight of the material passing through a 2 mm screen (Grain Trade Australia, 2021). Yield components included grain numbers and grain weights on both main stem and tiller panicles. Grain protein was determined by NIR spectroscopy (Grain trade Australia, 2021).

The Agricultural Production Systems Simulator (APSIM 7.10), APSIM-Sorghum, was used to simulate all trials and treatments. To simulate early sown sorghum crops with APSIM 7.10, we (i) removed the early frost sensitivity that would otherwise wrongly simulate a kill-crop event at the first frost event as sorghum tolerates frosts till the crop has seven leaves and (ii) used a decaying exponential function of plant population and sowing date (expressed as the number of days since 1-June) fitted to observed data over three latitudinal zones within the experiment data set i.e., Liverpool Plains, Darling Downs and Central Queensland. This was required as in APSIM 7.10; the fertile tiller number is calculated using an empirical function after 1st September, while in our trials, the earliest sowing date was in June. The tested model (see Figs. S2-S4) was then used to (i) derive environmental covariates for each combination of environment and hybrid, such as SeedSetStress (%) (Singh et al., 2017) and the water stress environment (Hammer et al., 2014), (ii) to study functional relationships between

Table 1
Site, latitude, longitude, irrigation treatment, time of sowing and sowing date.

Site	Latitude	Longitude	Irrigation (mm)	Time of sowing	Sowing date
Breeza	31.2481° S	150.4669° E	0	Early	6/9/2018
Breeza			158	Early	3/9/2018
Emerald	23.5243° S	148.1583° E	0	Early	26/7/2018
Moree	29.4653° S	149.8416° E	0	Early	8/8/2018
Surat	27.1519° S	149.0680° E	100	Early	8/8/2018
Warra	26.9303° S	150.9203° E	0	Early	27/7/2018
Breeza			0	Early	10/9/2019
Emerald			0	Early	20/6/2019
Emerald			180	Early	20/6/2019
Nangwee	27.5459° S	151.2923° E	0	Early	14/8/2019
Nangwee			227	Early	14/8/2019
Breeza			0	Spring	17/9/2018
Breeza			165	Spring	18/9/2018
Emerald			0	Spring	16/8/2018
Moree			0	Spring	12/9/2018
Surat			100	Spring	28/8/2018
Warra			0	Spring	19/10/2018
Breeza			0	Spring	7/10/2019
Emerald			0	Spring	22/7/2019
Emerald			180	Spring	22/7/2019
Nangwee			0	Spring	11/9/2019
Nangwee			265	Spring	11/9/2019
Breeza			0	Late	23/10/2018
Breeza			132	Late	16/10/2018
Moree			0	Late	27/9/2018
Surat			100	Late	24/1/2019
Warra			0	Late	9/11/2018
Breeza			0	Late	28/10/2019
Emerald			0	Late	19/8/2019
Emerald			180	Late	19/8/2019
Nangwee			0	Late	10/10/2019
Nangwee			265	Late	10/10/2019

measured and simulated crop, climate, and soil covariates, and (iii) to quantify the likelihood of heat and frost damages across the region. In APSIM, the SeedSetStress (%) is calculated from a heat stress factor that uses maximum daily temperatures during a period of 150°Cd, starting at 50°Cd before anthesis and observed flowering times (Singh, et al., 2017) (Eq. 1).

$$SeedSetStress(\%) \quad = \sum_{d=1}^{d=n} \frac{TTd}{150} \quad \times \quad (100-10) \tag{1}$$

Where TTd is the thermal time accumulated during any day within the 150°C window around flowering, and 10 is the SeedSetStress (%) if the maximum temperature would be 39°C continuously. As previously observed (Singh et al., 2015), the approach assumes that the reduction in the seed set starts at a maximum temperature of 33°C and is proportional to the duration of the high-temperature stress. The water stress environment type was derived from the simulated time course of the water supply/demand ratio for the period ± 400 °C days around anthesis (i.e., 1–5 as in Hammer et al., 2014 and 2020). The time course of the supply/demand ratio was classified into one of five environment types based on proximity assessed via least mean square distance. The water stress environment type was calculated for standard local agronomy i.e., solid configuration, 1 m rows and 6 plants m^{-2}, and hybrid (MR Buster).

The likelihood of frost damage was calculated from the frequency of frost days (i.e., air temperature at 1.8 m height lower than 0°C) after sorghum is sensitive to frost damage, i.e. seventh leaves or floral initiation. For conciseness, results from the simulations of heat and frost stress across eastern Australia are presented for a single variety (MR Buster) sown at fortnightly intervals between the 1st of June and the 15th of January for the period 1970–2018.

Readers should note that the sowing time was considered an environment as crops sown at different times will be exposed to contrasting climates and soil conditions (Table 1 and S1). The statistical analysis was a factorial combination of environments, the four target plant populations and eight hybrids. As in a previous article from this series (Mumford et al., 2023), an 'environment' was defined as growing conditions, i.e., climate and soil conditions, under which genotypes or management practices are tested. As in Mumford et al. (2023), these growing conditions were induced by site, time of sowing, and irrigation. The use of "management practices" to generate environmental cues is not new. In addition to Mumford et al., 2023), similar approaches were used previously by Coast et al. (2022), Fanning et al. (2018), Singh et al. (2015), and Borrell et al. (2014). Conversely, a management practice, e.g., plant density, was defined as the set of variables that are manipulated under the same 'growing' condition. Statistical analyses were performed for 11 traits (total yield, biomass, yield components and grain protein) using linear mixed models via the *ASReml-R* package (Butler et al., 2017; Welham and Thompson, 2021) in the *R* software environment. The analysis explored the three-way interaction effect between hybrid (G), environment (E), and target plant population (M), enabling us to investigate the presence of G×E×M interaction effects explicitly. A separate analysis was done for the (a) 2018/19 season and (b) 2019/20 season to explore G×E×M interaction effects within each season. Each of the terms contributing to G, E or M were fitted as fixed effects and the design terms for each trial were fitted as random. Heterogeneous residual variances were fitted for each trial, and spatial field trends were accounted for using environmental covariates in the mixed model (see Mumford et al., 2023, this special issue). Linear mixed models were run using the REML procedure in ASReml-R (Gilmour et al. (1997). The significance of the G×E×M and corresponding lower-order interaction and main effects were assessed using a Wald test with an approximate *F*-statistic (Kenward and Roger, 1997). Predictions obtained from the models were (empirical) Best Linear Unbiased Estimators (eBLUEs). The eBLUEs for the G×E×M interaction effect for each trait in each season were used to explore functional relationships between yield, yield components and environmental covariates. Associations between crop traits and environmental covariates were studied in biplots using the prcomp function from the pcaMethods package (Core Team, 2024).

