Understanding the diversity in yield potential and stability among commercial sorghum hybrids can inform crop designs

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ABSTRACT

Reducing yield gaps in dryland cropping depends on our capacity to identify combinations of genetics (G) and management (M) (i.e. crop designs, G × M) that best suit site and seasonal conditions (the environment, E). We combined empirical and modelling approaches to characterise and explain the yield stability and yield potential of commercial sorghum hybrids when grown under a range of agronomic managements and environments yielding between 3 and 12 t ha^{-1}. The empirical data includes two seasons (2014-15 and 2015–2016) of on-farm and on-research station trials conducted across six sites in Queensland, Australia. Agronomic management treatments included plant density, row configuration, level of irrigation and fertiliser inputs, and time of sowing. Six hybrids contrasting in maturity and tillering type were characterised relative to the industry standard MR-Buster in terms of yield potential, yield stability (b_i), and an expected utility index that combines both indices. A medium-late maturity and high tillering hybrid (MR-Scorpio), had the highest utility rank and showed high b_i values due to high tiller productivity. A variety of significant row spacing and configuration, and plant density effects on yield were observed, but these were inconsistent across sites and seasons. A long-term simulation experiment across contrasting environments was used to identify hybrid traits and managements capable of modifying yield stability. Combined with the empirical data, the simulations suggest hybrids showing high biomass production and multiple productive tillers can increase the response of yield to the productivity of the environment, whereas reducing the thermal time to floral initiation may increase the stability of yields across environments. Expected changes in hybrid rank due to such G × E interactions, along with the complex effects of management on yield, increase the need to match crop design to specific sites and seasons. The value of targeted crop design depends on the diversity of traits among commercial hybrids and the availability of a skilful seasonal climate forecast to allow farmers to match hybrids and management to prevailing and expected seasonal conditions.

1. Introduction

Increasing the productivity of dryland cereals is one of several strategies that will improve global food security (Stewart and Lal, 2018). With a reputation for drought tolerance (Blum, 2004) and recent yield gains (Potgieter et al., 2016), sorghum shows potential to contribute significantly to food production in semi-arid environments, including sub-Saharan Africa where food insecurity has increased in recent years (FAO et al., 2017). For the dryland cropping regions of Australia, between 1983–2011 shire-level sorghum yields showed annual increases of *ca.* 44 kg ha^{-1} year^{-1}, a gain of 2.4% year^{-1} (Potgieter et al., 2016). These values compare to global yield increases of *ca.* 1.5% for maize, and *ca.* 1% for rice, wheat and soybean (Ray et al., 2013;

Fischer et al., 2014). In addition, sorghum yield gains in Australia appear to have been higher in water-stressed (*ca.* 58 kg ha^{-1} year^{-1}) than non-water-stressed environments (*ca.* 23 kg ha^{-1} year^{-1}) (Potgieter et al., 2016). Yield gains in dryland cropping need to be understood as the result of gains from breeding, improvements in agronomic management, the cropping system, and their interactions. In Australia, emphasis on breeding for midge resistance and 'stay-green' (Henzell and Jordan, 2009); the widespread adoption of conservation agriculture practices (Radford et al., 1995; Brouder and Gomez-Macpherson, 2014); agronomic managements that minimise water use during vegetative stages (Whish et al., 2005); and rotations with legumes (Sadras et al., 2016), are likely to be responsible for relatively high yield gains in dry environments.

Table 1
Trial sites, experimental designs, treatments and minimum, mean and maximum oven dry yields. Additional information is provided in Table S1.

Site	Geographic coordinates (latitude, longitude)	Sowing dates	Experiment design (replications)	Plot length (m)	Hybrids[a]	Row spacing (m)	Config.	Targeted plant density (pl m^{-2})	Water regime[b]	Yield (t ha^{-1}) Min.	Mean	Max.
Brookstead	−27.76, 151.49	27/9/2014	Split plot (4)	100	1 – 7*	0.75	Solid	4.8, 7.2, 9.6, 12	R	6.6	8.8	12.6
Gatton	−27.55, 152.33	28/10/2014 6/10/2015	Split plot (3)	6	1 – 3, 6, 7	0.75	Solid	7	I or R* I	8.6 5.5	9.8 7.6	12.8 10.9
Warwick	−28.21, 152.46	30/10/2014 23/12/2014	Complete block (3)	4	1 – 3, 6, 7	0.76	Solid	5	I	10.0 6.3	10.4 7.5	11.0 9.0
Condamine	−26.94, 152.08	10/9/2015	Split plot (3)	12	1 – 3, 6	1	Solid, single skip*	4, 6, 8	R	3.0	3.9	5.0
Emerald	−23.54, 148.18	18/2/2016	Split plot (3)	12	3 – 6	1	Solid, single skip*	4, 6, 8	R	3.6	4.4	5.2
Pittsworth	−27.68, 152.46	25/9/2015	2 × complete block (3)[c]	14	6, 7	1	Solid Single skip	4, 6, 8	R	4.5	6.1	6.8

* Indicates the treatment assigned to the main plot in a split-plot design. See table 2 for the hybrid identification. [a] Refer to reference numbers in Table 2. [b] I = irrigated and rainfed, R = rainfed. [c] Each block featured solid or single skip row configuration as a treatment.

Genetic traits that increase drought tolerance, or risk averse agronomic managements that minimise losses in dry seasons, may also limit yields in high yielding environments. For example, while stay-green and low-tillering hybrids may be associated with yield benefits in low yielding environments (Tolk et al., 2013), higher plant densities would be required to increase yields in more favourable environments (Jordan et al., 2012; Hammer et al., 2014). Similarly, wide or skip rows and low plant densities can be used to shift water use from vegetative to reproductive stages but reduced yield in wetter seasons (Steiner, 1986, 1987). Risk averse nitrogen fertilisation strategies have also been shown to underpin the balance between profits and risks in variable climates (Sadras et al., 2016). In sorghum, combinations of genetic (G) traits (e.g. maturity, tillering and stay-green) and agronomic managements (M) create crop designs (G × M) that show contrasting responses across environments (E) (Hammer et al., 2014). This calls for a better understanding of how hybrid characteristics and agronomic managements could be used to increase crop productivity across variable environments.

A long-standing approach for characterising hybrid performance across environments is joint regression analysis (Finlay and Wilkinson, 1963). This method quantifies G × E interactions by modelling individual hybrid yield as a linear function of a continuous variable representing the effect of the environment:

$$GE_{ij} = b_i E_j + d_{ij} \qquad (1)$$

Where, GE_{ij} is the effect of the interaction between the i-th genotype and j-th environment (E_j), b_i is the linear regression coefficient for the i-th genotype and d_{ij} is the deviation associated with the i-th genotype in the j-th environment. The term E_j is often quantified by examining mean yield for each experimental site, referred to as the environmental index (Yates and Cochran, 1938). Hybrids having $b_i > 1$ have an above-average sensitivity to changes in E_j and are expected to be more productive in high yielding sites and seasons; genotypes having $b_i \approx 1$ have a responsiveness close to the group mean; and genotypes having $b_i < 1$ are 'stable': they are relatively insensitive to E_j and may be well suited to producing reliable yields in low-yielding sites and seasons. The yield stability parameter does not convey yield, so b_i is often used to evaluate genotypes in combination with mean yield across observations (Finlay and Wilkinson, 1963; Mutava et al., 2011). In the absence of information such as seasonal forecasts, variability across a production region will increase the demand and relative importance of broadly adapted genotypes, which have $b_i \approx 1$ and above-average yields (Finlay and Wilkinson, 1963; Chapman et al., 2000).

The main environmental determinant of productivity across Australian sorghum growing regions is crop available water during critical stages around anthesis. Water supply during this period is determined by the available soil water at sowing plus in-crop rainfall and its temporal distribution, less water evaporated from the soil or transpired by the crop (Hammer et al., 2010; Lobell et al., 2015). The particular evolution of these factors within a growing season has been used to identify a number of water stress environment types, which reflect contrasting temporal trends of the mismatch between water supply from the soil and crop water demand around anthesis (Hammer et al., 2014). Post-anthesis stresses are the most frequent, occurring in 25–60% of seasons across Australia's sorghum cropping region (Hammer et al., 2014). Simulation modelling suggests the likelihood of unprofitable yields could be reduced if G × M combinations could be informed at sowing to match specific sites and seasons (Hammer et al., 2014; Rodriguez et al., 2018).

In this manuscript, we (i) use the concept of yield stability to quantify G × E responses of commercial sorghum hybrids known to differ in time to maturity and propensity to tiller to alternative managements when grown across a wide range of environments and seasons; (ii) parameterise the most common hybrids in a tested crop simulation model (i.e. APSIM); and (iii) use simulation modelling to quantify the sensitivity of yield stability to hybrid traits and

Table 2

List of hybrids and their seed-company defined characteristics[a].

Reference number	Hybrid	Seed company	Maturity type	Tillering type
1	MR-Taurus	Pacific Seeds	Medium-early	Moderate
2	MR-Scorpio	Pacific Seeds	Medium-late	High
3	MR-Apollo	Pacific Seeds	Late	Moderate
4	MR-Bazley	Pacific Seeds	Medium-early	High
5	Pacific MR43[b]	Pacific Seeds	Medium	Moderate
6	MR-Buster	Pacific Seeds	Medium	High
7	G33[c]	Pioneer	Medium-early	Moderate

[a] Obtained from company websites (www.pacificseeds.com.au and www.pioneerseeds.com.au) and from consultation with company representatives.

