

Crop design for specific adaptation in variable dryland production environments

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Abstract. Climatic variability in dryland production environments (E) generates variable yield and crop production risks. Optimal combinations of genotype (G) and management (M) depend strongly on E and thus vary among sites and seasons. Traditional crop improvement seeks broadly adapted genotypes to give best average performance under a standard management regime across the entire production region, with some subsequent manipulation of management regionally in response to average local environmental conditions. This process does not search the full spectrum of potential $G \times M \times E$ combinations forming the adaptation landscape. Here we examine the potential value (relative to the conventional, broad adaptation approach) of exploiting specific adaptation arising from $G \times M \times E$. We present an *in-silico* analysis for sorghum production in Australia using the APSIM sorghum model. Crop design ($G \times M$) is optimised for subsets of locations within the production region (specific adaptation) and is compared with the optimum G across all environments with locally modified M (broad adaptation). We find that geographic subregions that have frequencies of major environment types substantially different from that for the entire production region show greatest advantage for specific adaptation. Although the specific adaptation approach confers yield and production risk advantages at industry scale, even greater benefits should be achievable with better predictors of environment-type likelihood than that conferred by location alone.

Additional keywords: crop improvement, crop modelling, $G \times E$, genotype by environment interaction, plant breeding, trait simulation.

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Introduction

In dryland crop production environments (E), where the amount of available water frequently limits crop growth, there are many plausible genetic trait (G) and agronomic management (M) manipulations available to improve crop growth and yield. In some instances, major gains in yield have been associated with combined $G \times M$ effects. For example, the continuous increase in maize (*Zea mays* L.) yield in the US over many decades has been associated with superior genotypes being grown at higher density (Duvick 2005). In more risky, dryland production environments where water limitation is more frequent, less intensive management systems that trade off yield potential for lowered risk of crop failure are often invoked, such as skip-row planting systems for sorghum (*Sorghum bicolor* Moench.) in Australia (Whish *et al.* 2005). While analyses have suggested the additional value that specific genotypes, such as those with reduced tillering, might

bring to such systems (Hammer 2006) progress towards $G \times M$ integration remains slow.

In general, approaches to crop yield improvement continue to separate G (i.e. plant breeding) and M (i.e. agronomic) approaches. Plant breeders search for superior genotypes that have improved performance across the target population of environments in the production system (Cooper and Hammer 1996; Jordan *et al.* 2006). This typically involves the benchmarking of yield of new genotypes against yield of existing genotypes using multi-environment trials, although replication of such trials in time and space is often limited by financial constraints. Hence, crop-improvement interventions are usually explored for a limited set of E types and nearly always with a single, standard management practice. Agronomists pursue improved performance by seeking to optimise management for elite genotypes developed by plant breeding (e.g. for maize in more marginal moisture environments in the

US; Lyon *et al.* 2003). Historically, plant breeding and agronomy have co-evolved, and both have contributed to improved crop performance, as described for wheat by Fischer (2009). Here, we consider the value that might be gained by a more integrated, location-specific $G \times M$ approach to crop improvement in variable dryland crop-production environments, using sorghum in Australia as the case study.

The nature of water limitation experienced by a crop through its life cycle can be characterised using simulation (Muchow *et al.* 1996; Chapman *et al.* 2000; Chenu *et al.* 2011). A central advantage of simulating water stress with crop models is the ability to compute potential daily soil water supply to the crop (determined by soil water content and root and soil properties), and crop soil water demand (determined by crop potential growth, intrinsic water-use efficiency, and atmospheric dryness). The ratio of soil water supply to crop water demand computed daily represents an integrated biophysical index of crop water status that can be used to quantify the temporal pattern or trajectory of water stress through the crop life cycle. When such trajectories are classified, they can define the specific types (seasonal patterns) of environments occurring in the target production region and their frequencies of occurrence. The intensity and timing of water shortage have major consequences for crop growth and yield.

The frequency with which particular environment types occur in the target production region is critical to the unravelling of genotype-by-management-by-environment ($G \times M \times E$) interactions and the design of crop-improvement strategies (Chapman *et al.* 2000; Chenu *et al.* 2011). The consequences of manipulating G and M attributes will differ depending on the E type (Hammer and Jordan 2007; Messina *et al.* 2009; Chenu *et al.* 2009; Tardieu 2012; Harrison *et al.* 2014). For example, in sorghum, combinations of tillering (G) and row configuration (M) favouring rapid canopy development and thus high water use will be advantageous in years with only minor water limitation through the crop cycle, but significantly disadvantageous in situations where water limitation becomes more pronounced as the life cycle progresses (Hammer 2006; Hammer and Jordan 2007).

Grain yield under water-limited conditions is strongly associated with the extent of crop water use after anthesis (Sadras and Connor 1991; Turner 2004; Hammer 2006). Simulation studies for wheat (*Triticum aestivum* L.) indicated a yield increase of 50–60 kg ha⁻¹ mm⁻¹ extra water uptake after anthesis (Manschadi *et al.* 2006). The main E factors are the distribution of rainfall and the storage capacity of the soil, but given these, numerous G and M factors can also influence the extent of water use after anthesis (van Oosterom *et al.* 2011). Beyond effects of manipulating phenology (Muchow *et al.* 1994), studies in sorghum have documented G and M effects via root-system architecture, row configuration, and the dynamics of water extraction (Whish *et al.* 2005; Singh *et al.* 2012), transpiration efficiency and transpiration regulation (Hammer *et al.* 1997; Sinclair *et al.* 2005; Gholipour *et al.* 2010), and aspects of canopy development associated with leaf appearance, leaf size, and tillering (Borrell *et al.* 2000; Kim *et al.* 2010b; van Oosterom *et al.* 2011; Alam *et al.* 2014).

Here we use this understanding of G and M effects on these major determinants of crop productivity to undertake a

simulation analysis of crop design for sorghum in Australia via use of a suitably structured crop model (Hammer *et al.* 2010). Our aim is to explore the value to crop improvement that might be gained by pursuing specific local adaptation rather than the typical, broad adaptation approach. Broad adaptation approaches seek genotypes giving best average performance under a standard management regime across the entire production region, with some subsequent manipulation of management regionally in response to average local environmental conditions. They do not search the full spectrum of potential $G \times M \times E$ combinations forming the 'adaptation landscape' (Cooper and Hammer 1996; Chapman *et al.* 2003; Messina *et al.* 2011). In specific adaptation, crop design ($G \times M$) is optimised for subsets of locations in the production region. We simulate the complete adaptation landscape for a range of G , M , and E , and then compare the outcomes for specific and broad adaptation approaches using a risk analysis framework in order to deal with the uncertainty generated by seasonal variation.

