

RESEARCH PAPER

Environment characterization as an aid to wheat improvement: interpreting genotype–environment interactions by modelling water-deficit patterns in North-Eastern Australia

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Abstract

Genotype–environment interactions (GEI) limit genetic gain for complex traits such as tolerance to drought. Characterization of the crop environment is an important step in understanding GEI. A modelling approach is proposed here to characterize broadly (large geographic area, long-term period) and locally (field experiment) drought-related environmental stresses, which enables breeders to analyse their experimental trials with regard to the broad population of environments that they target. Water-deficit patterns experienced by wheat crops were determined for drought-prone north-eastern Australia, using the APSIM crop model to account for the interactions of crops with their environment (e.g. feedback of plant growth on water depletion). Simulations based on more than 100 years of historical climate data were conducted for representative locations, soils, and management systems, for a check cultivar, Hartog. The three main environment types identified differed in their patterns of simulated water stress around flowering and during grain-filling. Over the entire region, the terminal drought-stress pattern was most common (50% of production environments) followed by a flowering stress (24%), although the frequencies of occurrence of the three types varied greatly across regions, years, and management. This environment classification was applied to 16 trials relevant to late stages testing of a breeding programme. The incorporation of the independently-determined environment types in a statistical analysis assisted interpretation of the GEI for yield among the 18 representative genotypes by reducing the relative effect of GEI compared with genotypic variance, and helped to identify opportunities to improve breeding and germplasm-testing strategies for this region.

Key words: Drought, environment classification, genotype–environment interaction, modelling, water deficit, wheat.

Introduction

Progress in plant improvement for yield relies on the identification of genotypes better adapted to their environment. However, the complexity of genotype–environment interactions (GEI), in particular in drought-prone environ-

ments, can reduce heritability of yield, i.e. the ability statistically to identify superior genotypes. In the ‘target population of environments’ (TPE), i.e. the set of environments in which cultivars can be grown within the

geographical area targeted by a breeding programme (Comstock, 1977), GEI impede plant breeding progress for both (i) broad adaptation across the TPE and (ii) adaptation to specific types of environments within the TPE (Cooper and Hammer, 1996; Löffler *et al.*, 2005; Dreccer *et al.*, 2008; Mathews *et al.*, 2008).

The effectiveness of genotype evaluation as part of breeding is influenced by (i) understanding of GEI and (ii) the degree to which the environments sampled in the multi-environment testing trials (MET) represent the TPE (Podlich and Cooper, 1998). While statistical approaches to estimate GEI have developed over more than 50 years, it has only been relatively recently that the cause of GEI has been investigated, with specific environment variables being included in mixed models (Voltas *et al.*, 1999; van Eeuwijk *et al.*, 2005) and with environment classifications being identified in principal component analysis (Annicchiarico and Perenzin, 1994; Yan *et al.*, 2000). In parallel with these methodological improvements to analyse GEI within a set of trials (MET), characterization of the complete TPE has been conducted based on (i) climate and soil data (Runge, 1968; Pollak and Corbett, 1993; Hodson and White, 2007), (ii) physiological traits that integrate various stresses that plants experience, for example, flowering date or yield (Chauhan *et al.* 2008; Hernandez-Segundo *et al.*, 2009), and (iii) stress index determined with crop models (Chapman *et al.*, 2000a, b).

In practice, breeders typically characterize their trials based on check-variety performance rather than environmental data, undertaking as many trials as resources allow. While this approach provides a solid platform for statistical analysis of GEI within their MET, it may often misrepresent the TPE, mainly due to cost limitation and the impracticality of large-scale MET to sample the TPE. By contrast, modelling tools applied to multi-site long-term studies allow a more comprehensive environmental sampling (Löffler *et al.*, 2005; Hammer and Jordan, 2007). Furthermore, these tools can also estimate local environmental variables and account for the interactions between the plants and their environment (*e.g.* Chelle, 2005; Chenu *et al.*, 2008), which thus allow more detailed physiological interpretation of GEI basis (Reymond *et al.*, 2004; Chenu *et al.*, 2007).