[b] Referred to herein as 'MR43'.

[c] Previously traded under the name '85G33'.

management across sites and seasons. We test the hypothesis that small differences in hybrid characteristics can result in significant changes in yield stability that are likely to be of value for informing farmers' practice and breeding programs.

2. Methods

2.1. Field trials

Field trials were sown on farmers' fields and research stations over two seasons (2014–2016) at six locations across Queensland's Darling Downs, Western Downs and Central Queensland, Australia. Trials consisted of the combination of two or three factors including hybrid, inputs (irrigation and nitrogen), plant density, and row configuration (Tables 1 and S1). The hybrid MR-Buster, released in the early 1990s, was used as a standard across all trials. The six other hybrids included in this analysis are described in Table 2.

At some sites, soil moisture and nitrogen at sowing were measured (0–1.8 m depth, 0.3 m increments, moisture determined gravimetrically, nitrogen by an external provider). Crops were sown into moist soil using a Monosem double-disc opener, vacuum precision planter within the recommended sowing window at each site. The dimensions of the experimental plots were four rows by 4–100 m. Crops were fertilised at recommended rates to avoid nutrient limitations, and were kept free of weeds, pests and diseases. Daily maximum and minimum temperature, total radiation and rainfall were recorded on-site using automatic weather stations (Vaisala HMP60 temperature and relative humidity probe, Apogee SP-212 pyranometer and Dyacon RGTB-6 rain gauge, logged with a Campbell Scientific CR800). Yield and biomass data was obtained on samples taken at grain physiological maturity from 2 lineal metres of central rows in each plot showing uniform plant density. On each sample the number of plants, stems and heads were recorded, and panicles were separated and threshed to determine yield components. Samples were oven dried to a constant weight at 65 °C.

2.2. APSIM simulations

The APSIM simulation model (version 7.10, revision 4176) (Holzworth et al., 2014) and its sorghum module (Hammer et al., 2010) were used to (i) characterise the water stress environment at each site and treatment during the observed field seasons using the parameterisation of MR-Buster; (ii) quantify the long-term (1889–2016) frequency of water stress environments at each site for a constant crop design (MR-Buster, 5 pl m^{-2}, 1 m solid rows); and (iii) estimate the sensitivity of yield stability to hybrid trait × management combinations across a subset of the trials sites using the long-term climate records. The water stress environment type is derived from the simulated time course of the water supply/demand ratio for the period ± 400 °C days around anthesis (ET1 to ET5, (Hammer et al., 2014)). Weather data for

(i) was recorded on-site using automatic weather stations, whereas for (ii) and (iii) weather data were obtained from the SILO database (Jeffrey et al., 2001). Measured soil moisture and nitrogen were used to initiate (i), then soil moisture was adjusted to minimise the offset between observed and simulated yield across treatments within a site-season. For (ii) and (iii), soil moisture at sowing was determined by calculating the mean water content at the date of sowing from a prior long-term simulation of fallow periods (Hammer et al., 2014), fertiliser was applied at sowing, and irrigation was omitted. In (iii) the simulated sites were chosen to encompass the range in sowing windows and ET1 frequencies observed in (ii). With two exceptions, parameters used to simulate hybrid traits in (iii) were the default values for MR-Buster, and the maximum and minimum values used to parameterise the commercial hybrids (see below). For canopy size, which is a multi-parameter simulated trait, all parameter sets were used. For the number of fertile tillers per plant (*FTN*), this value was either set to zero or defined by the model for MR-Buster (a high tillering hybrid: Table 2). Management treatments for (iii) were 5 and 10 pl m^{-2}, and solid and single skip row configurations. Soil parameters at each trial site were obtained from the APSoil database (Dalgliesh et al., 2012).

Commercial hybrids were parameterised in APSIM for phenology, canopy development, yield components and growth using results from a specifically designed on-research station trial at Warwick, Queensland (Tables 1 and S1). At this trial hybrids were sown at *ca.* monthly intervals across the conventional sowing window, between September 30, 2014 and January 20, 2015 (*n* = 5). Of the tested hybrids, this analysis focuses on those well-represented across the field trials (Table 2) and present in the Warwick trial (i.e. MR-Taurus, MR-Scorpio, MR-Apollo, G33 and MR-Buster). Anthesis dates were defined as the day anthers were visible approximately halfway down the panicle of the main stem. The second and fourth crops sown were sampled to measure biomass and leaf area distribution at early grain fill, and to measure biomass and yield components at grain physiological maturity to obtain data on representative biomass partitioning across the sowing dates. After parameterising phenology and leaf size (Carberry et al., 1993), adjustments were made to radiation use efficiency (*rue*) to reduce the offset between observed and simulated biomass (Hammer et al., 2010). Observed grain number was used to adjust the sensitivity of potential grain number to simulated biomass accumulation between floral initiation and the start of grain fill (*dm_per_seed*) (Heiniger et al., 1997).

2.3. Yield stability, yield potential and expected utility

Using the field trial observations, an index of yield stability was calculated for the yield of whole plants and tillers separately. In the absence of a constant set of hybrids and treatments across all sites, the yield of MR-Buster per site × season × treatment was used to represent E_j. Whole-plant stability indices were calculated by forcing a regression through the coordinate E_j:hybrid yield of 3:3 t ha^{-1} (Fig. 1). The b_i value for tillers was forced through the origin (Fig. 1). Forcing the regressions through coordinates was done to ensure the stability analysis is performed over a similar range of E_j and to reduce bias resulting from the absence of some hybrids at some lower yielding sites. Conducting simultaneous yield stability analyses on tillers (i.e. tested hybrid versus MR-Buster tiller yield) provided a method of conceptually dissecting the contribution of tillers to whole-plant yield. While the parameter b_i describes hybrid responsiveness to the productivity of the trial site and management combination, it does not convey relative yield. For this reason, b_i was examined with respect to a measure of yield potential calculated from the ratio of each tested hybrid over E_j at every site. Furthermore, because $b_i \neq 1$ implies that relative yield changes across sites and seasons, yield potential was calculated on subsets defined by MR-Buster yields below and above 6 t ha^{-1}, which approximates the median yield across sites. This division is meaningful in applied contexts because it separates regions with yields approaching 6 t ha^{-1} (e.g. Liverpool Plains and Inner Darling Downs) (Potgieter et al., 2005) from
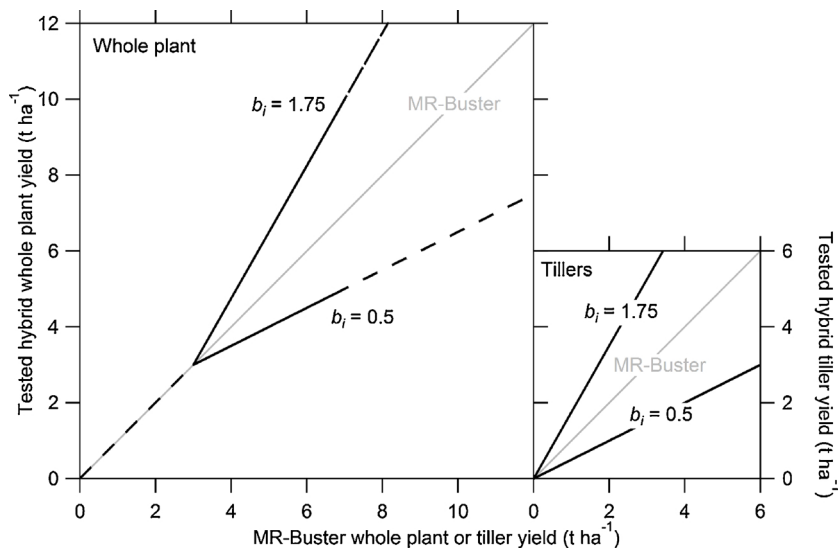
Fig. 1. The expected relationship between tested sorghum hybrids and MR-Buster yield. The grey lines indicate the values expected for MR-Buster. As explained in the text, whole-plant yields are expected to be similar between diverse hybrids and MR-Buster up to yields of *ca.* 3 t ha^{-1}. Beyond 3 t ha^{-1} the slope of this relationship (b_i, the stability parameter) may vary: the example b_i values are from multi-season simulations (Hammer et al., 2014, Fig. 9). For tillers, b_i values are repeated in the subplot, showing a linear relationship is expected between MR-Buster and tested hybrid tiller yield.
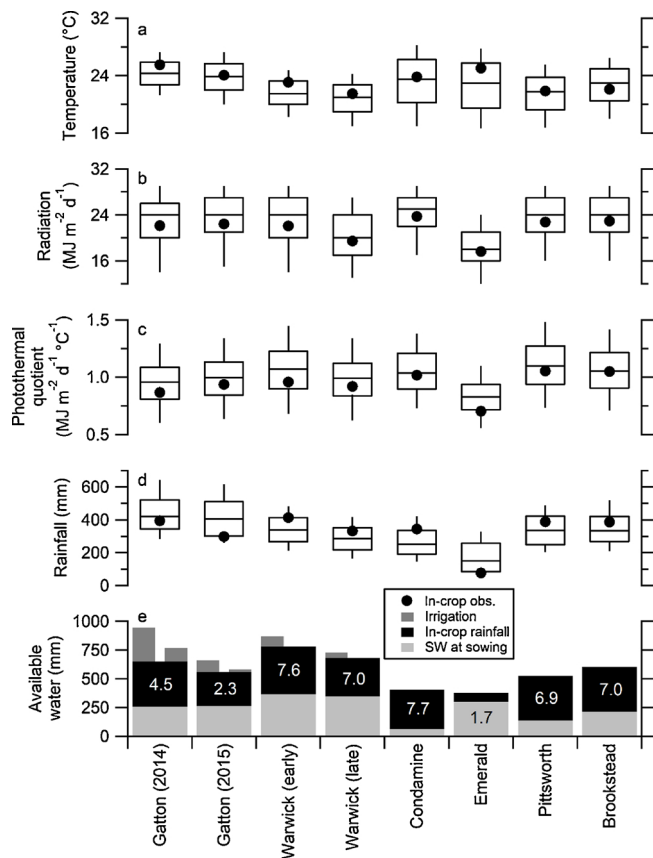