3. Results

3.1. *Sorghum emergence in cold soils*

Available data included emergence values from all sites, years, and six hybrids that warranted the fitting of a linear-plateau model (Fig. 1). The minimum soil temperature, i.e., minimum mean (9 am) soil temperature during the first week after sowing, that maximises crop emergence was as low as 13°C (Fig. 1). Though, differences between the tested hybrids were present. In Fig. 1, the lines were fitted through the largest values (90th percentile) of relative emergence, i.e., established plant population relative to the target plant population, for each of the hybrids. The approach is expected to minimise the influence of confounding factors such as differences in soil moisture or seed damage by pests and diseases. Therefore, temperature thresholds (Min T) and temperature responses (Slope) can be considered as mainly driven by soil temperature and the cold tolerance of the hybrid when sown under optimum soil bed moisture and low pest conditions. Results show that below 13°C losses can be significant. In Fig. 1b, differences between hybrids were tested for Min T and Slope, i.e. the threshold of soil temperature below which emergence starts to be reduced and the hybrid's tolerance to cooler soil temperatures. Some hybrids (F) showed cold tolerance and small seed losses (~95 % establishment) at 13 °C or higher soil temperatures. Other hybrids also showed small seed losses, though only when sown at about 15 °C or higher (D and G). Hybrid E showed some cold tolerance and some seed losses (85 % establishment). Some hybrids (B) only had high establishment rates above 16 °C.

3.2. *Yield components*

The combination of sites, times of sowing, and the use of supplementary irrigation created highly contrasting environments (Fig. S1), yielding between <0.5 t ha^{-1} to about 10 t ha^{-1} (dry basis) (Table 2 and Fig. 2a). Across environment yields (i.e., average yield across the G×M combinations for each environment), treatment yields varied ~60 % between the bottom and top yield deciles of hybrid and plant population combinations. This yield variation translated into a ~5.5-fold change in water use efficiency (Fig. 2b). Environment yields were weakly related to total plant available water (initial soil water plus in-crop rainfall), indicating that other environmental factors in addition to water availability were active, though the summer-sown crops tended to have lower values of water productivity (Fig. 2c).

The harvest index (Fig. 3a) tended to be larger for the early and spring-sown crops. Grain number per unit of area was the main determinant of grain yields and of the differences between early, spring, and summer-sown crops, while the early-sown crops showed consistently larger grain sizes (Fig. 3b).

Significant G×E (hybrids and environment) and E×M (environment and plant population) were observed for total biomass, grain yield and most yield components (Fig. 4a and b). G×M (hybrid and plant population) interactions were only observed for the yield of the main stems and for the grain numbers on the main stems, and only in the first season (Table 2). The main response to plant population was that of consistently lower yields for the lowest plant population across all levels of environment yield (Fig. 4a). Hybrid B performed particularly well in environments yielding less than 2000 kg ha^{-1}, and hybrids E and G in environments yielding more than 4000 kg ha^{-1}. The rest of the hybrids performed similarly across the whole range of environment yields (Fig. 4b).

The first two dimensions of a biplot, including yield components and environmental covariates, explained 73 % of the total variance in the dataset (Fig. 5 and Table S2). For the different sowing times, different environmental covariates were related to different yield components. The above-ground biomass (ABG), yield (Yield), and grain number (GN) were associated with higher values of total plant available water (TPAW) with the spring sowings. Grain quality parameters: grain weights and grain proteins were associated with higher values of the normalised photothermal quotient (NPTq, Rodriguez and Sadras, 2007), and seed set (SeedSetStress, Singh et al., 2015) associated with the early sowing, and negatively related to soil and air temperature and solar radiation. Table S2 shows the correlation coefficient and the *p*-value of the variables that were significantly correlated with the loadings from