Crop models capture feedback between plant growth and soil water depletion and have been shown to characterize water-limited environments better when compared with standard indices computed from climatic data (Muchow *et al.*, 1996). Applying this method, Chapman *et al.* (2000a) characterized the water-deficit patterns experienced by sorghum crops over a long-term period in six locations, and grouped them into environment types. The frequency of these environment types at specific locations correlated with the patterns of discrimination (principal component analysis) for yield among hybrids at those locations over *c.* 15 years of testing. Chapman *et al.* (2000b) also used these environment types to characterize the environment of the Australian sorghum-growing area during the 20th century and concluded, as did Podlich and Cooper (1998), that

weighting the multi-environment trials of breeding programmes, based on their representativeness in the TPE, would improve the rate of yield gain. Furthermore, a recent study on wheat showed that the negative influence of GEI on ranking of wheat genotypes could be reduced when trials were classified based on crop drought patterns (Chapman, 2008).

This study aimed to characterize the water-deficit patterns of an entire TPE and to demonstrate the utility of this broad characterization for local breeding trials. The focus here is on the north-eastern wheat-growing area of Australia, as this extensive TPE (more than 1500 km N–S and *c.* 500 km E–W) experiences large spatial and temporal variability in the seasonal pattern of water availability due to contrasting soil types, management systems, and inter-annual rainfall (Potgieter *et al.*, 2002). In such environments, genotype ranking varies greatly among locations and seasons, which limits the potential rate of genetic gain by decreasing the effective heritability for selection (Brennan *et al.*, 1981; Basford and Cooper, 1998). Here, the goals were to (i) use historical weather data to characterize the nature of the main water-deficit patterns occurring in the TPE, (ii) determine the frequency of these main environment types for each region within this area, for typical management and over a long-term period, and (iii) analyse a set of trials to demonstrate that this typology of the TPE can aid interpretation of GEI. Simulations were performed over 119 years, for 12 regions (14 locations) distributed across north-eastern Australia, with representative soil types for each region. Weighting factors were assigned to each site (location×soil combination) so that all sites corresponded to similar fractions of the total area of wheat planted. The nature and frequency of major environmental types were defined based on seasonal water-deficit patterns that were centred around flowering. These environment types were used to analyse and interpret the genotypic variability for yield of 18 lines selected from previous broad-scale evaluations in 16 irrigated and rain-fed trials (MET).

Materials and methods

Overview

The wheat-cropping area of north-eastern Australia was divided into 12 regions, each represented by 1–3 sites (combinations of weather station×soil; Table 1). These sites were chosen to have long-term and good quality climatic weather data, and to have soil characteristics as representative as possible of the region (soil information had been collected by local experts from the Agricultural Production Systems Research Unit (APSRU), <http://www.asris.csiro.au/grapher/APSRUkml.aspx> and from Daniells *et al.*, 2002). A weighting factor (Table 1) was assigned so that each site represented between 73 000 and 91 000 ha of wheat planted area (average data over 1975–1999; Australian Bureau of Statistics, <http://www.abs.gov.au/>).

Using the APSIM crop model (Wang *et al.*, 2002), an initial set of simulations was performed over 119 years of historical-climatic data to characterize sowing date and soil water profile at planting, which would be encountered at each site. Based on these initial

Table 1. Characteristics of the sites and soils chosen to represent the north-eastern wheat-cropping area of Australia

The main cropping areas (Central Queensland, South Queensland, and Northern New South Wales) were subdivided into smaller regions. Weighting factors were imposed for the sites (combination of weather station×soil) so that the number of situations per region was proportional to its average area planted to wheat. Plant available water content (PAWC) is indicated for the different soils used in the simulations. The five different levels of PAWC used at sowing in each site each corresponded to 20% of the sowing soil-water conditions estimated from an initial set of simulations.