Sorghum production in Australia and environment characterisation

Sorghum is the major dryland, summer grain crop grown in Australia. Over the 5 years to 2012–13, the average production of sorghum in Australia was 2.08 Mt, the crop occupied an average planted area of 0.63 Mha, and average yield was 3.27 t ha⁻¹ (ABARE 2013), but annual production is highly variable because of seasonal rainfall variability (Potgieter *et al.* 2005; Hammer 2006). Within Australia, sorghum production has been distributed relatively evenly between three geographic regions: central Queensland (CQ), southern Queensland (SQ) and northern New South Wales (NNSW) (Fig. 1). Cropping soils throughout this region vary in texture and depth but are often uniform, heavy clays with high water-holding capacity, with conservation tillage and long fallows (often in rotation with wheat) being standard practice. Sowing is reliant on occurrence of planting rains and adequate antecedent stored moisture and occurs from September to January, depending on location and timing of planting rains. Sorghum is grown as a row crop, with standard practice being 1-m row spacing and 50 000 plants ha⁻¹, but skip-row systems and reduced density are practiced in more marginal environments (Whish *et al.* 2005). Following the development and effective ongoing management of resistance to the major insect pest (sorghum midge, *Stenodiplosis sorghicola* (Coquillett)) and incorporation of stay-green to reduce lodging (Henzell *et al.* 2002) through the 1970s into 1990s, improving yield *per se* has become the main focus for crop improvement in sorghum (Jordan *et al.* 2006). Effective use of available water is critical to this approach.

Chapman *et al.* (2000) used a simulation approach to characterise the nature of water-limitation environments for sorghum in Australia and identified five types of environment that differed in extent and timing of water limitation in the crop life cycle. Here we update that environmental characterisation using the latest version of the sorghum module (Hammer *et al.* 2010) in the APSIM platform (Keating *et al.* 2003) and a more comprehensive range of sites and local M practice to better

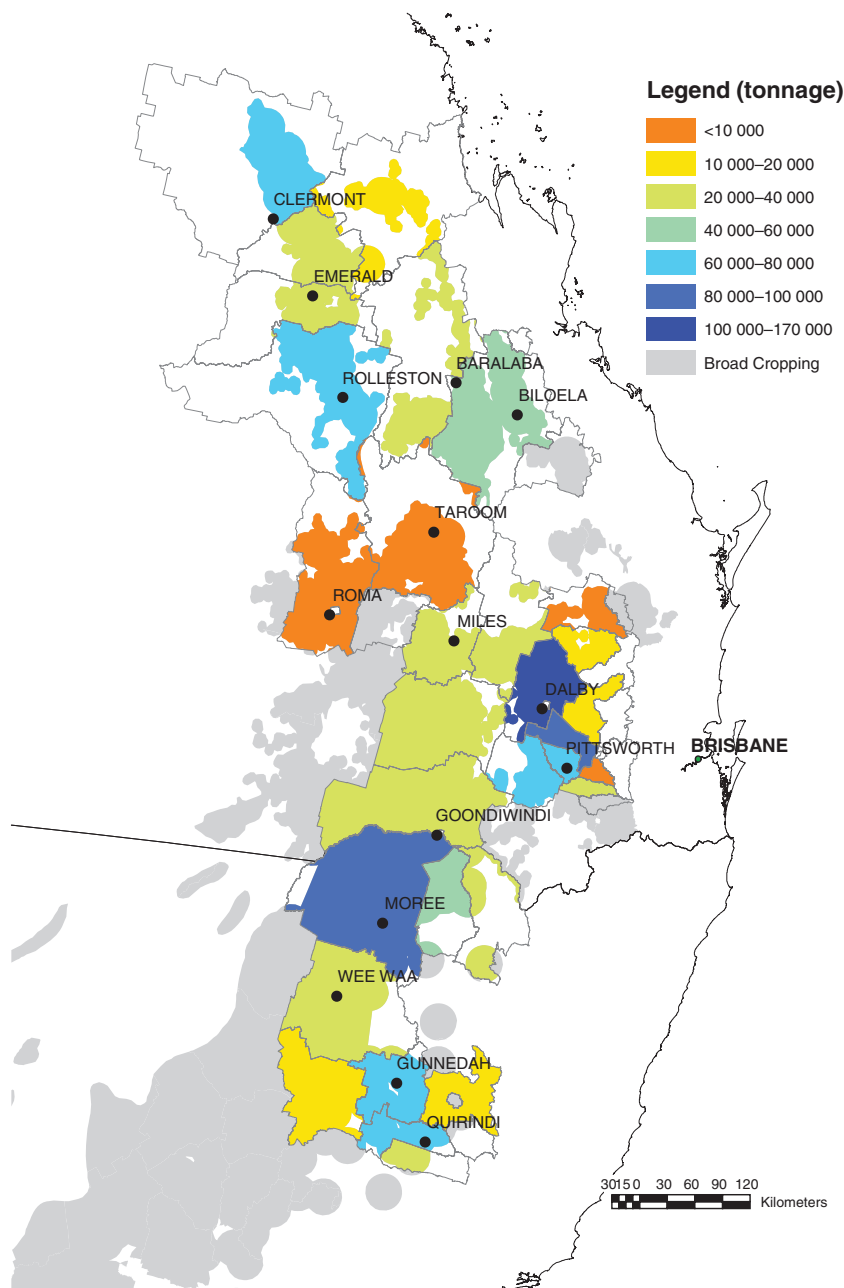


Fig. 1. Sorghum production in north-eastern Australia and the 15 locations chosen for environmental characterisation simulation. Shire boundaries are marked and shading indicates average annual production (t; 1983–2001) for each shire.

reflect the target population of environments experienced currently throughout the region (Fig. 1, Table 1). Sites were selected to cover the overall geographical spread of cropping, but in a manner that adequately reflected relative local magnitude of production. Soils reflected common cropping soils in the vicinity of each site, with detailed parameterisations drawn from the APSOIL database (Dalgliesh and Foale 2005). The water-holding capacity for each soil is given in Table 1. The simulations were conducted using a single common genotype (hybrid MR-Buster; Pacific Seeds, Toowoomba, Qld), with

parameterisation for crop growth and development characteristics as reported by Hammer *et al.* (2010). The number of fertile tillers (i.e. those tillers surviving to produce a panicle) is a required input of the model. Tiller number is known to depend on the growth environment (temperature and radiation), plant density and spatial arrangement (Lafarge and Hammer 2002; Kim *et al.* 2010a; Alam *et al.* 2014) via their effects on the amount of surplus assimilate available per plant to support tillering. For example, high temperature promotes growth of the main culm and suppresses tillering, and high

Table 1. Sorghum management practices and their frequency (%) for each site and soil type used in the environmental characterisation simulations