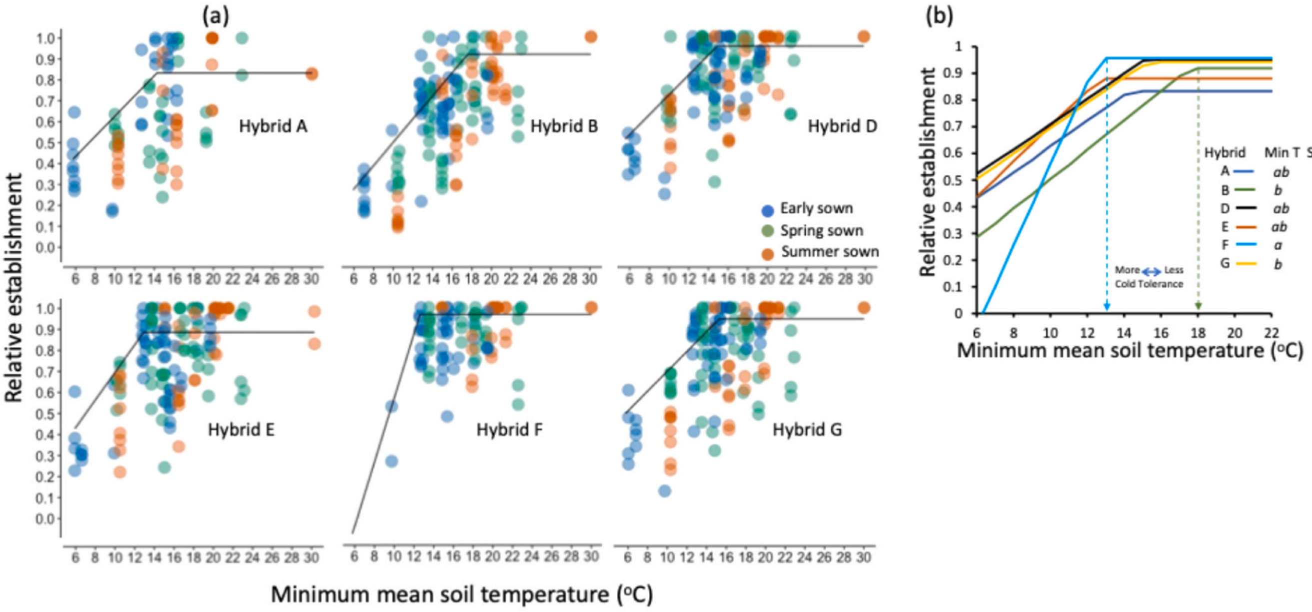

Fig. 1. Relative crop establishment, i.e., established plant population relative to the target plant population, as a function of the minimum mean soil temperature (9 am) at sowing depth during the first week after sowing (a) and (b) fittings in (a) plotted for comparison purposes between hybrids. In (b), *MinT* and *Slope* were derived from the fitting of a linear & plateau function through the 90th percentile of relative establishment values, using the function nlsLM in R. 90th percentile values were used to minimise the influence of limiting factors other than mean soil temperatures at sowing depth, e.g., low moisture, insect damage, diseases, etc. Difference letters for MinT and Slope in (b) indicate significant differences (t-tests p<0.05). In (a), blue circles are for early sown, green for spring sown and red for summer-sown crops. In (b) the different colour lines show the different.

Table 2
P-values obtained from the Wald tests for each trait by exploring the factorial combination of 32 environments (E) i.e., site and times of sowing, four target plant populations (M), and eight hybrids (G).

All sites 2018/2019 season							
	G	M	E	G×E	E×M	G×M	G×E×M
AGB	<0.0001	<0.0001	<0.0001	<0.001	<0.001	0.13	0.79
Yield	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.37	0.92
MSY	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0005	0.23
TiY	<0.001	<0.001	<0.001	<0.001	<0.001	0.051	0.87
MSGN	<0.0001	<0.0001	<0.0001	<0.001	<0.0001	<0.001	0.29
TiGN	<0.0001	<0.0001	<0.0001	<0.001	<0.0001	0.25	0.71
GN	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.65	0.63
MSGW	<0.0001	0.3	<0.0001	<0.0001	<0.0001	0.057	0.05
TiGW	<0.001	<0.01	<0.001	<0.001	<0.001	0.09	0.05
GW	<0.001	<0.05	<0.001	<0.001	<0.001	0.06	0.05
Prot	<0.001	<0.001	<0.001	<0.001	<0.001	0.37	0.92
All sites 2019/2020 season							
AGB	<0.0001	0.33	<0.0001	<0.0001	0.13	0.35	0.79
Yield	<0.0001	0.38	<0.0001	<0.0001	<0.05	0.69	0.73
MSY	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.51	<0.05
TiY	<0.0001	<0.0001	<0.01	<0.0001	<0.001	0.75	0.34
MSGN	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.49	0.71
TiGN	<0.0001	<0.0001	<0.05	<0.0001	0.1	0.24	0.13
GN	<0.0001	0.24	<0.0001	<0.0001	<0.0001	0.93	0.62
MSGW	<0.0001	<0.0001	<0.0001	<0.0001	0.15	0.89	<0.05
TiGW	<0.0001	<0.01	<0.001	<0.0001	<0.05	0.24	<0.01
GW	<0.001	<0.0001	<0.05	<0.001	0.1	0.24	0.13
Prot	<0.001	0.24	<0.001	<0.001	<0.001	<0.001	<0.05

G=hybrid; M=plant population; E=combination of sites and times of sowing; AGB = biomass; Yield = total yield; MSY = main stem yield; TiY = tiller yield; MSGN = main stem grain number; TiGN = tiller grain number; GN = grain number; MSGW = main stem grain weight; TiGW = tiller grain weight; GW = grain weight; Prot = grain protein (%).

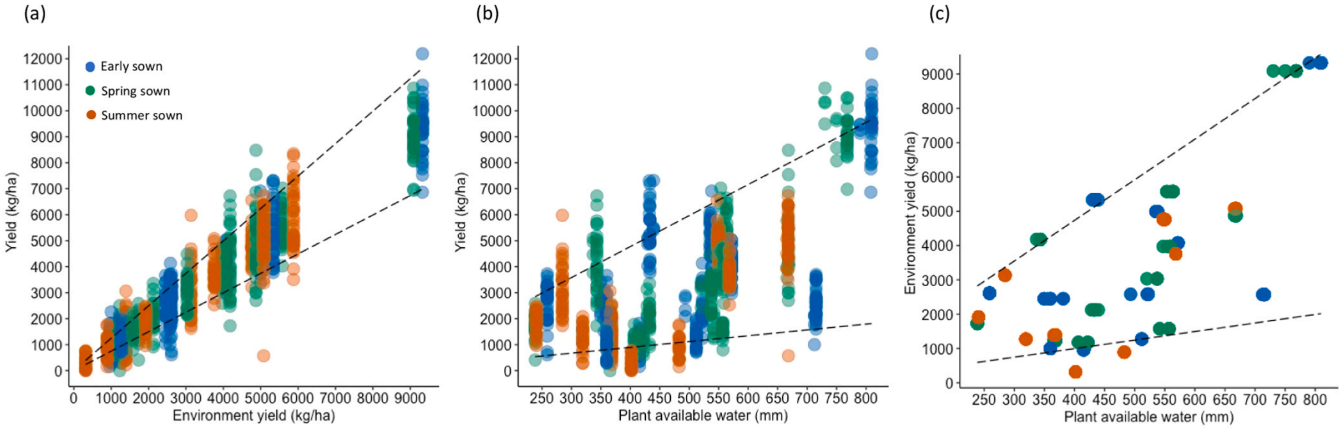

Fig. 2. Grain yields (kg ha^{-1}) (empirical Best Linear Unbiased Estimators) as a function of environment yields i.e., average of the estimated treatment (G×M) means for each environment (a); plant available water (mm) i.e., initial soil water plus rainfall, plus irrigation moisture (b); and environment yield (kg ha^{-1}) versus plant available water (c) (French and Schultz (1984), for three times of sowing "early", "spring" and "summer", and a combination of hybrids and plant densities, over two years of trials 2018–2020 across eastern Australia. Dashed lines were fitted through the deciles 9 and 1, in (a) $y_{(P=0.9)} = 1.25x$ and $y_{(P=0.1)} = 0.75x$; in (b) $y_{(P=0.9)} = 12.0x$ and $y_{(P=0.1)} = 2.2x$; and in (c) $y_{(P=0.9)} = 12.0x$ and $y_{(P=0.1)} = 2.5x$. Transparency was used to help with overlapping points.