Fig. 2. In-crop and long-term (1889–2016) records of temperature, radiation, photo-thermal quotient, rainfall and available water at each trial site and season. Box and whisker plots in (a), (b), (c) and (d) show the median (central line), 25th and 75th percentiles (box), and 10th and 90th percentiles (whisker) of long-term observations during the in-crop period. The circles in (a), (b), (c) and (d) show the in-crop mean or total observations at each trial. The temperature in (a) is the mean daily temperature calculated from the daily maximum and minimum temperatures. Radiation in (b) is total global radiation per day. Values in (c) are the ratio between the values in (a) and (b). Rainfall in (d) is the total for the season. Plot (e) shows the contribution of plant available soil water (SW) at sowing (modelled), in-crop rainfall and irrigation (high or low volumes matched to high or low nitrogen inputs) to total available water. The numeric labels in (e) indicate the trial in-crop rainfall decile relative to long-term observations.

those that exceed this mark with the use of high inputs (Kamoshita et al., 1998). An approach analogous to analysing the field trial data was used to run the sensitivity analysis of parameterised traits and management treatments on yield stability.

The expected utility index (*EUI*) (Eskridge and Johnson, 1991) was used to rank hybrids on the basis of both field-determined yield stability and yield potential. This enabled the values of yield stability and yield potential to be weighted to reflect changes in their relative importance (e.g. to breeders or farmers). This weighting was quantified using a stability preference coefficient, *a*:

$$EUI = \bar{Y}_i - (a/2)[(b_i - 1)^2 S_{\bar{y}}^2 (1 - 1/q) + S_{\delta_i}^2] \tag{2}$$

Where, $\bar{Y}_i = Y_i / E_j \times \dot{E}_j$ (i.e. test hybrid yield potential by MR-Buster yield across all environments in the subset), $S_{\bar{y}}^2$ is the variance associated with E_j, q is the number of environments represented by E_j and $S_{\delta_i}^2$ is the variance associated with b_i. The value of *a* define curves of varying concavity that relate yield to the utility of yield (Eskridge and Johnson, 1991). For example, preferences towards stable hybrids are prescribed by larger values for *a*, and result in yields from stable hybrids that are valued more than identical yields from genotypes with $b_i > 1$.

2.4. Statistical analysis

Residual maximum likelihood estimation was used to model variance in the response of total biomass, yield, grain number and weight, and tiller yield, for each trial to structural (block) and fixed (treatments and their interaction) effects ($\alpha = 0.05$). Initially, all statistical tests were performed using the *ASReml* package (Butler et al., 2007) in the R environment (R Core Team, 2017). To help estimate residual variation in the field, the analyses included all hybrids tested at each site. Where the model either failed to converge treatment effects were analysed using ANOVA (using *Statistica 13*, StatSoft Inc., Dell Software, Round Rock, TX, USA). Sensitivity of simulated yield stability to modified model parameters was estimated using ANOVA (aov function in the *stats* package of R version 3.4.1).

3. Results

3.1. Environments and stress environment types

The combination of sites and seasons created a wide range of water availability, temperature, radiation environments and crop yields, representative of some of the most productive dryland and irrigated sorghum growing environments in Australia. In-crop rainfall across
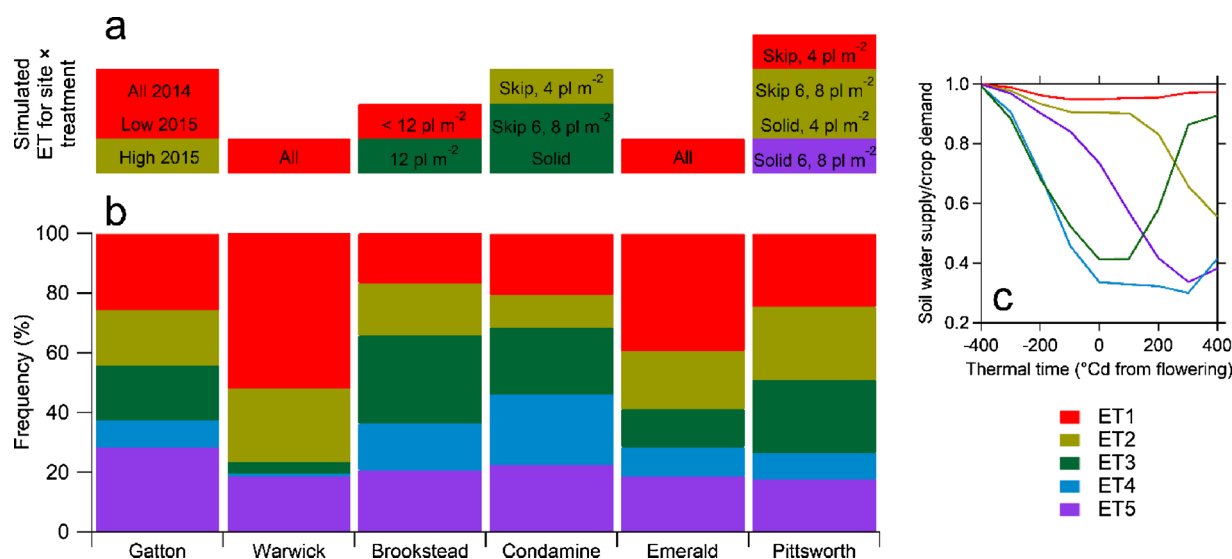
Fig. 3. Long-term (1889–2016) frequency of simulated water stress environment types for the hybrid MR-Buster at each trial site with constant agronomic management (b), and simulated environment type for MR-Buster at each site, season and set of treatments (a). The environment types as previously defined (Hammer et al., 2014) are also shown (c).

sites varied between long-term decile 2–8, and the diversity of in-crop temperature and radiation environments produced photo-thermal quotients between 0.7 and 1.1 MJ m^{-2} d^{-1} °C (Fig. 2a–c). The sum of soil moisture at sowing, in-crop rainfall and the application of irrigation supplied 580–940 mm of water to the trial sites at research stations. In contrast, the total water availability at on-farm trials sites was *ca.* 600 mm water or less (Fig. 2e). The simulation of a constant agronomic management for the hybrid MR-Buster at each site using long-term climate records generated frequency distributions of water stress environment types (Fig. 3b). Results showed that without irrigation, the highest frequencies of severe terminal stress environments (i.e. ET4 and ET5), are more likely for Gatton, followed by Condamine, Brookstead, Emerald and Pittsworth. Low water stress environments (ET1 and 2) were most frequent in Warwick and Emerald. Simulation of ETs for combinations of site, season and agronomic management (Table 1) for the hybrid MR-Buster within the trials (Fig. 3a) showed limited water stress (ET1 or 2) for Gatton (2014), Warwick, Brookstead (all but the highest density treatments), Emerald and Pittsworth (expect the higher density solid row treatments). Most treatments at Condamine, and the 12 pl m^{-2} treatment at Brookstead, were characterised by a strong water stress at anthesis that was relieved by rainfall during grain-filling (ET3). The higher density solid row treatments at Pittsworth were characterised by moderate water stress at anthesis, increasing to severe during grain fill (ET5).

3.2. Crop growth and yield

Hybrid, plant density, configuration and nitrogen treatments all showed statistically significant effects on different variables across the different trials (Table 3). Mean values for these variables are provided as supplementary data (Table S2). The only interaction between treatments was observed at Gatton during 2015 where the high input treatment interacted with hybrid for grain number and weight. Biomass production between treatments varied between 7.5 to more than 24 t ha^{-1} (Fig. 4). For all hybrids, tiller biomass responded strongly to increases in plant density, and was *ca.* 50% of the total at the largest biomass observations (Fig. 4).

Across sites, seasons and treatments, grain yields ranged between 3 to more than 12 t ha^{-1} (Fig. 5). The differences between hybrids was largest where E_j was more than 8 t ha^{-1}, and often associated with high MR-Scorpio yield (Fig. 5). At Condamine, the solid row configuration produced higher yields than the skip configuration, and at Emerald

increases in plant density had a strong positive effect on yield (Table 3). The largest yields (*ca.*12.5 t ha^{-1}) were observed for MR-Scorpio at Gatton (2014, both low and high input treatments) and at Brookstead (when sown at a high plant density, i.e. target of 9.6 pl m^{-2}). For treatments where $E_j < 6$ t ha^{-1}, the yields of all six other hybrids were similar, and only two hybrids (G33 and MR-Buster) had a substantial (> 1 t ha^{-1}) yield contribution from tillers (Fig. 5).