Management systems varied in row configuration (solid planting; single skip-row planting (SS); double skip-row planting (DS)) and planting density (35 000 (35K) or 50 000 (50K) plants ha⁻¹), but row spacing was maintained at 1 m. The weighting (estimated frequency, %) of each soil type, soil depth, and plant-available water capacity (PAWC) at each site is also given

Site	Soil type, depth (cm), PAWC (mm)	Weighting for soil (%)	Management system and weighting (%)					
			Solid		SS		DS	
			35K	50K	35K	50K	35K	50K
<i>Central Queensland</i>								
Clermont	Black Earth, 80,120	70	40	0	60	0	0	0
	Black Earth, 120, 150	30	40	0	60	0	0	0
Emerald	Black Earth, 80, 120	75	20	0	80	0	0	0
	Black Earth, 120, 150	25	30	0	70	0	0	0
Rolleston	Black Earth, 80, 120	25	30	0	70	0	0	0
	Black Earth, 120, 150	75	30	0	70	0	0	0
Baralaba	Grey Clay, 150, 260	100	0	70	0	30	0	0
Biloela	Grey Clay, 150, 260	100	0	70	0	30	0	0
<i>Southern Queensland</i>								
Taroom	Grey Clay, 120, 240	100	0	60	0	20	0	20
Dalby	Grey Clay, 150, 235	40	0	70	0	30	0	0
	Vertosol, 180, 324	60	0	100	0	0	0	0
Pittsworth	Grey Clay, 150, 235	100	0	80	0	20	0	0
Goondiwindi	Grey Clay, 120, 240	70	0	50	0	50	0	0
	Red Chromosol, 140, 185	30	0	30	0	35	0	35
Miles	Grey Clay, 120, 240	100	0	60	0	20	0	20
Roma	Black Earth, 80, 140	100	30	0	70	0	0	0
<i>Northern New South Wales</i>								
Wee Waa	Grey Clay, 150, 260	85	0	60	0	30	0	10
	Black Earth, 150, 280	15	0	100	0	0	0	0
Moree	Grey Clay, 150, 260	85	0	40	0	40	0	20
	Black Earth, 150, 280	15	0	90	0	10	0	0
Gunnedah	Grey Clay, 150, 260	60	0	100	0	0	0	0
	Black Earth, 200, 350	40	0	100	0	0	0	0
Quirindi	Grey Clay, 150, 260	15	0	100	0	0	0	0
	Black Earth, 200, 350	85	0	100	0	0	0	0

density reduces assimilate available per plant and also suppresses tillering. The estimates of fertile tiller number derived from this knowledge and local experiences are given in Table 2. To quantify the effect of seasonal variability, simulations were conducted using the long-term daily weather data available for each site (~120 years at each location) assuming planting of summer crop after winter fallow. Planting was simulated when 30 mm of rain had been received in a 3-day period within the planting window, provided there was a minimum of 75 mm available stored soil water. The planting window was set at 15 October–15 February for sites in CQ, and 15 September–15 January for sites in SQ and NNSW. The starting soil moisture for each sorghum crop in the time-series was determined by running the cropping system model through the fallow from the previous summer crop. The first 5 years of the simulation run were discarded to avoid any effects associated with starting conditions. An initial simulation was conducted at all site–soil combinations assuming a standard agronomy of 1-m row spacing and density of 50 000 plants ha⁻¹. For each year of each simulation run, sowing date and soil moisture condition at that date were captured and used for simulations of other

management systems (Table 1), to avoid confounding associated with differences in antecedent conditions. The simulation results were used to generate trajectories of crop water limitation through the season for the hybrid MR-Buster. In the analysis of environment types, those trajectories were weighted by the relative importance of soils and management systems for each location (Table 1), which were derived from experience of local agronomists.

Cluster analysis of the resultant trajectories of crop water limitation was employed to generate five distinct groups, with the mean patterns for soil water supply/water demand for these groups shown in Fig. 2. This number of clusters was chosen for comparison with the prior similar analysis of Chapman *et al.* (2000), which had identified the 5-group level from consideration of percentage variance explained by the grouping. Trajectories for each simulation of site–management–year combination were centred on flowering time and values of the ratio of soil water supply to crop water demand for 450 degree-days either side of flowering (averaged within nine 100-degree-day periods) used in the analysis. Classification of each of these trajectories into one of the five

groups was performed using k-means grouping (Hartigan and Wong 1979) in R (R Development Core Team 2008) to create the environment-type classifications.

The five environment types (ET1–ET5) (Fig. 2) were very similar in nature and overall frequency of occurrence across the entire production region to that found in the previous study by Chapman *et al.* (2000). A low stress type, ET1, experienced low levels of water limitation on average throughout the life cycle and occurred on 31% of occasions. There was an increasing degree of terminal water limitation for ET2 (19% overall frequency), ET5 (26%), and ET4 (13%), with the distinctions relating mainly to the timing in the crop cycle of onset of water limitation. In ET2, water limitation onset did not occur until after anthesis, whereas it had commenced by anthesis for ET5, and was early (pre-anthesis onset) and severe for ET4. Although

Table 2. Fertile tiller number used in regional simulation for sorghum for each subregion, planting date, and planting density for solid planting configuration, and double skip-row planting configuration

Region	Planting window	Planting date	Density (no. of plants m ⁻²)			
			2.5	5	10	15
<i>Solid planting (1-m rows)</i>						
Central Qld	1 Nov.–1 Feb.	<15 Dec.	1	0.75	0.25	0
		>15 Dec.	0.75	0.5	0.25	0
Southern Qld	1 Oct.–15 Jan.	<15 Nov.	2	1.5	0.5	0
		>15 Nov.	1.5	1	0.25	0
Northern NSW	1 Oct.–1 Jan.	<15 Nov.	2.5	2	0.5	0
		>15 Nov.	2	1.5	0.25	0
		>15 Dec.	1.5	1	0	0
		>15 Dec.	1.5	1	0	0
<i>Double skip-row planting</i>						
Central Qld	1 Nov.–1 Feb.	<15 Dec.	0.75	0.25	0.0	0
		>15 Dec.	0.5	0.25	0.0	0
Southern Qld	1 Oct.–15 Jan.	<15 Nov.	1.5	0.5	0.0	0
		>15 Nov.	1.0	0.25	0.0	0
Northern NSW	1 Oct.–1 Jan.	<15 Nov.	2.0	0.5	0.0	0
		>15 Nov.	1.5	0.25	0.0	0
		>15 Dec.	1.0	0	0	0
		>15 Dec.	1.0	0	0	0

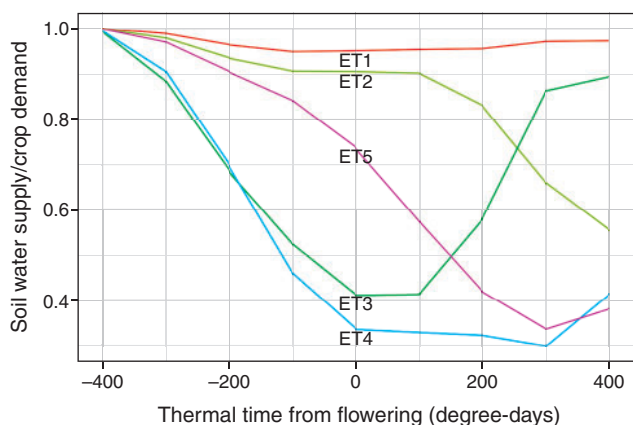


Fig. 2. Mean water limitation ratio (averaged by 100-degree-day periods) v. thermal time around flowering for all seasons within a group for the five environment types (ET) identified in the environmental characterisation simulation for sorghum in Australia (see text for details).