the first two principal components. Grain yield and environment yield were primarily associated with above-ground biomass and grain weight and most correlated with the first dimension in the biplot (Table S2). Environmental covariates associated with the summer sowing times were associated with the second dimension and included maximum and minimum temperatures and solar radiation as well as per cent screenings (per cent of grains smaller than 2 mm).

3.3. *Determinants of final grain number and grain yield*

Observed grain numbers (eBLUEs) were affected by both water and heat stresses in different ways across early, spring, and summer-sown sorghum. Calculated values of SeedSetStress % (Singh, et al., 2015) were highest for the early sown crop, followed by the spring and summer sowing times (inset in Fig. 6a). The lowest values of SeedSetStress% were in the summer-sown crops, and were also associated with severe terminal water stresses, as per the simulation of stress environments with APSIM (Stress environments 4 and 5) (Fig. 6a and b). Fig. 6b shows that summer crops were predominantly affected by severe terminal stresses and had primarily low seed set values. Even though early and spring-sown crops were exposed to terminal stress, most of the crops showed high values of seed set, indicating stress avoidance. Early and spring-sown crops also had a high frequency of no or mild stresses.

For the complete MET dataset, very small differences in grain yield were observed between sowing times (Fig. 7a). However, when the data was partitioned into sites and years where heat stress around flowering was present, i.e., a calculated SeedSetStress value lower than 40 and 50 % (inset in Fig. 6a), the yield of the early sown crops was much larger

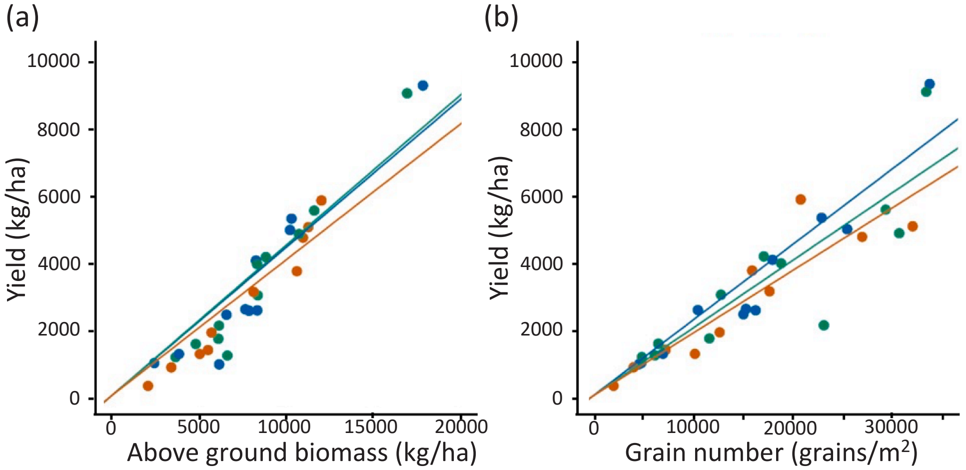

Fig. 3. Grain yields (kg ha^{-1}) (empirical Best Linear Unbiased Estimators (eBLUEs)) as a function of above-ground biomass (kg ha^{-1} eBLUEs) (a), and (b) grain yield as a function of grain number (grains m^{-2} eBLUEs). The regression lines in (a) are $Yield\_Early = 0.44*AGB$, *adj.* $R^2=0.94$ $p<0.001$; $Yield\_Spring = 0.45*AGBN$, *adj.* $R^2=0.95$ $p<0.001$; $Yield\_Summer = 0.40*AGB$, *adj.* $R^2=0.96$ $p<0.001$; and in (b) are $Yield\_Early = 0.22*GN$, *adj.* $R^2=0.96$ *95* $p<0.001$; $Yield\_Spring = 0.20*GN$, *adj.* $R^2=0.92$ *95* $p<0.001$; $Yield\_Summer = 0.18*GN$, *adj.* $R^2=0.95$ *95* $p<0.001$. *In (a), using the functions lsmeans and lstrends from R, the slopes were different, TOS1-TOS2* $p<0.05$, *TOS1-TOS3* $p<0.0001$, *TOS2-TOS3* $p<0.0009$; *and in (b), TOS1-TOS2* $p<0.0001$, *TOS1-TOS3* $p<0.0001$, *TOS2-TOS3* $p<0.0009$.