Cropping area	Region	Weather station	Latitude	Longitude	Soil PAWC (mm)	PAWC at sowing (mm)	Weighting factor
Central Queensland	Central Highlands	Emerald	-23.53	148.16	134	107-125-131-134-134	1
	Dawson Callide	Biloela	-24.38	150.52	198	121-154-186-196-198	1
South Queensland	Western Darling Downs	Roma	-26.57	148.79	119	94-109-118-119-119	1
	Central Darling Downs	Miles	-26.66	150.180	159	105-134-149-159-159	1
					201	105-137-167-191-201	1
	Eastern Darling Downs	Dalby	-27.17	151.27	205	119-164-193-203-205	1
					285	124-169-206-234-282	1
	St George	St George	-28.04	148.58	169	91-120-147-164-169	1
	Southern Darling Downs	Goondiwindi	-28.55	150.31	159	94-121-146-157-159	1
					222	102-129-158-189-222	1
Northern New South Wales	Moree	Moree	-29.50	149.90	153	90-116-141-150-153	1
					194	93-122-149-180-194	3
					238	100-124-155-190-233	1
	Narrabri	Narrabri	-30.34	149.76	232	107-151-181-220-232	2
		Walgett	-30.04	148.12	232	93-109-132-165-225	1
	Coonamble	Coonamble	-30.98	148.38	197	87-106-134-160-191	2
	Dubbo	Dubbo	-32.21	148.57	128	109-128-128-128-128	1
					142	104-131-141-142-142	1
	Gunnedah	Coonabarabran	-31.27	149.27	142	128-139-142-142-142	1
		Gunnedah	-30.98	150.25	153	92-121-142-151-153	1
					282	102-135-169-206-262	1

conditions, a second set of simulations was run to characterize the seasonal water-deficit patterns occurring at the different sites for the 119 years. Cluster analysis was applied to this dataset to identify the major environment types of the wheat-growing area of north-eastern Australia.

A third set of simulations was performed to characterize the water-deficit pattern of 16 irrigated and rain-fed trials and to identify the environment type of each trial. This environmental classification was used in genetic analyses to interpret the GEI for yield in this MET.

Determination of the initial conditions (sowing date and soil water at sowing) in the target population of environments (TPE)

To be successful in this summer-dominant rainfall area, wheat crops require a rainfall event before planting, and sufficient stored water for access later during their development. To characterize the initial conditions (sowing date and soil water content at planting) occurring in each location×soil combination (called 'site'), cropping system simulations were run using the APSIM-Wheat crop model (Keating *et al.*, 2003) for each site for the years 1889 to 2008. In each simulation, a fallow (5–8 months) followed by a wheat crop (Hartog cultivar, no nitrogen limitation, minimum tillage, and no weed, pest or disease) and followed by another fallow was simulated to mimic farmer practices and estimate (i) the timing of planting events and (ii) the moisture retained in the soil at these dates. The planting opportunities were estimated within an 8-week planting window specific to each region, as consistent with local farmer practice. Based on consultations with experienced agronomists and previous studies (Hammer *et al.*, 1987), a planting opportunity was defined to occur when (i) the fraction of extractable water was between 0.6 and 0.9 in the surface soil layer, so that

seeds could germinate, but the soil was dry enough for sowing traffic, (ii) the extractable stored soil water in the entire profile was higher than 80 mm, and (iii) cumulative rainfall in the previous 10 d was at least 10 mm.

This initial set of simulations revealed that sowing opportunities were uniformly distributed throughout the planting window. Given this uniform distribution in planting opportunities, sowing dates for the second set of simulations (see next section) were chosen to be 2-weeks apart within the planting window, with each date representing around 20% of the sowing opportunities occurring at each site. Sowing dates were: 15 April, 1 May, 15 May, 1 June, and 15 June for Central Queensland; 1 May, 15 May, 1 June, 15 June, and 1 July for South Queensland; and 15 May, 1 June, 15 June, 1 July, and 15 July for northern New South Wales. For each site, the initial soil water conditions were found to be similar for all the sowing opportunities, showing that rainfall occurring during the previous fallow was more important than the small rainfall events occurring during the planting window. Hence, the second set of simulations used five different initial soil water conditions for each site (without distinction across sowing dates; Table 1), each representing 20% of the conditions encountered during the planting window for the considered sites over 119 years.