As expected, grain yield was primarily explained by grain number (Fig. 6b & c), though different relationships between grain number and grain weight were observed between hybrids (Fig. 6a). All hybrids showed a negative correlation between grain number and weight, but this relationship was only significant for MR-Buster ($p < 0.05$). Hybrid had a highly significant effect on grain weight in nearly every trial ($p < 0.001$) (Table 3). G33 had a large contribution of tillers to total grain number and the average grain weight was 23.7 mg, which is about 4 mg less ($p < 0.05$) than the average across the other hybrids (Fig. 6a).

Within sites, plant density significantly affected yield (Table 3), though when yield was plotted for each hybrid relative to E_j a weak (not statistically significant) yield response to plant density was observed in the range of -1 to 2% for each additional pl m^{-2}. The exception was MR-Apollo which increased its yield by about 2 ± 1% for each additional pl m^{-2} (Fig. 7). Plant density had a significant effect on fertile tiller number wherever it was applied as a treatment (Table 3). The ratio of main stem yield to total plant yield tended to increase in the lower yielding sites where fewer fertile tillers per plant were observed (Figs. 6a and 7). In higher yielding sites, most hybrids tended to produce fewer tillers than MR-Buster, which had a large proportion of unfertile tillers.

3.3. Yield stability, potential and expected utility

There was large diversity in the values of yield stability and yield potential between hybrids (Fig. 8). Some hybrids had higher values of b_i and yielded more than MR-Buster in both above and below median yielding environments (i.e. MR-Scorpio and -Apollo). Other hybrids had lower values of b_i, and yielded less than or similar to MR-Buster in both environments (i.e. MR-Taurus, MR-Bazley and G33). MR43 consistently had b_i values and yields similar to MR-Buster. Only the hybrids MR-Scorpio and -Apollo showed b_i values for tillers significantly greater than those of MR-Buster. There were no hybrids with a tiller yield potential significantly different from that of MR-Buster.

Table 3

Within-site effects of genotype, management and environment on the biomass, yield, grain number and size, and number of fertile tillers.[a,b].

Site	Year sowing window opened	Variable	Row configuration	Hybrid	Plant density	Nitrogen supply	Hybrid × nitrogen supply	Hybrid × plant density	Hybrid × row configuration	Plant density × row configuration	Hybrid × plant density × row configuration
Brookstead[c]	2014	Biomass		***	*			ns			
		Yield		***	*			ns			
		Grain number		***	*			ns			
		Grain size		***	ns			ns			
		Fertile tillers		*	***			ns			
Gatton	2014	Biomass		–		–	–				
		Yield		***		ns	ns				
		Grain number		***		ns	ns				
		Grain size		***		***	ns				
		Fertile tillers		**		ns	ns				
Gatton	2015	Biomass		**		***	ns				
		Yield		*		***	ns				
		Grain number		***		***	**				
		Grain size		***		*	*				
		Fertile tillers		***		***	ns				
Warwick	2014 (early)	Biomass		ns							
		Yield		ns							
		Grain number		ns							
		Grain size		***							
		Fertile tillers		**							
Warwick	2014 (late)	Biomass		ns							
		Yield		**							
		Grain number		ns							
		Grain size		***							
		Fertile tillers		ns							
Condamine	2015	Biomass	–	–	–			–	–	–	–
		Yield	***	ns	ns			ns	ns	ns	ns
		Grain number	***	ns	ns			ns	ns	ns	ns
		Grain size	Ns	**	ns			ns	ns	ns	ns
		Fertile tillers	Ns	*	**			ns	ns	ns	ns
Emerald	2015	Biomass	***	*	***			ns	ns	ns	ns
		Yield	Ns	ns	***			ns	ns	ns	ns
		Grain number	Ns	ns	***			ns	ns	ns	ns
		Grain size	Ns	***	***			ns	ns	ns	ns
		Fertile tillers	Ns	ns	*			ns	ns	ns	ns
Pittsworth (single skip)	2015	Biomass		ns	***			–			
		Yield		ns	*			ns			

Table 3 (continued)

Site	Year sowing window opened	Variable	Row configuration	Hybrid	Plant density	Nitrogen supply	Hybrid × nitrogen supply	Hybrid × plant density	Hybrid × row configuration	Plant density × row configuration	Hybrid × plant density × row configuration
		Grain number		**	*			ns			
		Grain size		***	ns			ns			
		Fertile tillers		**	***			ns			
Pittsworth (solid)	2015	Biomass		ns	**			ns			
		Yield		ns	*			ns			
		Grain number		ns	**			ns			
		Grain size		***	**			ns			
		Fertile tillers		ns	*			ns			

a *, ** and *** refer to $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.
b ns = not statistically significant ($p > 0.05$), and em dash (–) = data not available.
c Variance estimated using linear model ANOVA.

When evaluated using an expected utility index, hybrid ranks did not change across a wide range in weightings for the model coefficient a (0–4.15) (Eskridge and Johnson, 1991) representing preferences between yield potential and yield stability (Table 4). Hybrids MR-Scorpio then -Apollo were consistently the top ranked hybrids but there were shifts in the minor rankings. In the lower-yielding environments, MR-Taurus and G33 were ranked higher than MR43 and MR-Bazley, but the opposite was true in the higher yielding environments. MR-Buster had a moderate rank regardless of the productivity of the environment.

3.4. Hybrid trait parameterisation

Using results from the on-research station trial at Warwick, adjustments were made to the APSIM sorghum module MR-Buster values for parameters controlling phenology, canopy development, yield components and growth (Table 5). Changes to phenological thermal time targets (*photoperiod_slope, tt_endjuv_to_init, tt_flag_to_flower, tt_flower_to_maturity*) for the commercial hybrids produced simulations that closely matched field observations of flag leaf ligule appearance and anthesis. For example, for the second trial sown at Warwick (Fig. 9), simulated thermal time to anthesis for MR-Taurus, -Scorpio, -Apollo and G33 were 675, 639, 753 and 646 °C d respectively, and within 45 °C d of the observed anthesis date. However, the default MR-Buster values over-estimated thermal time to anthesis (790 °C d) by about 130 °C d. Similar results were observed for the penultimate trial sown at Warwick (Fig. S1).

The MR-Apollo distribution of leaf area with respect to leaf position was similar to that of MR-Buster, whereas the largest leaf tended to be located at more apical nodes for MR-Taurus, -Scorpio and G33 (*aX0*, Table 5). The area of the largest MR-Apollo leaf also showed the greatest sensitivity to final leaf number (*aMaxS*, Table 5). These canopy trait parameters produced leaf biomass that was close to observed values, although the proportion of biomass allocated to G33 leaves tended to be under-estimated, and senescence of MR-Scorpio leaves tended to be over-estimated (Figs. 9 and S1).

An *rue* of 1.75 g MJ^{-1} was used to reproduce the observed high biomass of MR-Apollo and MR-Scorpio (Table 5). For MR-Taurus and G33 parameterisation, the MR-Buster *rue* of 1.25 g MJ^{-1} was capable of supporting observed yield formation but tended to under-estimate leaf and stem biomass (Figs. 9 and S1). Modifications to potential grain number (*dm_per_seed*) (Table 5) were in accord with observations across the field trials (Fig. 6), with MR-Apollo setting a relatively small number of large grains, vice versa for G33, with the other hybrids showing intermediate tendencies.

When the hybrid parameterisations obtained from the Warwick trial were used to simulate all site × season × treatment combinations across the multi-environment trial, APSIM accurately simulated the yield of most hybrids and managements (RMSE 0.8 to 2.2 t ha^{-1}) (Fig. S2). However, there was a tendency to under-estimate yields approaching or greater than 10 t ha^{-1}.