ET3 (11%) also had early onset, the limitation was relieved during the grain-filling period after anthesis.

Locations varied considerably in their frequency distributions of ETs (Fig. 3). For example, in more favourable soil–site situations (e.g. Dalby with 180 mm soil water-holding capacity, Fig. 3), there was an increased frequency of lower stress environments (ET1 and ET2) relative to their overall occurrence rates and a decreased frequency of more severe stress types (ET4 and ET5). The opposite occurred in some other situations (e.g. Wee Waa with 150 mm soil water-holding capacity, Fig. 3), and in some instances (e.g. Emerald 80 mm, Fig. 3), there was a relatively uniform distribution of frequencies across all ETs.

Simulating the G × M × E adaptation landscape

A comprehensive yield-adaptation landscape was simulated for the entire sorghum production region using a plausible range of M and G factors for the site–soil combinations and historical seasonal climates that formed the E used in the environmental characterisation. This study focused on the main production-limiting factor (water) and did not consider issues associated with fertility, subsoil constraints, and biotic factors. The sorghum crop model of Hammer *et al.* (2010) in the APSIM platform (Keating *et al.* 2003) had been structured to be sufficiently robust for this purpose. Simulations were conducted using three fixed sowing dates and three antecedent soil-water conditions at each sowing date for each site–soil combination. These values were determined from the data captured from the initial simulation run conducted for the environmental characterisation (see details in previous section). Sowing dates were found to be uniformly spread through the planting window (data not shown), so the sowing dates chosen here were spread (early, mid, late) over that interval. Similarly, the distribution of antecedent moisture levels extended uniformly from 75 mm (the minimum requirement for sowing) to full (or near full, depending on soil type) (data not shown), so the levels chosen here (low, medium, high) were based on quartile values from those distributions.

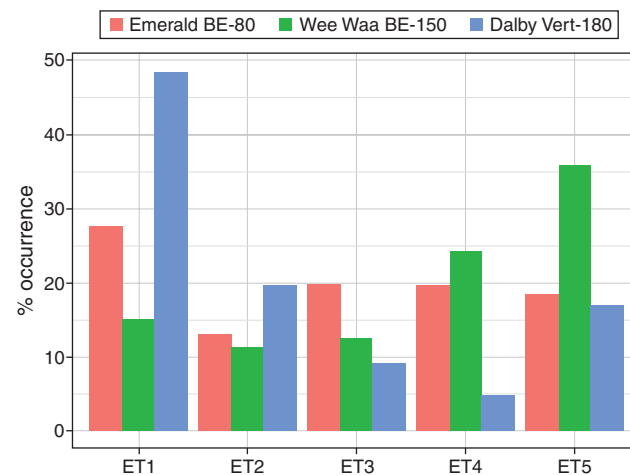


Fig. 3. Frequency of occurrence (%) of each of the five environment types found for sorghum in Australia for three site–soil combinations (bars left to right): Emerald, Black Earth, 80 cm deep; Wee Waa, Black Earth, 150 cm deep; Dalby, Vertosol, 180 cm deep).

The environment type associated with each sowing date–antecedent soil water–site–year combination was determined from the simulation with the standard genotype and management practice. The pattern of soil water supply/water demand for that simulation was compared with that for the five defined groups (Fig. 2), and the group with the lowest mean-square distance was assigned.

Attributes for M employed in the simulations included three types of row configuration (solid 1-m rows; single skip-row;

double skip-row; Whish *et al.* 2005) and four levels of plant density (3.5, 5, 6.5, 8 plants m⁻²). The G attributes included nine levels of maturity (Ravi Kumar *et al.* 2009), nine levels of tillering (Kim *et al.* 2010b), and five levels of root-system architecture (Singh *et al.* 2012). Levels of maturity were introduced by varying the time from end juvenile stage to floral initiation within the range -30 to +30 degree-days relative to the standard hybrid (with value 160 degree-days) using steps of 7.5 degree-days to generate the nine types. In