Crop simulation and environmental characterization in the TPE

Simulations were performed for a standard check variety, Hartog, at the 25 sites distributed over the actual wheat-cropping area of north-eastern Australia (Table 1). Simulations were performed in APSIM, for the years 1889 to 2008, with no biotic constraint, no nitrogen limitation (180 kg ha⁻¹ of nitrogen in the soil at sowing), with minimum tillage, for the five planting dates and five initial soil water conditions identified above (25 simulations per year and per site), i.e. *c.* 75 000 simulations in total.

Each environment (location×year×sowing date×initial soil water combination) was characterized based on a daily crop water stress index, corresponding to the ratio between water supply and demand. This index indicates the degree to which the potential water supply that depends on the volume and wetness of soil explored by roots is able to match the water demand of the canopy, which is influenced by radiation and temperature and air humidity conditions (Chapman *et al.*, 1993, 2000a, b).

For each simulation, the temporal pattern of this water stress index was centred at flowering and averaged every 100 °Cd (between emergence and maturity). A cluster analysis was applied to these 75 000 water-deficit patterns using the partitioning clustering function *clara* in the R statistical package (R Development Core Team, 2008) in order to identify the three major environment types ('ET1-2-3') encountered in the TPE. This method is based on minimizing the sum of the dissimilarities (i.e. pair-wise distances) between the pattern of water stress index of (i) each environment of the TPE and (ii) the median situation of the environment type considered. The partitioning clustering method is better suited to this large dataset than the hierarchical method that was used for smaller datasets in previous studies. An average pattern of water deficit was calculated to describe each environment type. The occurrence of different environment types was interpreted with respect to different regions, years, starting soil water conditions, and sowing date.

Multi-environment trials (MET): experimental conditions and simulations

Eighteen wheat lines (*Triticum aestivum* L.; Cooper *et al.*, 1997) were grown in 16 field trials (Qiao *et al.*, 2000, 2004) in the north-eastern wheat-growing area of Australia, between 1994 and 1996 (Table 2). These lines were selected in a breeding programme to represent advanced CIMMYT lines and a few local check genotypes, for yield performance and GEI for yield in Queensland drought environments (Cooper *et al.*, 1994a, b). The released cultivars ('named' genotypes, e.g. 'Hartog') and broadly-adapted wheat lines from the 17th International bread wheat nursery

distributed by CIMMYT, Mexico ('numbered' genotypes, e.g. '17IB206') that were studied here are: Hartog ('G1'), Cunningham ('G2'), Banks ('G3'), Pelsart ('G4'), 17IB7 ('G5'), 17IB30 ('G6'), 17IB31 ('G7'), 17IB38 ('G8'), 17IB53 ('G9'), 17IB64 ('G10'), 17IB92 ('G11'), 17IB129 ('G12'), Seri (17IB206, 'G13'), 11IB50 ('G14'), Genaro ('G15'), 17IB173 ('G16'), Sunco ('G17'), and Kite ('G18').

In the 16 trials, plants were sown at a density of 85–100 plants m⁻², in c. 15 m² plots, with a triple lattice, three replicate design (Qiao *et al.*, 2000, 2004). In order to test the model, above-ground biomass was measured twice before flowering and flowering date was recorded for the standard Hartog cultivar. Yield was measured at maturity for the 18 lines.

MET trials were simulated for cultivar Hartog using climatic and soil data collected at each site, and their water-deficit patterns were determined as described above for the TPE. The trials were classified based on which environment type from the TPE they were the most similar to, i.e. based on the minimum sum of squared differences for the trial water-deficit pattern compared with the water-deficit pattern of the TPE environment types.