3.5. Simulated sensitivity of yield stability to site, hybrid traits and management

Condamine, Emerald, and Warwick were chosen as sites to simulate a long-term series of seasons because they represent a diversity of environments with respect to the simulated frequency of ET1 (Fig. 3). The inclusion of Emerald further increased the diversity of the environments by increasing the latitudinal range (with consequent temperature and photoperiod effects) and introducing a contrasting sowing window. Across the 1152 trait × management combinations, each simulated at all three sites across approximately 120 seasons, yields ranged between 0.4–11.7, 0.4–11.3, and 1.3–14.3 t ha^{-1} at Condamine, Emerald and Warwick, respectively. Median yields at these sites were 3.0, 3.8, and 6.2 t ha^{-1}, respectively. A line fitted through all combinations of hybrid and MR-Buster yield had a slope of 0.88 and crossed the 1:1 line at the
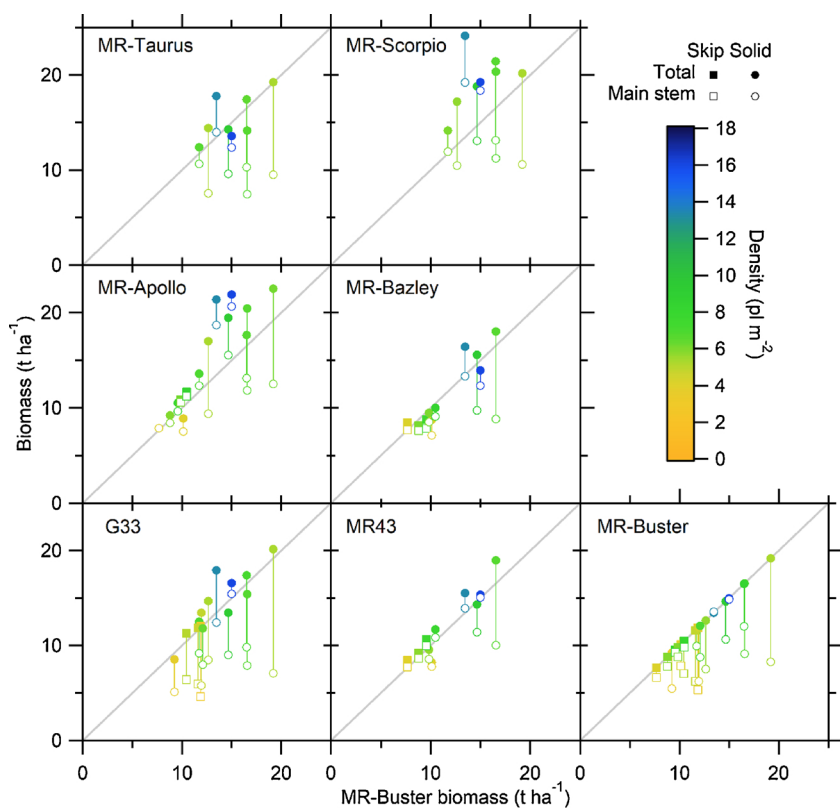
Fig. 4. Contribution of main stem and tillers to the total biomass relative to the mean biomass of the check hybrid MR-Buster. Filled and open symbols represents mean total and main stem biomass, respectively, per site × season × treatment; circles and squares represent solid and skip row configurations, respectively; and the symbols are colour-coded according to observed plant density. The length of the line joining pairs of symbol represents the contribution of tillers to total biomass. The grey reference line represents the 1:1 relationship between hybrid and MR-Buster total biomass.
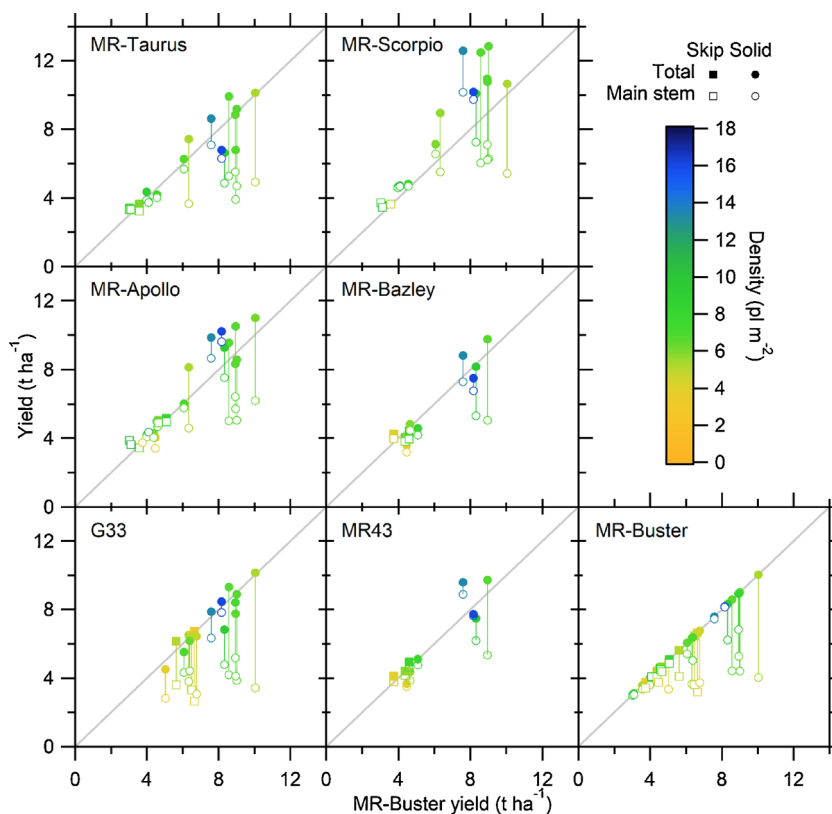

Fig. 5. Contribution of main stem and tillers to the total yield relative to mean yield of the check hybrid MR-Buster. The symbols and reference line are explained in Fig. 4.
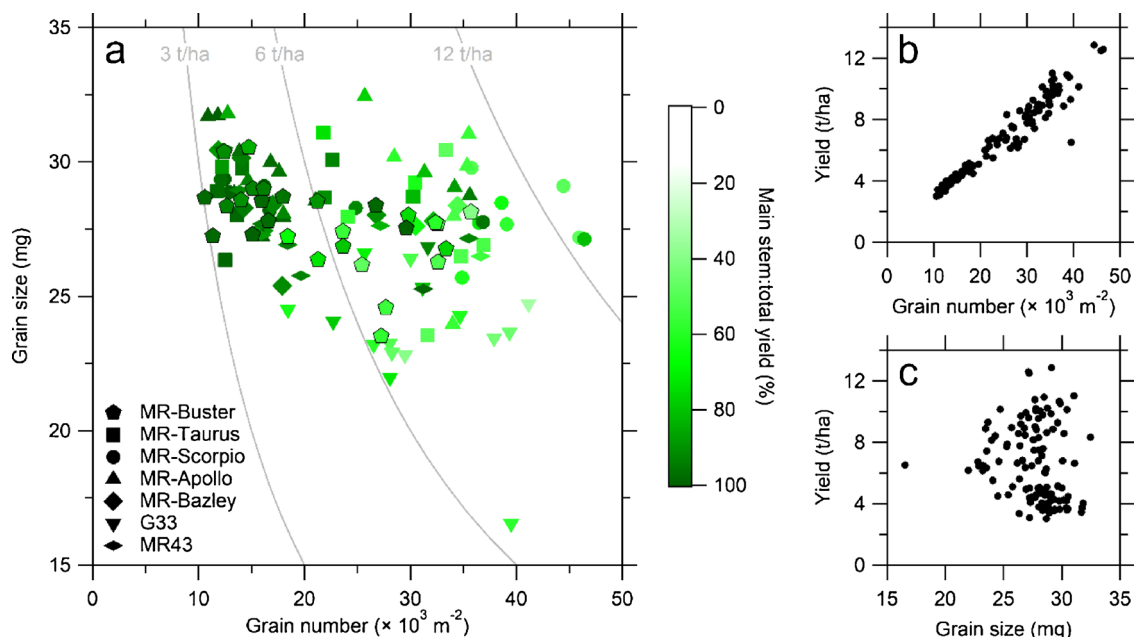
Fig. 6. Grain size as a function of grain number across all site × season × treatment combinations (a). The subplots show the relationships between grain yield and grain number (b) and grain weight (c). In (a) symbol shape varies by hybrid and symbol colour varies according to the percentage contribution of the main stem to total yield, and the grey curvilinear reference lines are isolines of grain number and grain weight that produce yields of 3, 6 and 12 t ha^{-1}. In (a) the only significant slope was observed for MR-Buster.

coordinate 0.3:0.3 t ha^{-1}, supporting the contention drawn from the field data, that hybrid choice becomes less important where $E_j < 3$ t ha^{-1}.

Values for b_i calculated where MR-Buster simulated yields > 3 t ha^{-1}, ranged between 0.22 and 1.40, with a median of 0.92. Of the trait and management treatments tested, *dm_per_seed* had the strongest effect on b_i (Fig. 10). Values of 0.0006 and 0.0015 g grain^{-1} showed the highest and lowest median yields across the simulation. Similarly, decreasing *dm_per_seed* (increasing potential seeds set) appeared to

increase b_i (Table 6). However, further testing (results not shown) showed *dm_per_seed* had a non-linear effect on b_i: values between 0.0005 and 0.0007 g grain^{-1} produced b_i values close to unity, whereas values out to 0.0003 or 0.0014 g grain^{-1} tended to show values as low as $b_i = 0.7$. Furthermore, variability was large (range in yields of 2 t ha^{-1}) where *dm_per_seed* < 0.0006 g grain^{-1}.