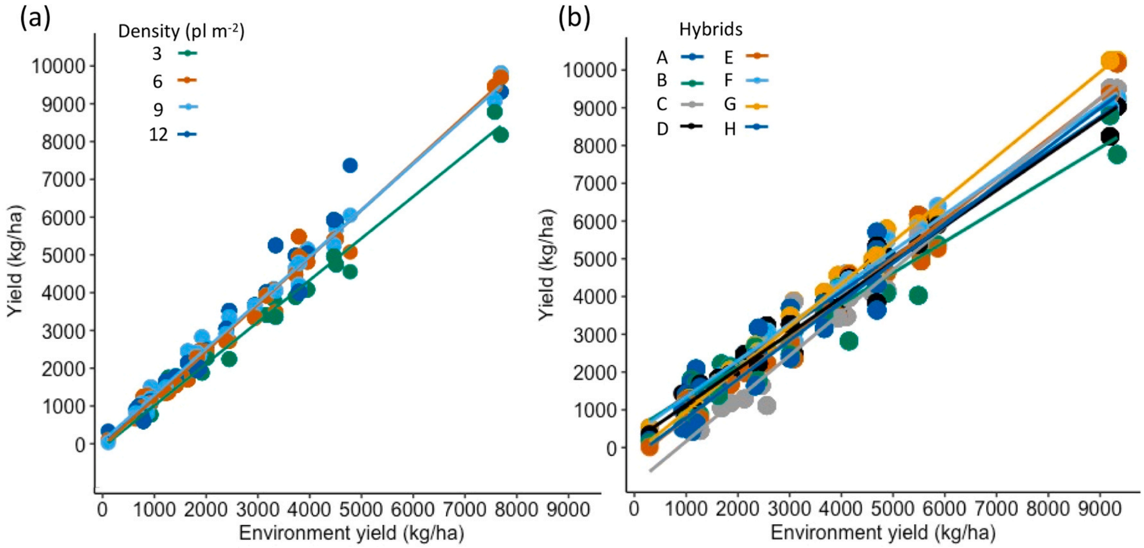

Fig. 4. Environment yield plotted against grain yield (empirical best linear unbiased estimators) for the (a) M×E (a) (b) G×E (b) interaction. Dashed lines show regression lines through the origin for deciles 1 and 9. In (a), regression lines are $y_{(Density=3)}=0.90x$ *adj.* $R^2=0.99$ $p<0.001$; $y_{(Density=6)}=1.02x$ *adj.* $R^2=0.99$ $p<0.001$; $y_{(Density=9)}=1.03x$ *adj.* $R^2=0.99$, <0.001; $y_{(Density=12)}=1.02x$ *adj.* $R^2=0.99$, <0.001. In (b), regression lines are $y_{(Hybrid=A)}= 1.06x$ *adj.* $R^2=0.97$ $p<0.001$; $y_{(Hybrid=B)}=0.93x$ *adj.* $R^2=0.98$ $p<0.001$; $y_{(Hybrid=C)}=0.95x$ *adj.* $R^2=0.98$, <0.001; $y_{(Hybrid=D)}=0.98x$ *adj.* $R^2=0.99$, <0.001; $y_{(Hybrid=E)}=1.02x$ $R^2=0.99$, <0.001; $y_{(Hybrid=F)}=1.03x$ *adj.* $R^2=0.99$ $p<0.001$; $y_{(Hybrid=G)}=1.09x$ *adj.* $R^2=0.99$ $p<0.001$; $y_{(Hybrid=H)}=0.95x$ *adj.* $R^2=0.95$ $p<0.001$. Tests of slopes are presented in Table S3 and S4.

than that of spring (Fig. 7b) and summer (Fig. 7c) sown crops.

3.4. PSIM simulations

The capacity of APSIM-Sorghum to simulate the tested G×M combinations, sites and years is presented in Figures S2, S3 and S4. Considering that most of the trials were conducted on farmers' fields, the capacity of APSIM to simulate these trials was acceptable and comparable to those in the APSIM-Sorghum documentation (https://www.apsim.info/documentation/model-documentation/crop-module-documentation/sorghum/).

Even though total plant available water was similar between the early and spring-sown crops (Fig. S1c), the simulated median water use between flowering and maturity was larger in the early-sown crop, followed by the spring and summer-sown crops (Fig. 8). Small differences in crop water use were simulated between emergence and seven leaves, and seven leaves and flowering.

3.5. Simulated risk of heat stress and frost damage

For the early sowing dates, the number of days between sowing and flowering shortened just one month for ~3 month delay in sowing. Across eastern Australia, sowing early or late reduced the likelihood of heat stresses (Fig. 9a, b and c). However, for the most southern locations (i.e., Liverpool Plains), the risk of frost during sensitive crop stages significantly increased for sowings after the 15th of December and in the Darling Downs for sowings before the 15th of August. For the most northern region, the Central Highlands, the risk of frost damage is

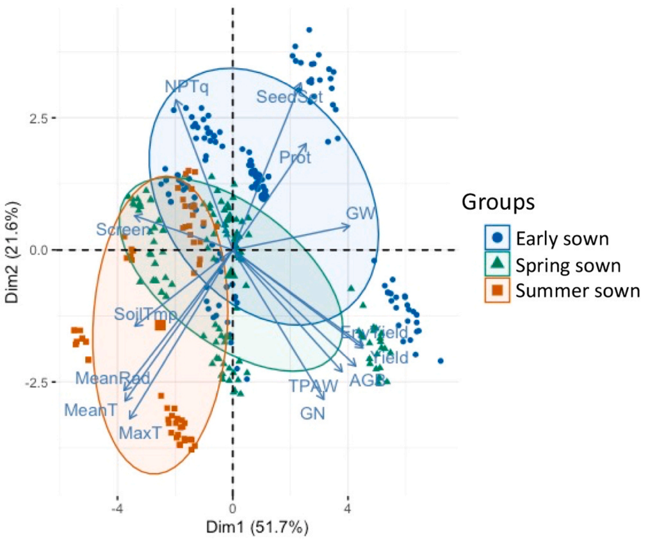

Fig. 5. Principal component analysis on above ground biomass (AGB – kg/ha), grain yield (Yield – kg/ha), grain number (GN – g m^{-2}), grain weight (GW – g 100 $grains^{-1}$), percent screenings (Screen - %), grain protein (Prot - %), and environmental covariates, total plant available water (TPAW - mm 0–1.2 m), environment yield (EnvYield – kg ha^{-1}), seed set (SeedSetStress - %, as in Singh et al., 2015), mean normalised photothermal quotient between floral initiation and flowering (NPTq - MJ m^{-2} d °C kPa, as in Rodriguez and Sadras, 2007), mean soil temperature at sowing depth a week after sowing (SoilTmp, °C), mean solar radiation (MeanRad – MJ m^{-2} d^{-1}), mean air temperature (MeanT - °C), and maximum temperatures (MaxT - °C) from sowing to maturity. Concentration ellipses are just grouping the three times of sowing for easier visualisation.

negligible, and the largest reduction in the likelihood of heat stresses was for sowings between June and July.