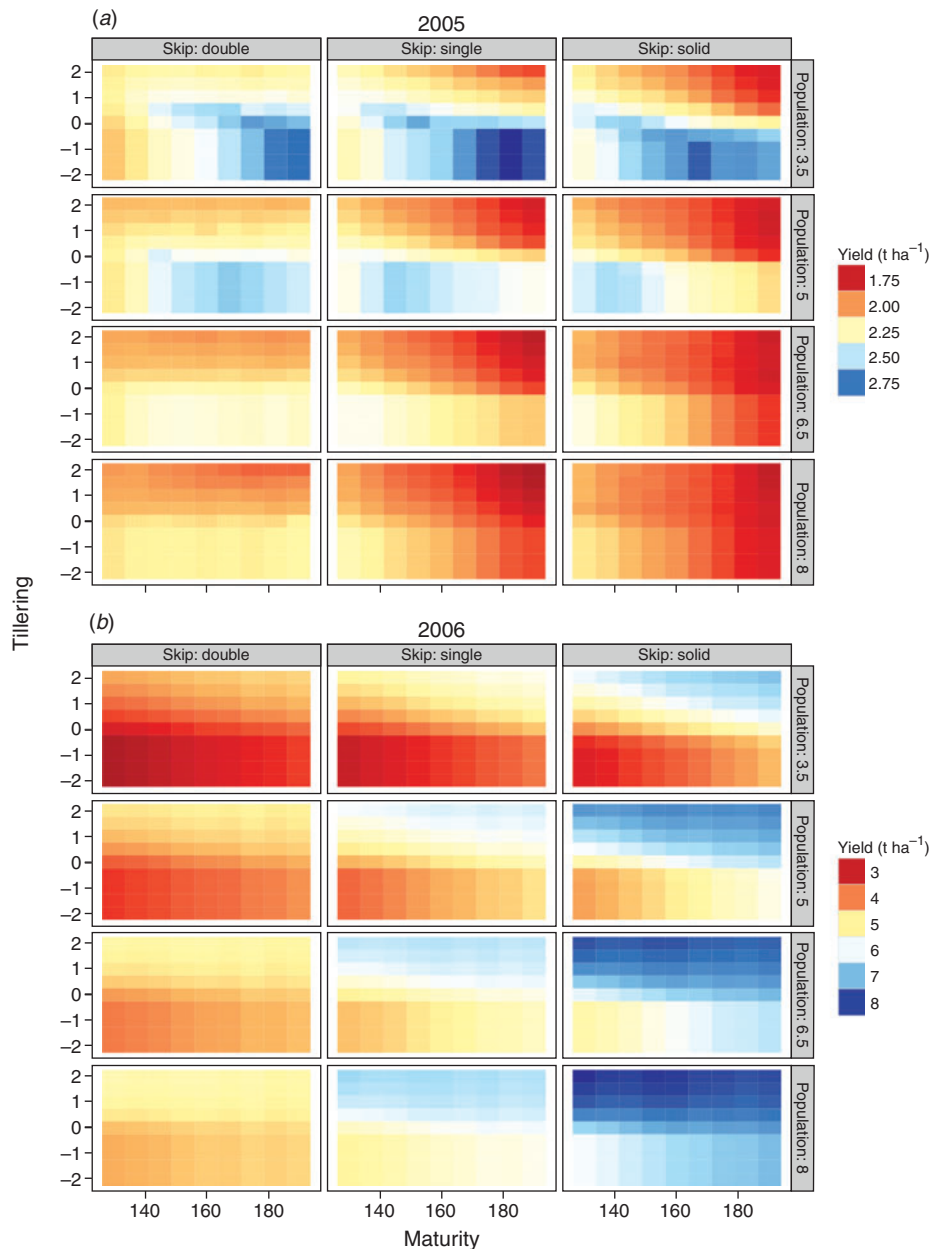


Fig. 4. Simulated landscapes of sorghum grain yield (t ha⁻¹) at Emerald in (a) 2005 and (b) 2006 for genotypes varying in tillering (positive values for high tillering types) and maturity (high thermal time requirement values for late maturing types. see text), and crop management varying in row configuration (double skip, single skip, and solid 1-m rows) and density (3.5–8 plants m⁻²). The landscapes are for a standard root architecture and sowing date in each year.

addition to the effect on crop duration, this generates a change in total leaf number and hence the pattern of leaf area development through the crop life cycle (Hammer *et al.* 1993). The range employed generates difference from the standard hybrid (17 leaves) within the range -1.5 to $+1.5$ total leaf number (Ravi Kumar *et al.* 2009). Levels of tillering were introduced by adding to, or subtracting from, the fertile tiller numbers defined in

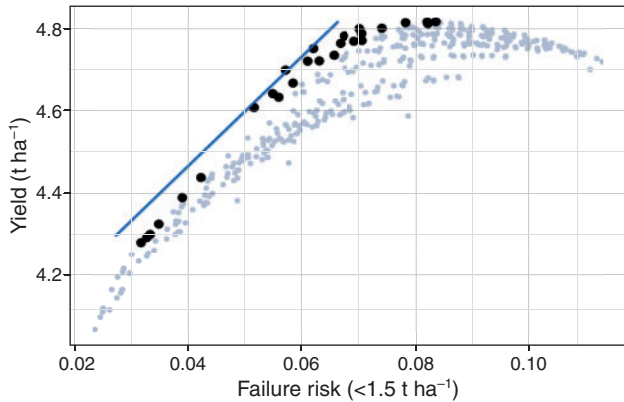


Fig. 5. Average yield *v.* failure risk for each genotype from simulations conducted across all environments (site years) for the standard management practice (solid row configuration; density 5 plants m^{-2}). Points highlighted in black indicate the superior genotypes forming the ‘technology frontier’ as identified by quantile regression at the 90th quantile (see text). The line represents an indicative trade-off between yield and risk for a risk-averse individual. The degree of risk aversion determines the slope of this line (greater slope indicates greater risk aversion).

Table 2. Tiller number was modified within the range -2 to $+2$ tillers relative to the standard hybrid using steps of 0.5 fertile tillers to generate the nine types. For the lowest tillering type, this generates a plant that is unicum in nearly all situations. Fertile tiller number affects maximum potential plant leaf area and hence the pattern of leaf area development through the crop life cycle (Hammer *et al.* 1993). Variation in root system architecture was introduced via nominal effects linked to the root angle of the first flush of nodal roots (Singh *et al.* 2012). For nodal root angle varying from 45° to 25° , in steps of 5° , an additional 5 mm potential available soil water below 1 m depth in the soil (where possible) was assumed. Hence, for the narrowest root-angle type, an additional 20 mm of water was potentially available at depth in the soil profile.

The total number of $G \times M \times E$ combinations resulted in a simulation of $\sim 7.4 \times 10^8$ crop years. The computing architecture utilised was the CondorHT Harvesting Service of CSIRO and a submission and simulation management platform, ClusterRun (B. Zheng and S. Chapman, unpubl.). All simulations were completed in 15 h on 8000 processors, with the potential to explore further billions of combinations of $G \times M \times E$.

The simulated yield adaptation landscapes cannot be viewed in their entirety but it is possible to view summaries of the data using heat maps of yield across several variables. Figure 4 presents yield levels for two consecutive years at Emerald, illustrating grain-yield landscapes associated with variation in tillering, maturity, row configuration, and planting density. In 2005 (Fig. 4a), which was lower yielding, the highest yield occurred with a low-tillering, late-maturing type grown at low population in a single skip-row configuration. By contrast, in