Increasing *rue* from 1.25 to 1.75 g MJ^{-1} increased b_i, resulting in $b_i = 1.16$ if applied to the APSIM MR-Buster parameterisation (Table 6). However, *rue* was about one-third as effective as *dm_per_seed*
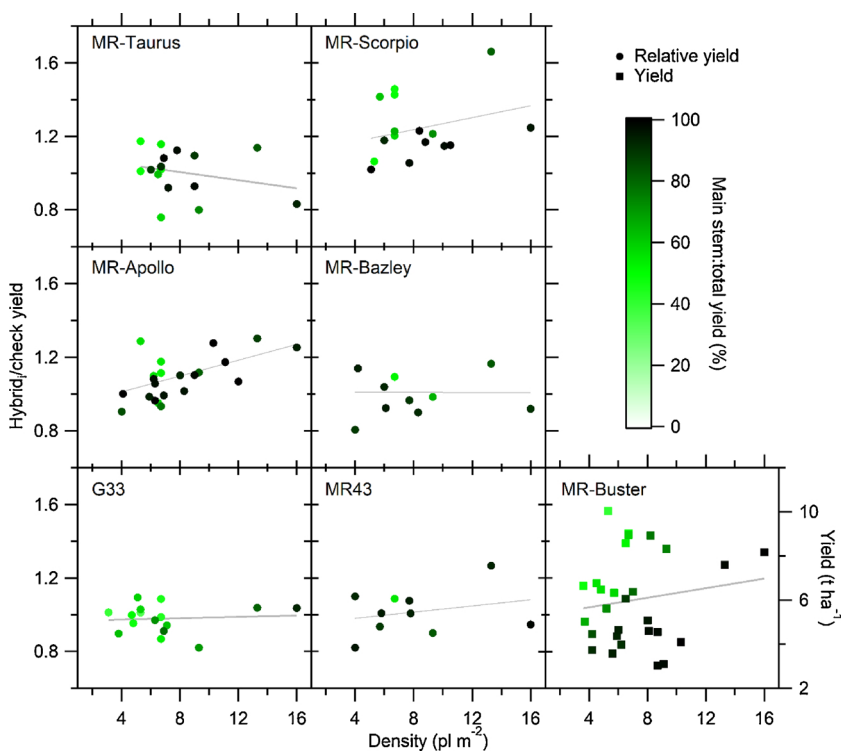

Fig. 7. Response of hybrid yield to actual plant density. With the exception of the lower right-hand sub-plot, the figure shows the relative yield response of each hybrid (expressed with respect to the yield of MR-Buster) to actual plant density (circular symbols). The lower-right hand sub-plot shows the response of the MR-Buster yield to actual plant density (square symbols). Symbol colour varies according to the percentage contribution of the main stem to total yield. The grey lines are linear least-squares regressions. The only significant slope was observed for hybrid MR-Apollo.
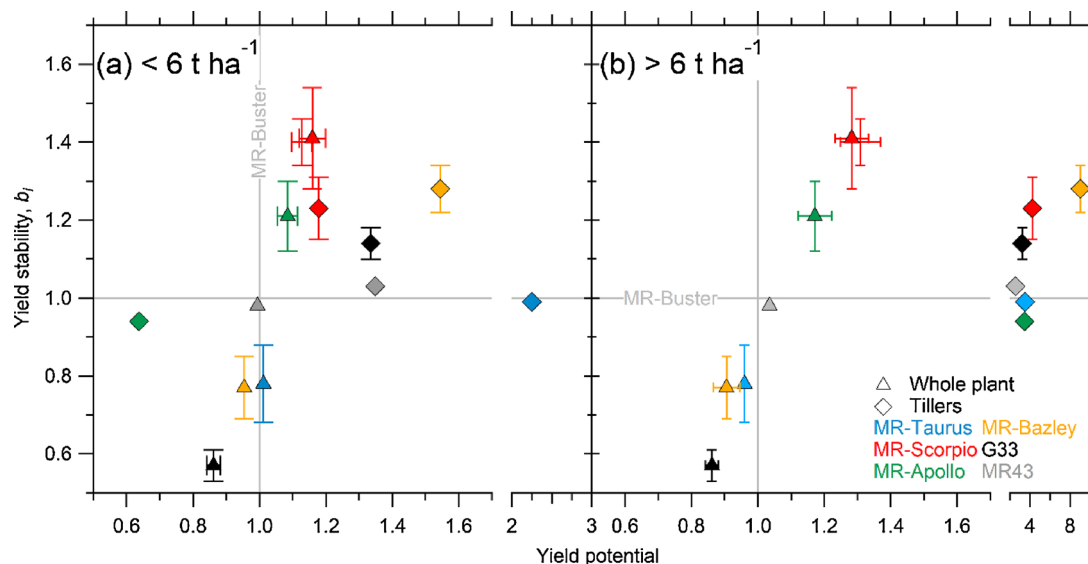
Fig. 8. The yield stability and yield potential of the whole plant and of tillers. As explained in the text and Fig. 1, the b_i values were obtained by linearly regressing hybrid treatment mean yields against those of MR-Buster, forcing the lines through the coordinate 3:3 t ha^{-1} for the whole plant and 0:0 t ha^{-1} for the tillers. Symbols indicate data points corresponding to whole plants and tillers, and colours denote different hybrids (see legend). The yield potential was calculated as the ratio of the hybrid yield over the yield of MR-Buster, for yields below (a) or above (b) an MR-Buster yield of 6 t ha^{-1}, and separately for the whole plant and for tillers. Error bars (± 1 SE) are provided where values are significantly different from the expected mean of MR-Buster.

Table 4
Hybrid ranks determined using the expected utility index of the utility maximisation model (Eskridge and Johnson, 1991), for environments yielding less and more than 6 t ha^{-1}.

Hybrid	Rank (< 6 t ha^{-1})	Rank (> 6 t ha^{-1})
MR-Scorpio	1	1
MR-Apollo	2	2
MR43	6	3
MR-Bazley	7	4
MR-Buster	5	5
MR-Taurus	3	6
G33	4	7

at explaining variance in b_i (Fig. 10). Setting *FTN* to zero reduced b_i, with the effect stronger at plant densities of 5 than 10 pl m^{-2} (Table 6). Reducing *tt_endjuv_to_init* relative to that of MR-Buster decreased b_i, whereas increasing this thermal time, or that of *tt_flower_to_maturity*,

increased b_i (Table 6). Individually, none of the other traits or managements tested explained more than 1% of the total sum of squares across the simulation (Fig. 10). Overall, there was a strong tendency for the b_i values of the traits discussed above to be positively correlated with their overall median yield across the simulation (results not shown).

4. Discussion

Australia's sorghum cropping region is characterised by a high level of season to season climate variability (Fig. 2). Rainfall variability, in amount and distribution, combines with a large variability in soil plant available water holding capacity, hybrid traits and agronomic management to create a diversity of water stress environments (Hammer et al., 2014). This temporal and spatial variability presents the opportunity to match hybrids and managements (i.e. crops design), to best fit site and expected seasonal conditions (Hammer et al., 2014). This also

Table 5
Values and descriptions for parameters modified to simulate phenology, grain set, canopy and growth traits of commercial hybrids in the APSIM sorghum module. Values for MR-Buster are the defaults in APSIM 7.10.

Traits			Hybrids and parameter values[a]				
Description	APSIM parameter	Units	MR-Taurus	MR-Scorpio	MR-Apollo	G33	MR-Buster
Sensitivity of *tt_endjuv_to_init* to photo-period	*photoperiod_slope*	°Cd h^{-1}	7.5	0	0	0	**11.5**
Thermal time from the end of the juvenile phase to floral initiation	*tt_endjuv_to_init*	°Cd	**118**	130	**185**	118	**160**
Thermal time from flag leaf ligule appearance to anthesis	*tt_flag_to_flower*	°Cd	150	**120**	130	150	**170**
Thermal time from anthesis to grain physiological maturity	*tt_flower_to_maturity*	°Cd	**810**	**810**	**810**	810	**761**
Relation between biomass accumulated from floral initiation to the start of grain filling and the potential number of grains set	*dm_per_seed*	g grain^{-1} ×10^{-4}	6.5	6.5	**15.0**	6.0	**8.3**
Position of the largest leaf relative to final leaf number	*aX0*[b]	–	**0.80**	**0.83**	**0.71**	0.86	**0.687**
Slope of the line defining the relationship between final leaf number and area of the largest leaf	*aMaxS*[b]	cm^2 leaf^{-1}	**1**	**2.3**	**37**	0	**22.25**
Intercept of the line defining the relationship between final leaf number and area of the largest leaf	*aMaxI*[b]	cm^2	**451**	**514**	**-101**	542	**92.45**
Efficiency at which intercepted radiation is converted into above-ground biomass	*rue*	g MJ^{-1}	**1.25**	**1.75**	**1.75**	1.25	**1.25**

[a] Values highlighted in bold were used to represent MR-Buster and the range in the commercial hybrids in the long-term simulations.
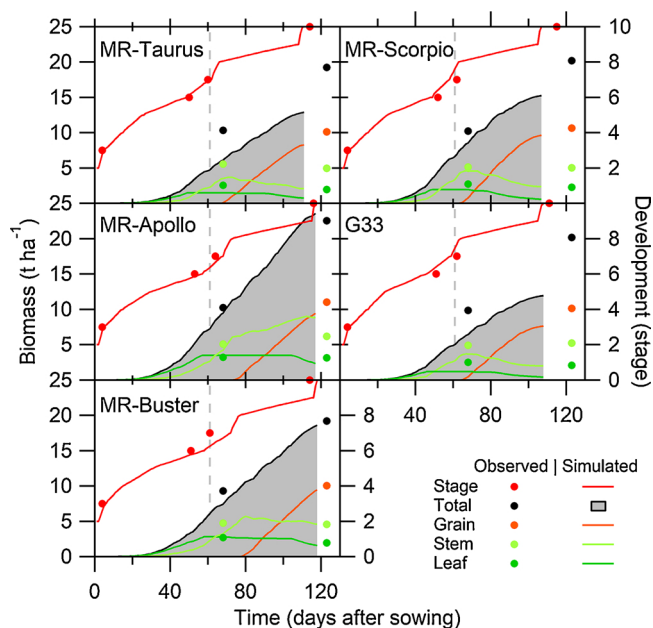[b] These parameters are collectively referred to as 'canopy'.