MET: statistical analyses and heritability

The variance components for the genotype and GEI were estimated for both:

- (i) the classical compound symmetry model:

$$P = E + G + GEI + \varepsilon \quad (1)$$

- (ii) and a nested compound symmetry model to test the G and GEI contribution within each environment type:

$$P = E + G_{\text{within each ET}} + GEI_{\text{in each ET}} + \varepsilon \quad (2)$$

where P is the phenotype (yield); E is the fixed environment effect; G and $G_{\text{within each ET}}$ are the random genotype effects in all environments and within each environment type, respectively; GEI and $G_{\text{within each ET}}$ are the random genotype-by-environment effects

Table 2. Characteristics of the multi-environment trials (MET), which comprised 16 trials carried out across the north-eastern wheat-cropping area of Australia (experiments described by Qiao *et al.*, 2000, 2004)

Trial	Year	Location	Latitude	Longitude	Sowing date	Fertilization ^a (kg ha ⁻¹)	Irrigation treatment	Total water supply (mm) ^b	Environment type
E1	1994	Gatton	-27.55	152.33	10 May	174	Irrigated	473.4	ET1
E2	1994	Jimbour	-6.94	151.13	19 Jun	150	–	111.3	ET3
E3	1994	Meandarra	-27.32	149.87	21 Jun	150	–	75.4	ET3
E4	1994	Oakleigh	-27.32	151.44	31 May	150	–	145.3	ET3
E5	1994	Fernless	-23.92	148.39	08 May	106	–	4	ET3
E6	1994	The Gum	-27.33	150.20	13 Jun	150	–	79.8	ET3
E7	1995	Billa Billa	-28.10	150.31	28 May	150	–	86.8	ET3
E8	1995	Biloela	-24.40	150.50	22 May	130	Partially irrigated	336.2	ET3
E9	1995	Bungunya	-28.42	149.65	28 May	128	–	133.7	ET3
E10	1995	Gatton	-27.55	152.33	14 May	174	Partially irrigated	248.7	ET2
E11	1995	Tummalville	-27.87	151.48	25 Jun	150	–	406.3	ET2
E12	1996	Bungunya	-28.42	149.65	27 May	120	–	152.3	ET2
E13	1996	Gatton	-27.55	152.33	23 May	196	Irrigated	288.7	ET1
E14	1996	Jimbour	-26.94	151.13	06 Jun	150	–	239.9	ET1
E15	1996	Moonie	-28.33	150.30	02 Jun	150	–	254.9	ET2
E16	1996	Fernless	-23.92	148.39	10 May	111	–	100.8	ET2

^a Fertilization at sowing.

^b Cumulative rain and irrigation for the sowing-harvest period.

Table 3. Heritability (A) and mixed model analyses of yield in the MET either without (B), or with (C), the environment characterization. (B) Classical compound symmetry model (equation 1). (C) Compound symmetry which nests the components for the genotypes (G) and for the genotype–environment interactions (GEI) within independently assigned environment types.

(A) Heritability		
Environment group	Heritability	
All trials	0.592	
ET1 trials	0.564	
ET2 trials	0.408	
ET3 trials	0.467	

(B) Classical GEI model		
Source	Variance component	Standard error
G	0.053	0.022
GEI	0.193	0.018
Residual variance	0.073	

(C) Model with the environment characterization		
Source	Variance component	Standard error
$G_{\text{within ET1}}$	0.124	0.072
$G_{\text{within ET2}}$	0.054	0.039
$G_{\text{within ET3}}$	0.036	0.018
$GEI_{\text{within ET1}}$	0.214	0.057
$GEI_{\text{within ET2}}$	0.268	0.049
$GEI_{\text{within ET3}}$	0.130	0.018
Pooled residual variance	0.073	

in all environments and within each environment type, respectively; and ε is the residual trial error.

The genotype mean heritability (h^2) was estimated for each environment type and for all trials of the MET, as:

$$h^2 = G / (G + GEI/n_E + \varepsilon/n_E \times n_R) \quad (3)$$

where G , GEI , and ε are the variance components and the residual error described above, n_E is the number of environments (i.e. number of trials for the considered environment type or for the MET), and n_R is the number of replications per trial (three for these trials).

In order to estimate the number of trials needed to have an acceptable heritability in the different environment groups (as presented in Fig. 7), an expected heritability was also calculated for a number of trials (n_E) varying from 1 to 10 for each group of environments, with the values of G , GEI , and ε as observed in the MET (Table 3), and with two repetitions ($n_R=2$; as in a usual breeding trial).