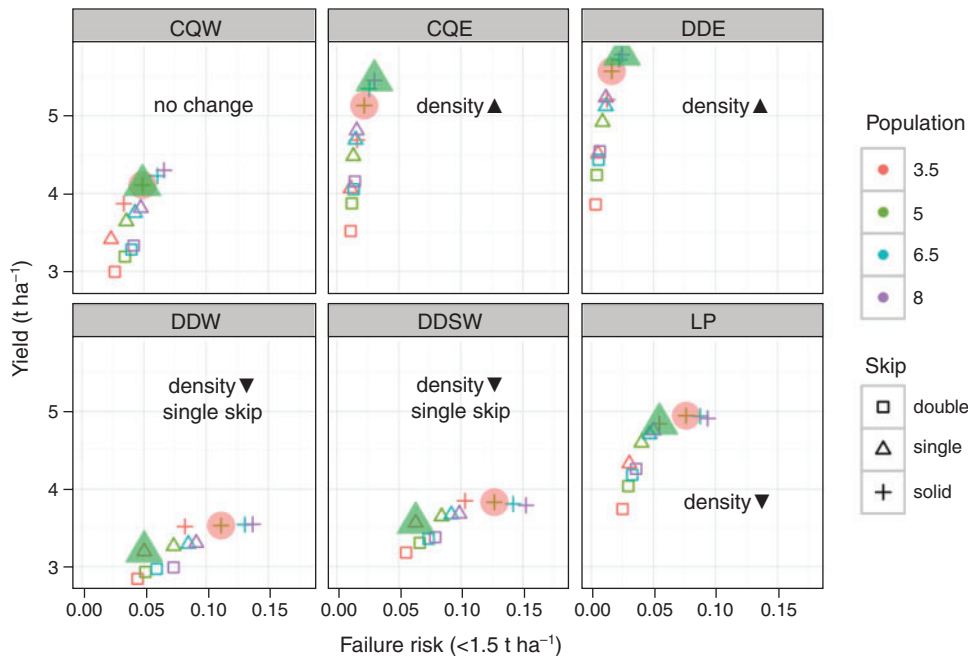


Fig. 6. Average yield *v.* failure risk for the globally adapted genotype from simulations conducted across environments within defined subregions (see text) for a range of management practices (row configuration; plant density). The filled circle indicates result for standard practice (solid rows; 5 plants m^{-2}) and the green filled triangle the local optimum management practice. Comments in each panel indicate change in management practice from standard to local, with a black triangle indicating increase or decrease in density.

2006, with the same starting conditions (Fig. 4b), yields were greater, with the maximum yield occurring with a high-tillering, relatively early-maturing type grown at high population in a solid row configuration. This contrast demonstrates the instability in the adaptation landscape, with different combinations of $G \times M$ being favoured depending on E, and highlights the difficulty in seeking broad adaptation in such variable production environments.

Simulated broad adaptation

Genotypes with best overall broad adaptation at the standard M practice of solid row configuration and planting density of 5 plants m^{-2} were identified by determining the average yield of each G combination across all E for this standard M that is typically used in all breeding trials in the region. To accommodate production risk associated with climate variability, average yield for each G was plotted against the proportion of years (i.e. risk) in which that G did not exceed a threshold yield level (Fig. 5), which was set at 1.5 t ha^{-1} , because this approximates the economic break-even yield for sorghum in these production systems. Such yield-risk plots quantify the trade-offs between potential profit (yield) and the chance of making a financial loss (risk) and facilitate identification of the technology frontier (deVoil *et al.* 2006) of superior genotypes, which are those

achieving greatest yield for a given risk, or lowest risk for a given yield. A quantile regression method (Koenker 2013) was used to identify the points (at 90th percentile) on the frontier of these plots, and we then determined which genotype factors were most represented in these points. Genotypes at the technology frontier are those demonstrating superior broad adaptation. In this instance, the attributes of those genotypes tended to be early-medium maturity, medium-high tillering and narrow root angle.

A set of genotypes remains populating the technology frontier, and to determine the preferred individual genotype, the desired approach to trading off profit (yield) and financial risk must be defined. This will depend on personal attitude to risk. Here we assume a risk-averse position and define this trade-off by accepting lower average yield only if it is accompanied by reduced risk of a loss, and this is used to identify the set of preferred genotypes (Fig. 5). The degree of risk-aversion can vary, and this will change the level of trade-off accepted. A more risk-averse person will accept a greater reduction in average yield for the same degree of risk reduction. By applying the assumed level of risk-aversion (Fig. 5) and considering the general traits of the selected genotypes, we identify the standard, broadly adapted genotype (at standard M practice) as one with medium maturity, medium tillering, and narrow root angle.

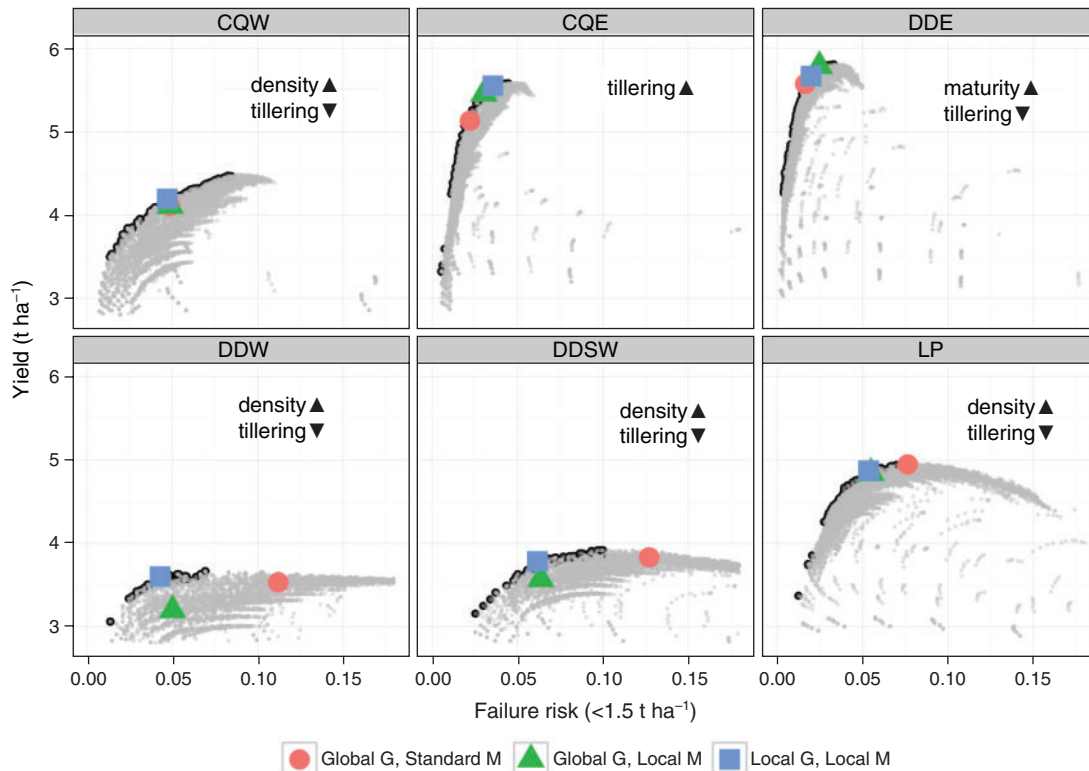


Fig. 7. Average yield v. failure risk for all genotype and management combinations from simulations conducted across environments within defined subregions (see text). Small black circles indicate combinations forming the technology frontier as per Fig. 5. The pink circle indicates result for standard, broadly adapted genotype with standard management practice, the green triangle the local optimum management practice with that genotype (both as per Fig. 6), and the filled blue square the locally optimal combination of genotype and management. Comments in each panel indicate change in genotype and management in moving from broad to specific adaptation, with black triangles indicating any direction of change.