Fig. 9. Observed and simulated biomass and development of sorghum hybrids parameterised as part of this research. Results are also shown for MR-Buster, using field observations and APSIM parameters. The crops were sown at Warwick on October 30, 2014. In temporal order, the stages correspond to emergence, flag leaf ligule appearance, 50% anthesis and grain physiological maturity. Results are shown for total above-ground, grain, stem and leaf biomass for plants harvested after grain set and physiological maturity. The dashed grey reference line shows the observed 50% anthesis day for MR-Buster.
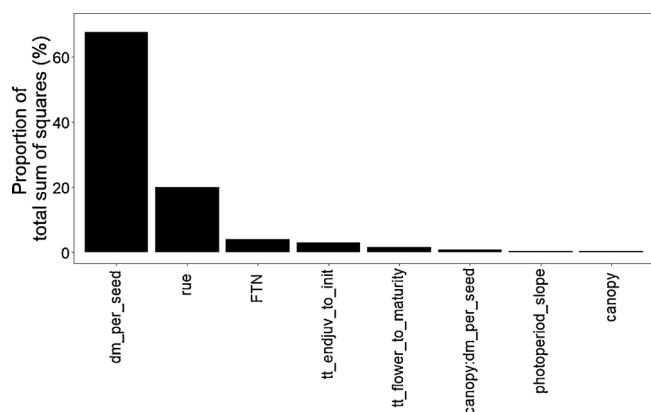

Fig. 10. The proportion of variance in yield stability explained by hybrid traits, management, and sites across *ca.* 120 years of simulated seasons, calculated using ANOVA. Results are truncated to show those factors that individually explained > 0.4% of the total sum of squares: those shown collectively account for 98% of the total. Model parameters are described in the text and Table 5.

highlights the potential value of skilful seasonal climate forecasts at the time of sowing (Wang et al., 2009; Rodriguez et al., 2018). Here, we (i) used the concept of yield stability to quantify G × E responses of a range of commercial sorghum hybrids differing in maturity and propensity to tiller to alternative managements when grown across environments yielding between 3 to more than 12 t ha^{-1}; (ii) parameterised the most common hybrids in the APSIM sorghum module; and (iii) used APSIM to quantify the importance of the range in traits parameterised for these common hybrids, as well as management practices and contrasting environments, on simulated yield stability. Results are discussed in terms of the opportunity to inform crop designs that are better adapted to specific subsets of environments rather than broad adaptation across environments (Cooper and Byth, 1996).

4.1. G × M effects across environments

The combination of trial sites, seasons and G × M treatments created a range of growing conditions, stress environments and yields typical of generally favourable seasons within the highly variable and changing environment of Australia's Northern Grains Region (Hammer et al., 2014; Rodriguez et al., 2014; Potgieter et al., 2016). Across the tested environments, the most frequent water stress environment types were ET1 and ET2, with ET3 less frequent and ET5 restricted to a single site × treatment combination. At Condamine, irrespective of the plant density, the single skip yielded less than the solid row configuration (by *ca.* 1 t ha^{-1}), a result consistent with a reduced canopy capacity to intercept solar radiation. At Emerald, the skip row configuration showed higher values of harvest index (Figs. 4 and 5) probably associated with an improved soil water availability during grain filling; and plant density was positively associated with yield. Similarly at Pittsworth, a low stress environment, there was no benefit of skip over solid row configurations but high plant densities were negatively correlated with yield in the skip configuration, possibly due to fewer fertile tillers at the high intra-row plant spacing (Table 3). These results provide further evidence of the complex dynamics and interactions between crop – climate – soil. To be of practical benefit for targeted crop design, this complexity must be understood at sowing in the context of likely seasonal conditions (Rodriguez et al., 2018).

4.2. Yield stability, potential and expected utility

The quantification of G × E interactions is most effective when assessed across sites that capture the range (Eberhart and Russell, 1966) and frequency (Piepho, 1998) of climate variability encountered across the target set of environments. Yield is often used to represent the effect of the environment not only because it is the key agronomic output, but also because no other measure adequately integrates the many interacting factors that determine plant performance across a cropping season (Freeman and Perkins, 1971). Our results show there is diversity among Australian hybrids in terms of yield stability and yield potential. Genotype by environment interactions were quantified using the yield stability parameter b_i, and an index of yield potential, both relative to the yield of the industry standard hybrid, MR-Buster. No hybrid showed the broadly-adapted trait of a low b_i value and a high yield potential. The hybrid showing consistently larger yields than MR-Buster with $1 < b_i < 1.3$ was MR-Apollo. In environments where $E_j > 6$ t ha^{-1}, MR-Scorpio had the largest b_i value and the highest yield, suggesting this hybrid is well adapted to high productivity environments. MR-Scorpio was also the highest yielding hybrid across environments where $E_j < 6$ t ha^{-1}. At Condamine, the lowest yielding site MR-Scorpio was tested, the yields of this hybrid were not significantly different from those of others: while reduced hybrid effects may be common in ET3 seasons due to the low terminal water stress, this result also suggests the traits that enabled MR-Scorpio to produce the highest yields across the trials were not associated with a yield penalty as mean site yield approached 3 t ha^{-1}. However, at the individual trial level, in any experiment with a significant hybrid effect, the highest yields were obtained with MR-Scorpio but these were not significantly larger than those of -Apollo.

The utility maximisation model (Barah et al., 1981; Eskridge and Johnson, 1991) was used to combine yield stability and yield potential to rank hybrids. Overall, rank was insensitive to the utility maximisation model coefficient *a* that defines the perceived importance of yield relative to stability. This shows that hybrid contrasts in yield potential were sufficient to overcome contrasts in yield stability: MR-Scorpio then -Apollo were top ranking in environments where E_j was below or above 6 t ha^{-1}. While the lowest ranked hybrids changed between these environments, the rank of MR-Buster remained close to the median. This was due to its moderate yield potential and b_i value, which indicate it has broad adaptation to a wide range of environments, characteristics that may explain why MR-Buster has been persistently

Table 6

Simulated b_i values obtained when the APSIM trait parameterisation for MR-Buster was changed by a single parameter characterising the range in values used to model commercial sorghum hybrids. Unless otherwise indicated, the b_i values were calculated across all sites, densities, row configurations and seasons comprising the long-term multi-environment simulation. Results are shown for the parameters in Fig. 10 (*sans* the *canopy:dm_per_seed* interaction). One-tailed Student's *t*-tests indicated all b_i values are significantly different ($p < 0.001$) from that of the check hybrid used to define E_j, MR-Buster ($b_i = 1$). Traits are described in Table 5.

Trait	Value[a] defining range for commercial hybrids	$b_i \pm$ SE	r^2
dm_per_seed	0.0006 g grain^{-1}	1.06 ± 0.006	0.97
	0.0015 g grain^{-1}	0.50 ± 0.004	0.93
rue[b]	1.75 g MJ^{-1}	1.16 ± 0.012	0.92
FTN[c]	0	0.84 ± 0.005	0.97
tt_endjuv_to_init	118 °Cd	0.89 ± 0.004	0.98
	185 °C d	1.03 ± 0.003	0.99
tt_flower_to_maturity	810 °Cd	1.10 ± 0.001	> 0.99
photoperiod_slope	0 °Cd h^{-1}	0.95 ± 0.003	> 0.99
canopy	MR-Taurus	0.89 ± 0.004	0.98
	MR-Scorpio	0.93 ± 0.004	0.98
	MR-Apollo	1.03 ± 0.001	> 0.99
	G33	0.87 ± 0.005	0.97

[a] Or set of values in the case of 'canopy'.

[b] With *rue* = 1.75 g MJ^{-1}, the relatively large uncertainty in b_i is due to the effect of environment type on yield: ET 1, 2, 3, 4, and 5 showed b_i values of 1.43 ± 0.01, 1.06 ± 0.01, 0.86 ± 0.02, 0.56 ± 0.07, and 0.65 ± 0.02, respectively.

[c] With *FTN* = 0, the overall linear trend is comprised of two distinct linear trends representing plant densities of 5 or 10 pl m^{-2}, with b_i values of 0.69 ± 0.006 and 0.94 ± 0.002, respectively, both of which are significantly different from $b_i = 1$.

popular in the sorghum seed market since its release in the early 1990s.

Previous results showed positive correlations between sorghum maturity and yield stability, whereby early maturing genotypes had more stable yields (Saeed and Francis, 1983; Wade and Douglas, 1990). Our results show a close relationship between how seed companies described maturity type (Table 2) and yield performance relative to MR-Buster. High yielding and high b_i hybrids MR-Scorpio and -Apollo were designated medium-late and late maturity types, respectively. Conversely, G33, the hybrid with a yield potential and b_i value significantly lower than those expected of MR-Buster, was identified as a medium-early hybrid. MR-Taurus and -Bazley are also medium-early types and the only other hybrids to show b_i values significantly less than that expected of MR-Buster. MR43 is a medium maturity type that had values of b_i and yield potentials close to those of MR-Buster. Such a close link between maturity type and yield can be expected in environment types characterised by limited post-anthesis water stress (ET1, 2 and 3) (Blum et al., 1989; Haussmann et al., 1998), which were the environment types most common in this set of trials (Fig. 3). Early flowering hybrids show a reduced duration of vegetative growth (Quinby, 1974), conserving water for later grain-filling stages (Blum, 1970), though the reduced size of the source (leaf area) limits yield potential (Jordan et al., 1983; Hammer et al., 2014). Conversely, late flowering hybrids are likely to be more sensitive to soil moisture (higher b_i values) after anthesis, due to a larger water use during vegetative growth. The larger leaf area and biomass of late-maturing genotypes produces favourable conditions for grain-filling when post-anthesis soil moisture is adequate. The performance of these commercial sorghum hybrids provides strong support for the contention that phenology must be closely matched to seasonal water availability (Ludlow and Muchow, 1990).