4. Discussion

Adaptation to more frequent and intense heat and drought stresses in summer cereals will require a combination of genetic and agronomic solutions that increase tolerance and or avoid the occurrence of stresses during critical crop stages. Here, we showed that early sowing of sorghum, a summer cereal, in late winter and early spring into cool and moist soils has the potential to reduce the likelihood of heat stresses around flowering and terminal drought stresses (Fig. 6) and maintain yields during the hottest years (Fig. 7b and c). Though sowing sorghum, a summer crop, into soils cooler than 13°C is likely to affect crop emergence (Fig. 1). Other advantages include the transfer of water use to grain filling stages (Fig. 8) that are likely to result in increased grain quality parameters, e.g., grain weight and grain protein (Table 2 and Figs. 3 and 5).

Avoiding the overlap between crop-sensitive stages around flowering and the hottest times in the year should be an obvious option to minimise grain set losses due to pollen sterility (Reynolds et al., 2016). However, sorghum is a subtropical crop known to be affected by temperatures below 15°C during germination and emergence, early vegetative, and reproductive stages (Casto et al., 2021; Emendack et al., 2021; Maulana and Tesso, 2013). Existing guidelines recommend sowing sorghum when soil temperatures are between 15 and 19°C and increasing and the likelihood of frost events after floral initiation (~7 leaves) is low. Sowing sorghum into cold soils can result in delayed emergence, patchy stands, increased weed competition, and yield penalties (Emendack et al., 2021). Paradoxically, sorghum appears to have been undirectedly selected against chilling/cold tolerance, as the trait is linked to poor grain quality traits such as high concentration of tannins, as well as tall stature and propensity to lodging, and open panicles in Chinese sorghums (Marla et al., 2018). Our results show that sowing sorghum early into soils at 13°C or higher should be feasible with small or no reduction in plant stands (Fig. 1a) or yield (Fig. 7a). Differences in cold tolerance between the small number of Australian commercial hybrids tested here can be of significance. This is because a difference in soil bed temperatures between 13°C for hybrid F and 18°C for hybrid D, in Fig. 1, can represent having to delay sowing by ~15–20 days, with loss of soil bed moisture, and eventually loss of sowing opportunities (Rodriguez et al., 2018).

Our results also show that at the hottest sites and years, early sown crops were able to produce higher grain yields (Fig. 7b and c) while reducing the likelihood of severe terminal stresses, i.e., stress environments 5 and 4 (Fig. 6b). This is most likely associated with the transfer of water use from vegetative to reproductive stages (Fig. 8) and the enhanced contribution of tillers to final grain numbers in early sown crops.

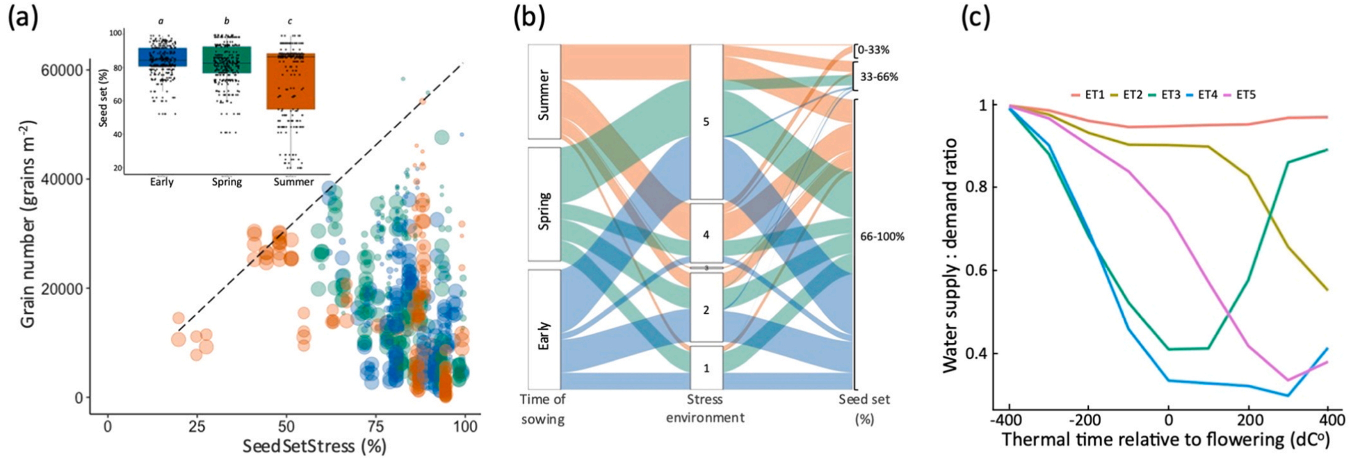

Fig. 6. Observed grain numbers (eBLUEs) versus calculated SeedSetStress (%) (a). In (a) the increasing size of the circles represents the stress environment type as simulated by APSIM (Environment Types 1= small circles (no stress); and increasingly larger symbols represent more severe stresses or stresses of different dynamics, as in Hammer et al., (2014). In (a), the inset shows boxplots of the calculated SeedSetStress (%) for the early, spring and summer-sown crops. The dashed line in (a) is a p=0.99 quantile regression of the form y=x * b, representing the potential grain number under no (heat or water) stress. Transparency was added to the graph to facilitate interpretation. In (b), the Alluvial graph shows the influence of the time of sowing on the frequency of stress environments and the values SeedSetStress (%) across the thirty-two simulated environments. In (c) the stress environments 1–5 are defined as in APSIM-Sorghum. ET1 and 2 indicate low and mild terminal water stresses, ET3 and 4 more severe stresses around flowering, and ET5 severe terminal stresses.