Given the best G over all Es under the standard M practice for a breeding program, it is plausible to adapt the management used for that best genotype in each subregion to best suit local conditions. Here, broad adaptation accepts the globally adapted G from a breeding program operating across the entire region and undertakes agronomic research to optimise local M within subregions; that is, in the real world, this step would be used in the recommendation and marketing of the genotype. To implement this process, we identify six subregions, based on agro-climatology, local experience and plausible geographical marketing segments. The northern zone (CQ) is partitioned into east and west, with CQE containing sites Biloela, Baralaba and Taroom, and CQW containing sites Clermont, Emerald and Springsure (Fig. 1). The central zone (Darling Downs, DD) is also partitioned into east and west, with DDE containing sites Dalby, Pittsworth and Miles, and DDW containing Roma (Fig. 1). The southern zone consists of the Darling Downs south-west (DDSW) containing sites Goondiwindi and Moree, and Liverpool Plains (LP) with sites Gunnedah, Quirindi and Wee Waa.

For each of these six subregions, locally optimal M can be determined by examination of average yield *v.* risk plots for simulations conducted using the standard genotype across the range of available management practices for the sites in the subregion (Fig. 6). The optimal M practice is identified using the same degree of risk aversion as for identifying the standard, broadly adapted genotype (Fig. 5). Whereas in CQW this results in no change to the standard M practice (i.e. solid row configuration; 5 plants m^{-2}), this is not the case in all other subregions. In the higher yielding subregions (CQE, DDE), a shift to greater density is predicted, and this is associated with

increased yield and risk, although risk remains low. In the lower yielding subregions (DDW, DDSW), a reduction in density and shift to single skip-row configuration is predicted, and although this is associated with a slight reduction in average yield, there is a substantial reduction in associated risk (Fig. 6).

Simulated specific adaptation

The previous result considers a fixed, broadly adapted genotype. It remains to determine whether adapting both G and M simultaneously within subregions (i.e. specific adaptation) can add value beyond that found for broad adaptation. For each of the six subregions, locally optimal G \times M can be evaluated by examination of average yield *v.* risk plots for simulations of all possible G and M combinations for the sites in the subregion (Fig. 7). The optimal G \times M practice is identified using the same degree of risk aversion as for broad adaptation. These results indicate that there is the capacity to shift the technology frontier favourably for four of the six subregions, i.e. greater yield at a given level of risk is achievable via specific adaptation for G \times M. These shifts are most noticeable for DDW and DDSW subregions, where an average yield increase of 0.22–0.41 $t\ ha^{-1}$ and slight reduction in failure risk was associated with increasing planting density while planting a genotype with reduced tillering. Similar but smaller shifts in the technology frontier also result for CQW and LP. The changes found for the remaining two subregions (CQE, DDE) are associated with shifts along the technology frontier, rather than with shifts in the frontier. These shifts to more preferable average yield–risk positions are associated with combinations of changes in tillering and maturity.

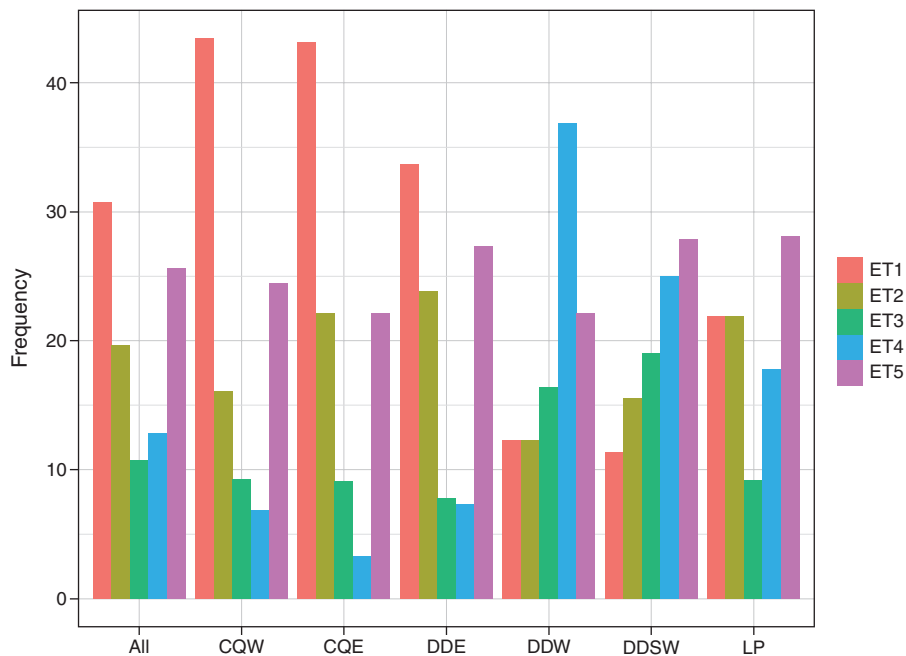


Fig. 8. Frequency of occurrence (%) of each of the five environment types found for sorghum in Australia (colour coded as in Fig. 1) within each of the six subregions defined (CQW, CQE: central Queensland west and east; DDE, DDW, DDSW: Darling Downs east, west, south-west; LP, Liverpool Plains) and over all subregions.

Discussion

Advantage of specific adaptation was greatest in subregions where environment-type frequencies differed most from the distribution for the entire production region

Examination of the frequency of ETs by subregion (Fig. 8) indicated that the two regions showing greatest advantage of specific adaptation (i.e. DDW and DDSW) had distributions of ETs differing greatly from that found over the entire region; that is, these two subregions had the greatest mismatch of ET frequencies to the entire region, with both subregions having fewer mild terminal stress environments (i.e. ET1 and ET2 combined) and a greater proportion of severe terminal stress environments (i.e. ET3 and ET4 combined). There was little difference in the frequency of ET5 across all regions, which highlights its likely importance for broad, but not specific, adaptation. Although the differences in ET frequencies for DDW and DDSW were reflected in lower average yield in these subregions and an associated advantage of moving to skip-row management systems with lower density for broad adaptation (Fig. 6), there was also a considerable additional advantage associated with specific adaptation via a reduction

in tillering combined with an increased density. This likely reflects the value of better matching of canopy leaf-area development with the dynamics of water supply through the crop life cycle in these more water-limited environments. An improved interfacing of the degree of water availability with patterns of water use through the crop life cycle can allow enhanced water use post-anthesis and improved yield even though total water use over the entire crop may not be changed (Sadras and Connor 1991; Turner 2004; Hammer 2006; van Oosterom *et al.* 2011). The dynamic perspective through the crop cycle, facilitated by the modelling approach, exposes a degree of interdependence between timing of water use as transpiration and realised harvest index, which is not captured in static models, for example, in relationships between total crop evapotranspiration and yield (Passioura and Angus 2010). This finding is also consistent with that found for skip-row configurations (Whish *et al.* 2005) where pre-anthesis 'water-saving' was shown to enhance yield in severe terminal drought situations by extending growth in the post-anthesis period and thus improving harvest index without changing total water use and total biomass production.