As expected, grain number was the yield component that best explained differences in yield. In general, grain weight did not respond to changes in productivity (measured by E_j), though hybrid differences

were observed. Grains of the hybrid G33 were significantly smaller than those of all other hybrids. The lack of sensitivity of grain weight to the tested M × E is a consequence of moderate stresses during grain-filling (Heiniger et al., 1997); a relatively low plasticity in grain size is also common among tillering crops (Sadras, 2007). In contrast, grains head^{-1} (i.e. total grain per plant with respect to fertile tillers plus main stem) and head m^{-2} showed significant plasticity with respect to E_j. The trends in grains head^{-1} suggests that the tested hybrids are similar in terms of stress sensitivity on source activity during panicle development (Gerik et al., 2004). The strong positive response of head m^{-2} to E_j suggests that the tested hybrids responded similarly to early season stresses that inhibit tillering, such as reduced light interception, warmer temperatures and increased plant density (Kim et al., 2010; Alam et al., 2017). The differences in b_i values among the tested hybrids, are most likely due to the contribution from tillers (i.e. tiller-specific b_i values, Fig. 8). Hybrids MR-Scorpio, -Apollo, as well as G33, had tiller b_i values significantly greater than MR-Buster. However, of these hybrids G33 was the only one without main stem b_i values greater than MR-Buster (results not shown). The high b_i values and yield potential of hybrids MR-Scorpio and -Apollo are therefore most likely the product of all culms responding strongly to improvements in the environment.

4.3. Effects of hybrid traits and management on simulated yield stability

The simulation of hybrid traits and managements across three sites and approximately 120 seasons showed the value of *dm_per_seed* had the most important effect on simulated yield stability (Fig. 10). This effect was due to the MR-Apollo *dm_per_seed* value of 0.0015 grain g^{-1}, which is similar to the value used to parameterise a genotype with relatively low grain set (Hammer et al., 2010). This value constrained grain number across the treatments to < 20,000 grains m^{-2}, and the associated increases in grain weight of up to > 50 mg grain^{-1} were insufficient to compensate yield. Where *dm_per_seed* = 0.0015 grain g^{-1} the highest yield was *ca.* 7.5 t ha^{-1}, which places most yields for this parameterisation below the 6 t ha^{-1} isoline in Fig. 6a, and therefore within the narrow range of the grain number and yields shown by MR-Apollo in the field trials. Thus, while the simulation shows the importance of *dm_per_seed* as a determinant of b_i, the inability to reproduce the yield components of a relatively large-grain commercial hybrid suggests the results over-emphasise the likely sensitivity of potential grain set to yield stability in applied contexts. Nonetheless, more subtle changes to *dm_per_seed* showed an effect on b_i of similar magnitude to other important trait treatments (Table 6), thus it remains possible that genetic determinants of grain number are an important determinant of simulated yield stability.

The upward adjustment of *rue* from 1.25 to 1.75 g MJ^{-1} is high for sorghum but within the range of other C$_4$ crops (Sinclair and Muchow, 1999; Hammer et al., 2010). In the APSIM sorghum model, increasing *rue* potentially has pronounced effects on simulated yield stability via (i) increasing biomass accumulation in reserve tissues (until this process ceases when grain filling commences), and (ii) increasing biomass accumulation during the critical period for setting potential grain number. Effect (i) provides reserves to support *rue*-enhanced biomass accumulation during grain filling, leading to higher yields in favourable seasons. Effect (ii) should make sink-size less-limiting for yield formation, and therefore (i) and (ii) should increase b_i. Leaf area development less limited by biomass accumulation may not be advantageous in seasons characterised by terminal water stress: for example, across the ET1 seasons in the simulation, the increase in yield per unit of maximum leaf area index was an order of magnitude greater than for ET4 (results not shown). The interaction between source size, water stress and yield potentially explains why the simulation of MR-Buster with *rue* = 1.75 g MJ^{-1} showed a close correspondence between b_i and environment type (Table 6).

Imposing no tillers, as opposed to allowing APSIM to set *FTN*, simulated $b_i < 1$. Zero tillers reduced the leaf area index, thus the effect

on b_i can be understood in terms of reduced source size, leading to slower growth during critical stages, reduced grain numbers and capacity to fill grains in favourable seasons. Zero tillers can be expected where plant density is > 10 pl m^{-2} or an intra-row plant spacing of ≤ 5 cm (Hammer et al., 2014), thus *FTN* = 0 may be an extreme setting. Nevertheless, this aspect of the simulation provides strong support for the conclusion drawn from the multi-environment trials, that tillers and their productivity are important contributors to hybrids showing high b_i values.

Increasing *tt_endjuv_to_init* and *tt_flower_to_maturity* increased b_i, but the earlier period had a stronger effect due to its influence on canopy development. Across the tested range in *tt_endjuv_to_init*, increasing the thermal time target (i.e. 118 vs 185 °C d) increased the duration for leaf initiation (by *ca.* 12 d), final leaf number (*ca.* three leaves), and leaf area (*ca.* 1.3 ×). These changes were associated with increases in mean biomass, grain number and yield (*ca.* 0.3 t ha^{-1}) (results not shown). Although diverse, the *tt_endjuv_to_init* values (Table 2) are within the range of previous observations (Chapman et al., 2002; Akinseye et al., 2017). Similarly, the *tt_flowering_to_maturity* value used for the commercial hybrids is within the limits of previous reports (Ravi Kumar et al., 2009; Hammer et al., 2010). Increasing *tt_flowering_to_maturity* had a simple effect on b_i by extending the duration of the crop cycle by approximately three days, an effect that increased mean yield by 0.2 t ha^{-1} (results not shown).

In contrast to MR-Buster, for several commercial hybrids the timing of floral initiation had no sensitivity to photoperiod, which was simulated by setting *photoperiod_slope* to zero. Photoperiod insensitivity is typical of genotypes adapted to temperate production regions where it promotes homeostasis in thermal time to anthesis (Craufurd et al., 1999). Photoperiod insensitivity reduces b_i by negating any increase in *tt_endjuv_to_init* in response to increased photoperiod. The constraint placed on canopy development by photoperiod insensitivity can conserve soil water for use during grain fill, but will also constrain biomass accumulation, thus reducing the ability of the crop to respond to increases in the potential productivity of the environment, as reflected in $b_i < 1$.

Parameters defining the distribution of leaf area within the canopy and plant density had minor effects on b_i relative to the traits discussed above (Fig. 10). The minor effect of density on b_i may be due in part to the method used to define yield stability: it is conceptualised as a genotypic trait, so b_i was defined as hybrid yield relative to the yield of the check hybrid (MR-Buster) at the same combination of site, season and management (E_j). Defining E_j using a constant management (e.g. 1 m solid rows and 5 pl m^{-2}, as per Fig. 3) may have increased the importance of plant density as a determinant of b_i, but this approach was not applicable to the varied design of the multi-environment field trials.

In combination with the field results, the simulations identified several traits that may enhance the identification of hybrids with relatively high or low yield stability. Hybrids simulated with high *rue* had high biomass (Fig. 9) and $b_i > 1$ (Table 6), and in the field trials the high biomass hybrids, MR-Scorpio and -Apollo (Fig. 4), also showed the highest b_i values (Fig. 8). Although empirical evidence is required to confirm the *rue* assigned to MR-Scorpio and -Apollo, the field and simulated experiments are nonetheless consistent in showing genotypes capable of producing high aboveground biomass can be expected to show high b_i values. The field and simulated experiments are also consistent in demonstrating productive tillers can lead to higher b_i values. The simulations show shortened *tt_endjuv_to_init* may be an important trait when seeking to identify genotypes with relatively low b_i values, especially if the trait can be combined with a canopy that generates $b_i < 1$ (Table 6). This combination of traits may explain why MR-Taurus and G33 showed $b_i < 1$ across the multi-environment field trials. Of the thermal time targets, shortened *tt_endjuv_to_init* appear to be more effective at lowering b_i than *photoperiod_slope* or *tt_flag_to_-flower*.

5. Conclusions

We showed commercial hybrids known to vary in maturity and tillering have contrasting yield stability and yield potential. Hybrids showing both a large biomass and large number of productive tillers appear to be better adapted to the more productive environments, a finding supported by crop modelling. Medium-early maturity hybrids showed the most stable yields across environments, and crop modelling underpinned by observations of phenology and leaf area suggests this stability may be due to reduced thermal time to floral initiation and/or a conservative canopy. Hybrid-specific information on these traits is therefore valuable to growers, agronomists and breeding companies to inform targeted crop designs. Results also highlight the value of crop models able to integrate genotype (G), management (M) and environment (E) to explore targeted combinations of genotypes and managements that best suit stress environments. We conclude that (i) even the limited diversity in maturity type and tillering among the tested hybrids produced important G × E interactions, thus the ability to design specifically adapted crops may be readily aided by diversifying these and other agronomically important traits, and (ii) given the importance of the stress environment in determining the final yield, access to skilful seasonal climate forecasts is likely to increase our capacity to target crop designs (G × M) to specific environments (E).

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fcr.2018.10.010.

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