Analyses were performed with genotype means (BLUEs, Best Linear Unbiased Estimates) and relative weights from existing analyses (Qiao *et al.*, 2000), using the ASREML software (Gilmor *et al.*, 1997, 2002) and the methods described by Cullis *et al.* (1996) and Chapman *et al.* (2000a).

Phenotypic correlations among the original BLUEs were calculated for all possible pairs of trials, both within and across environment types, with R (R Development Core Team, 2008). A principal component analysis was applied to the $G \times E$ matrix of BLUEs with the environment standardized data transformation

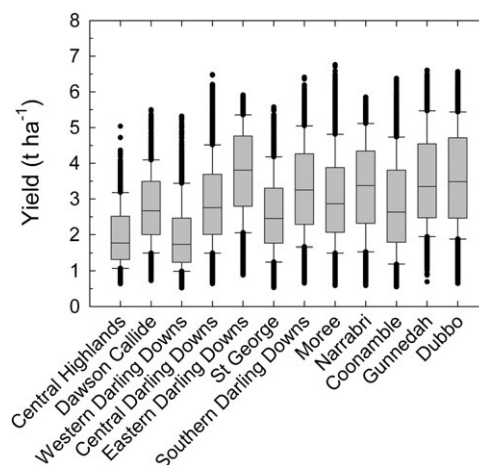


Fig. 1. Distribution of the simulated yield of cv. Hartog over 119 years for the different regions, ordered north to south. Upper and lower dimensions of the boxes represent the third and first quartiles, the medians are indicated by bars inside the boxes, and the circles represent outlying values below the 10th and above the 90th percentiles.

(Fox and Rosielle, 1982; Cooper and DeLacy, 1994). The analysis and the resulting biplot were produced using R.

Results

Three main environment types for the wheat-cropping area of north-eastern Australia

Long-term simulations in the wheat-cropping area of north-eastern Australia highlighted the high variability of wheat yield across years and regions (Fig. 1), in accordance with wheat production data (Potgeiter *et al.*, 2002). Average yield ranged between 2.0 t ha⁻¹ (Central Highlands and Western Darling Downs) and 3.7 t ha⁻¹ (Eastern Darling Downs), with an inter-annual range of more than 4 t ha⁻¹ between the most extreme years in each region. The occurrence of water-deficit patterns was also highly variable across regions and seasons, ranging from stress-free environments where the simulated yield reached close to 7 t ha⁻¹, to severely stressed crops that yielded 0.5 t ha⁻¹. Given the initial soil-water conditions required for planting, there was no crop failures. Note that in the real-world, crop failures can occur as the result of a catastrophic event due to pests, flooding etc (not simulated here) or when farmers choose to plant crops in high-risk conditions (e.g. low initial soil water).

Using a cluster analysis, three major water-deficit patterns were identified, explaining 65% of the variation in the c. 75 000 simulations (Fig. 2): the first environment type (ET1) comprised situations where plants were effectively not limited by water or experienced only short-term water deficit; the second environment type (ET2) was characterized by mid-season water deficit, starting during the vegetative period and relieved by rainfall events during grain filling; and the third environment type (ET3) also had

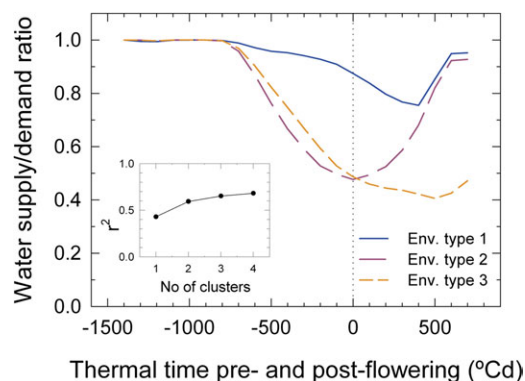


Fig. 2. Water-stress index throughout the crop cycle, represented as a function of thermal time relative to flowering, for three environment types (ET1–2–3) identified in the north-eastern wheat-growing area of Australia, for cv. Hartog. Inset, coefficient of determination for the clustering of the different number of environment types. This water stress index corresponds to a water supply/demand ratio that integrates the crop demand (potential transpiration depending on the climate and plant status) and resource supply available to the roots on the considered date. A ratio of 1 indicates no water stress, while a ratio of 0 corresponds to a full-stress, with no water available to the crop. Data of all the environments of the TPE were centred at flowering, averaged every 100 °Cd and clustered in three environment types. The data presented here correspond to the average of the water stress index of the different environments of the TPE that belonged to ET1–2–3, respectively.

a mid-season water deficit beginning at around the same time as in ET2, but continuing through to plant maturity.