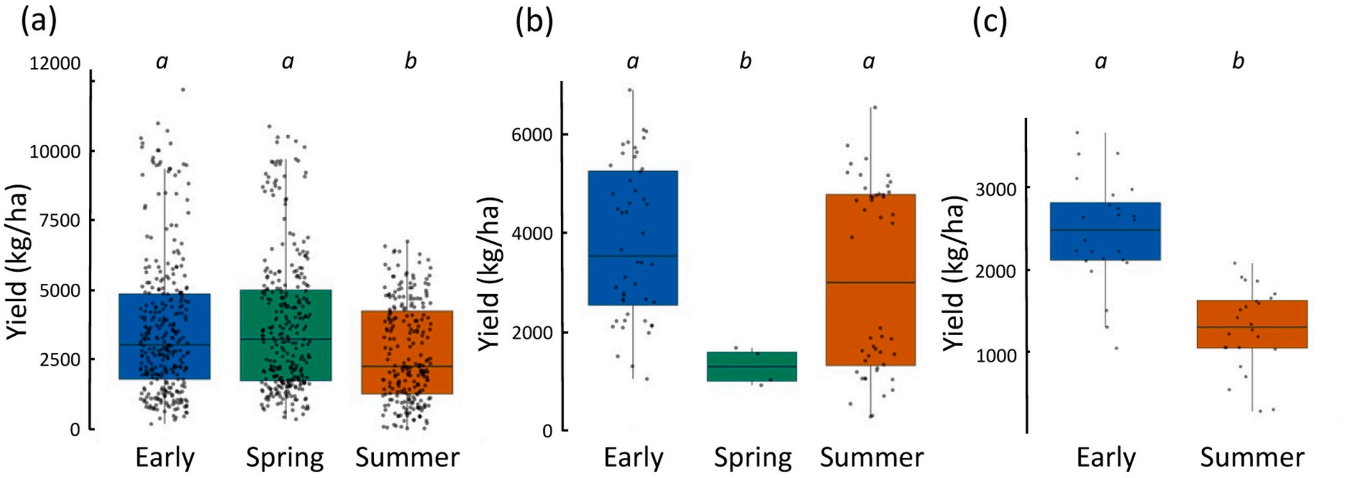

Fig. 7. Observed grain yields (eBLUEs) for the collective data set i.e., all sites and years (a), and for those years having SeedSetStress % values lower than 50 % (b), and lower than 40 % (c) (see inset in Fig. 6a).

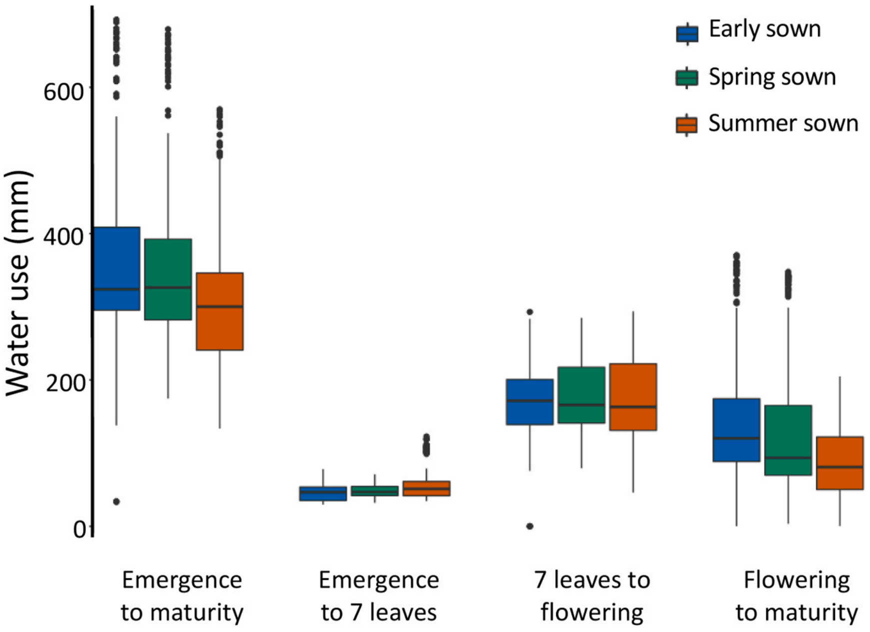

Fig. 8. Boxplots of simulated crop water use between emergence and maturity, emergence and seven leaves (floral initiation), seven leaves and flowering, and flowering to maturity for early, spring and summer-sown sorghum from the simulation of all trials in Table S1.

Significant E×M and G×E interactions were present on yield and most yield components, indicating the potential to optimise the matching of hybrids to environments or population densities to sites and expected seasonal conditions (Rodriguez et al., 2018; Rotili et al., 2020). Fig. 4a shows that up to 1 t ha^{-1} of yield would be missed if a low plant population is used in high-yielding environments, with no significant risk of yield loss in poor-yielding environments. The different hybrids showed differences in yield across environments, with some hybrids performing well in the higher-yielding environments and others in poorer-yielding environments (Fig. 4b). Similar plastic responses with some of the same hybrids were previously found by Clarke et al. (2018). E×M and G×E interactions are plastic phenotypic responses, i.e., "the amount by which the expressions of individual characteristics of a genotype are changed by different environments'' (Bradshaw, 1965), also discussed in evolutionary terms (Sadras, 2007).

However, even though a large number of G×M combinations (and yield environments) were tested here, no significant G×M or G×E×M interactions on yield or yield components were present (Table 2). This contrasts with the vast *in-silico* crop design (G×M) literature (Cooper et al., 2023; Hammer et al., 2014; Rodriguez et al., 2018). Disparities between *in-silico* and *in-vivo* results could be attributed to data quality deficiencies from on-farm experimentation, the lack of phenotypic diversity in Australian commercial hybrids, or, most likely, the lack of readiness in available modelling tools to simulate G×E×M interactions (Stöckle and Kemanian, 2020; Wang et al., 2019). In this work, significant effort was invested in the development and application of uniform protocols for trial design, data collection and analysis across multiple sites and years, while to a point, the APSIM model was able to reproduce the empirical results (Figs. S2, S3 and S4). We do not discard the possibility that some of the trials might have been affected by factors outside our control e.g., un-noticed pests or diseases. Our results show highly significant yield differences between the tested hybrids when averaged across all environments and all target plant populations, as well as for most yield components across both years of trials ($p<0.0001$, Table 2), indicating that phenotypic differences between hybrids were present. Some of the hybrids in this dataset were also present in our