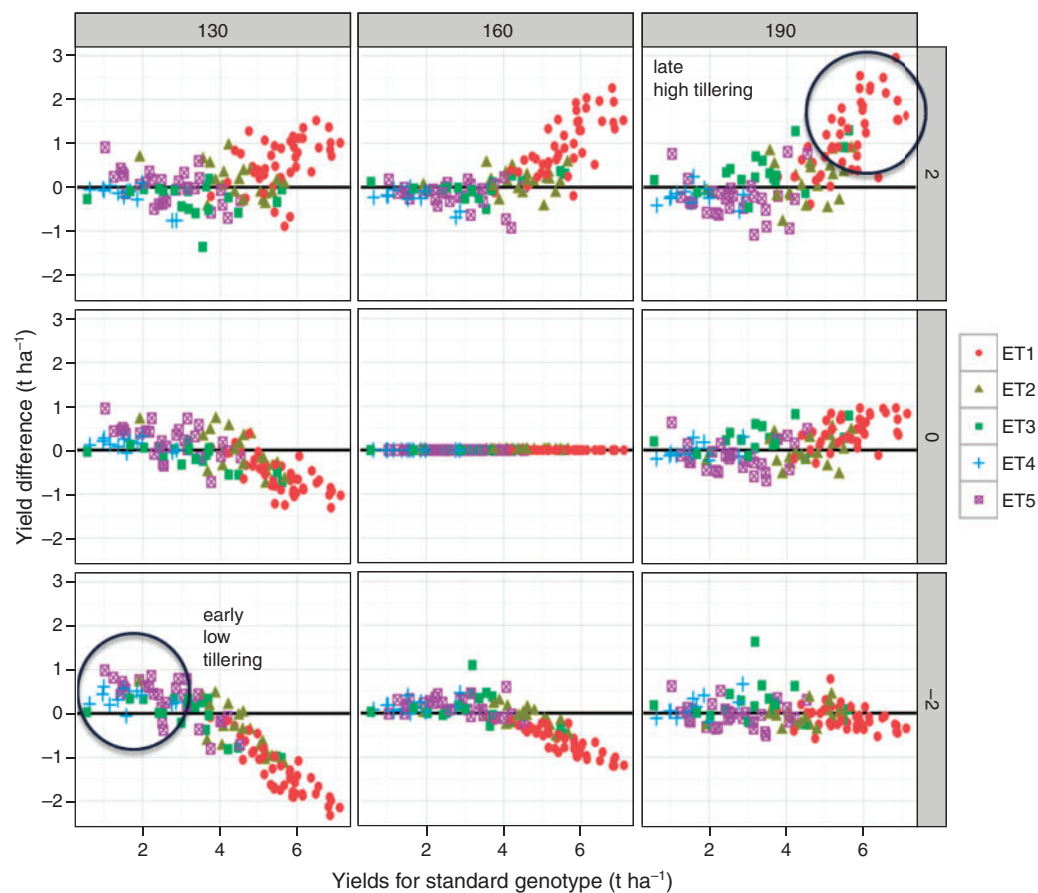


Fig. 9. Yield difference v. yield of the standard genotype (medium-maturing (160 degree-days thermal time requirement) and medium-tillering (0)) for genotypes differing in maturity (earlier (130 degree-days requirement) to later (190 degree-days requirement) columns from left to right) and tillering (high (+2) to low (-2) rows from top to bottom) for a sample long-term simulation at Emerald. Each point represents 1 year of the simulation and colours indicate the environment type for that year.

Although subregions differ in frequency of ETs, each subregion retains considerable variability in the occurrence of different ETs, so that even in DDW and DDSW, there remains a >20% occurrence of mild terminal stress environments (ET1 and ET2). Hence, effects of specific adaptation $G \times M$ options within each subregion are averaged over a diverse set of ETs. This likely diminishes any advantage associated with specific adaptation based solely on subregions.

Environment type dominates effects on specific adaptation

Examination of yield advantages associated with specific trait combinations indicated strong association of yield advantage with environment type (Fig. 9). For the specific simulation example (planting date, soil condition, row spacing, density) presented for Emerald, CQ, there is a significant yield advantage to a late-maturing, high-tillering type in most years classified as ET1 or ET2, whereas an early-maturing, low-tillering type was advantageous in most years classified as ET4 or ET5. There was no clear distinction for years classified as ET3. As noted above, this finding likely reflects the better matching of canopy development and demand for water with the available supply. In ET1 or ET2 seasons, the more favourable availability of moisture allows a larger canopy to develop and flourish, and generate higher yield. However, this is disadvantageous in ET4 or ET5 seasons because the water supply is inadequate, so the larger canopy will deplete available moisture more rapidly, leaving less available for post-anthesis growth and causing yield deficit. In these situations, the more conservative canopy development and earlier flowering associated with early maturity and lower tillering generates yield advantage by retaining more water for post-anthesis growth (van Oosterom *et al.* 2011). The overall effect on specific adaptation for a region (Fig. 7) will ultimately depend on the mix of environment types.

This finding suggests that specific adaptation based on ET, rather than on location, would likely be more useful. However, this would require forewarning of ET to be implemented. Although it is possible to consider advance indicators of ET, such as soil water content at sowing combined with seasonal climate indicators based on phase of the El Niño Southern Oscillation (Stone *et al.* 1996) or other factors, unless this generates reliable forecasts, the degree of advance over accepting the mix of ETs associated with location will likely be limited. An additional complication for breeding companies would be the need to have greater seed stocks on hand to support a more dynamic choice of hybrids close to sowing time. Nonetheless, research into this approach is warranted to consider how to improve recommendations of hybrids, especially where starting conditions and local weather conditions favour a greater likelihood of specific ETs in a given year.

Concluding remarks

We have explored the value to crop improvement of sorghum in Australia that might be gained by pursuing specific local adaptation for $G \times M$ rather than the more traditional, broad adaptation approach. The results of the simulation study suggest that significant improvements in yield and or failure

risk are possible through seeking locally optimal $G \times M$ combinations, but the degree of advantage varies with subregion. Geographic subregions with the greatest mismatch of frequencies of major environment types compared with those for the entire production region show greatest advantage for specific adaptation. The value of adopting specific adaptation in crop improvement will depend on the size of the potential benefit *v.* associated additional costs of implementing such a program. This will likely depend on the size of the market in areas of greatest effect. In this study, substantial market growth in some areas would be needed for this to be the case. However, the dilemma is that different plant types and management would be advantageous in fostering such industry growth.

The variability in environment types from year to year within subregions remains the main factor limiting the value of specific adaptation in production. Our results suggest that considerably greater value from specific adaptation would be possible if it could be based on environment type rather than geography. However, this would require better advance indicators or predictors of environment-type likelihood than that conferred by location alone. This would be a suitable avenue for further research.

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