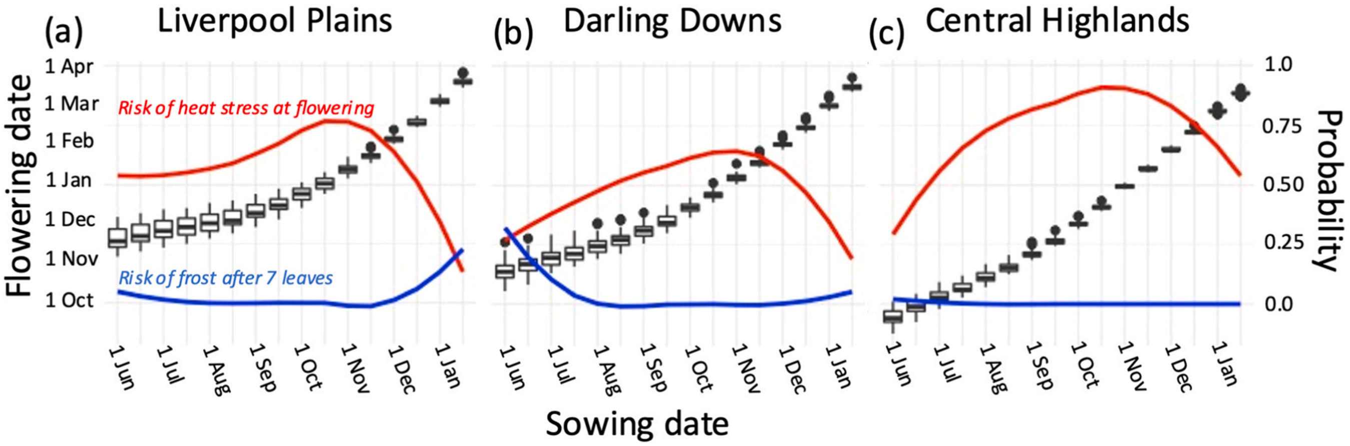

Fig. 9. Boxplots of simulations of flowering dates for MR Buster sown at fortnightly intervals between the 1st of June and the 15th of January for the period 1970–2018 (n=48), and the likelihood of frost (blue line) and heat stress (red line) events, at the Liverpool Plains – Breeza in NSW (a), the Darling Downs – Dalby QLD (b), and the Central Highlands – Emerald QLD (c), Australia. Simulations were run assuming sorghum was sown after a wheat crop that at harvest left 20 % of plant available water in the soil profile. Simulations started on the first of January every year.

previous research (Clarke et al., 2018; Zhao et al., 2022 and 2024; and Mumford et al., 2023) and showed similar results across similar environments, agronomic management and yield environments. The use of crop models and *in-silico* analyses remains an important research tool. Models are a repository of knowledge, and their use has value in ex-ante foresight and predictive analyses to inform practice change (Clarke et al., 2019; Rodriguez et al., 2018) and in the integration of crop models with genome prediction tools to support plant breeding (Messina et al., 2009; Wang et al., 2019). Some of the most obvious critical gaps in GxExM modelling have been recently reviewed by (Stöckle and Kemanian, 2020). In addition to those identified before, we propose that areas requiring improved understanding should include the modelling of adaptive phenotypic plasticity (Via et al., 1995) in multi-environment G×M experimentation (Clarke et al., 2019; Sadras et al., 2013; Trentacoste et al., 2011) for highly plastic crops such as sorghum. This is important because depending on (drought) stress dynamics, sorghum is known to be able to compensate for canopy size, root angle distributions (Hammer et al., 2009), root growth and soil water uptake (Singh et al., 2012; Zhao et al., 2022 and 2024), yield (Clarke et al., 2019), and grain weights (Gambín and Borrás, 2007). Most likely, crop models that do not account for these plasticities will be more likely to exaggerate the presence of G×M interactions when commercial varieties, instead of virtual or actual isogenic lines, are modelled.

At the cropping system level, the inclusion of early sown sorghum in the crop sequence seems simple, though its implementation and consequences are not. A sorghum crop sown early in late winter will have a longer emergence period that will increase the likelihood of some seeds running out of soil moisture and the risk of soil insects or disease-damaging seeds resulting in patchy plant stands with implications for weed competition, crop evenness and yield (Fig. 1). On the upside, early sowing widens sowing windows, may increase the opportunities for managing ground cover in regions where spring rainfall is highly variable or infrequent. Early sowing is also likely to increase cropping intensity, as earlier harvests will increase the likelihood of double cropping after a short summer fallow, particularly in summer rainfall-dominant environments (Sadras and Rodriguez, 2007). There might also be significant benefits at the farm level through increased confidence in the inclusion of sorghum in the rotation, particularly in marginal environments more prone to severe terminal drought stresses, having additional cropping opportunities, broadening sowing windows and easing of logistical time constraints around sowing and harvest due to less overlap between winter and summer crop time requirements.

5. Conclusions

Early sowing of sorghum can reduce the likelihood of heat stresses around flowering as well as the likelihood of terminal drought stresses. Advantages include reduced yield losses in the hottest years and a transfer of water use to grain filling stages, likely to increase grain yield and improve grain quality parameters. However, for the practice to be de-risked, there is a need to increase cold and chilling tolerance in sorghum or to identify interventions that enhance seed germination and seedling early vigour when sown into cold soils. Despite the irony, we propose that to increase adaptation to heat stress around flowering, breeders should consider including early cold tolerance as a target trait in sorghum breeding programs.

CRediT authorship contribution statement

Mark Hellyer: Methodology. **Daniel Rodriguez:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Jane Auer:** Methodology. **Darren Aisthorpe:** Methodology. **Joe Eyre:** Methodology. **Ian Broad:** Methodology. **Peter de Voil:** Writing – review & editing, Formal analysis, Data curation. **Loretta Serafin:** Writing – review & editing, Investigation, Data curation. **Dongxue Zhao:** Writing – review & editing, Formal analysis. **Michael Mumford:** Writing – review & editing, Formal analysis.

Declaration of Competing Interest

Declare no conflict of interest.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2024.109592.

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