Occurrence of the environment type highly varied across regions, over time and among management practices

The distribution of the three environment types varied across regions (Fig. 3). For the entire north-eastern Australian wheat-growing area, the frequency of occurrence of the environment types ET1:2:3 was 16:34:50%, respectively. The generally stress-free conditions (ET1) only represented between 6% and 38% of the years among the different regions, while the severe ET3 stresses occurred at 33–65% depending on the region. Except for ET3, which was more frequent in the driest years, the frequency of occurrence of the environment types was poorly correlated with the cumulative rainfall within the season (data not shown). For example, the Dawson Callide in the north is one of the regions with lowest rainfall, but it had a similar frequency of ET1 to the highest rainfall regions in the south (Dubbo and Gunnedah).

High variability in the frequency of different environment types has also been observed over the years (Fig. 4A). Decades when more than 50% of sites in the wheat-growing area experienced an ET1 were relatively rare (0–3 years per decade), while they frequently had more than 50% of sites with ET3 (2–7 years per decade). Note that the results

presented here do not correspond with the historical occurrences of these environment types but to their occurrence when considering years as independent, using identical initial conditions (sowing date and soil water at sowing). This remark also applies to the simulated yield results. Nonetheless, the results reflected well the incidence of El Niño Southern Oscillation (ENSO) events and their effect on wheat yield (Potgieter *et al.*, 2002).

Simulated yield was highly constrained by the water-deficit pattern (Figs 3, 4A). In each region, crops grown in ET1 seasons had the highest yield (Fig. 3). In ET2, crops tended to yield more than in ET3; however, the yield distribution in ET2 and ET3 was similar for many regions (e.g. Central Highlands). The range of simulated yield for each environment type remained broad, and the large overlaps in yield performance among environment types indicated (i) the importance of other environmental factors not included in this analysis (e.g. due to warmer temperatures and shorter times to flowering, mean yields in the ET1 seasons in the northern regions (Central Highlands and Dawson Callide) were at least 0.6 t ha⁻¹ lower than in other regions), and (ii) the limitation of clustering so many environments into three groups, so that short-term stresses affecting yield were smoothed in the averaging and clustering process.

Management practice also had an impact on the frequency of occurrence of the different environment types. For the standard variety used (Hartog), delaying sowing reduced the occurrence of ET1, and increased the occurrence of ET2 (Fig. 4B): later-sown crops were subjected to more water stress around flowering, as this period of their development occurred under higher temperature and water demand conditions in the latter part of spring.

As might be expected, increased initial soil water at any sowing date led to an increase in the frequency of ET1 and a decrease in the frequency of ET2 and ET3. This impact of initial water was greatest at the earlier sowing dates, and decreased with the later sowing dates.

Environment characterization helped in understanding the genotype–environment interactions in the MET

Sixteen trials of a breeding programme (MET; Fig. 5A) were simulated and their water-deficit patterns were characterized for the cultivar Hartog. The simulations over-predicted biomass production slightly, but predicted final yield well for this genotype (Fig. 5B, C), suggesting that transpiration patterns and water-deficit responses were reasonably well approximated.

Compared with the entire TPE, the 16-trial MET, which included several partially-irrigated trials, slightly over-represented ET1 (22% versus 16% in the TPE), and slightly under-represented ET2 (28% versus 34%), while both the TPE and the MET had the same proportion of ET3 (50%).

In the MET, average yield decreased substantially from ET1 to ET3 for all lines (Fig. 6A), with the GEI variance component being more than three times that of the genotype component (Table 3). Three broadly-adapted lines

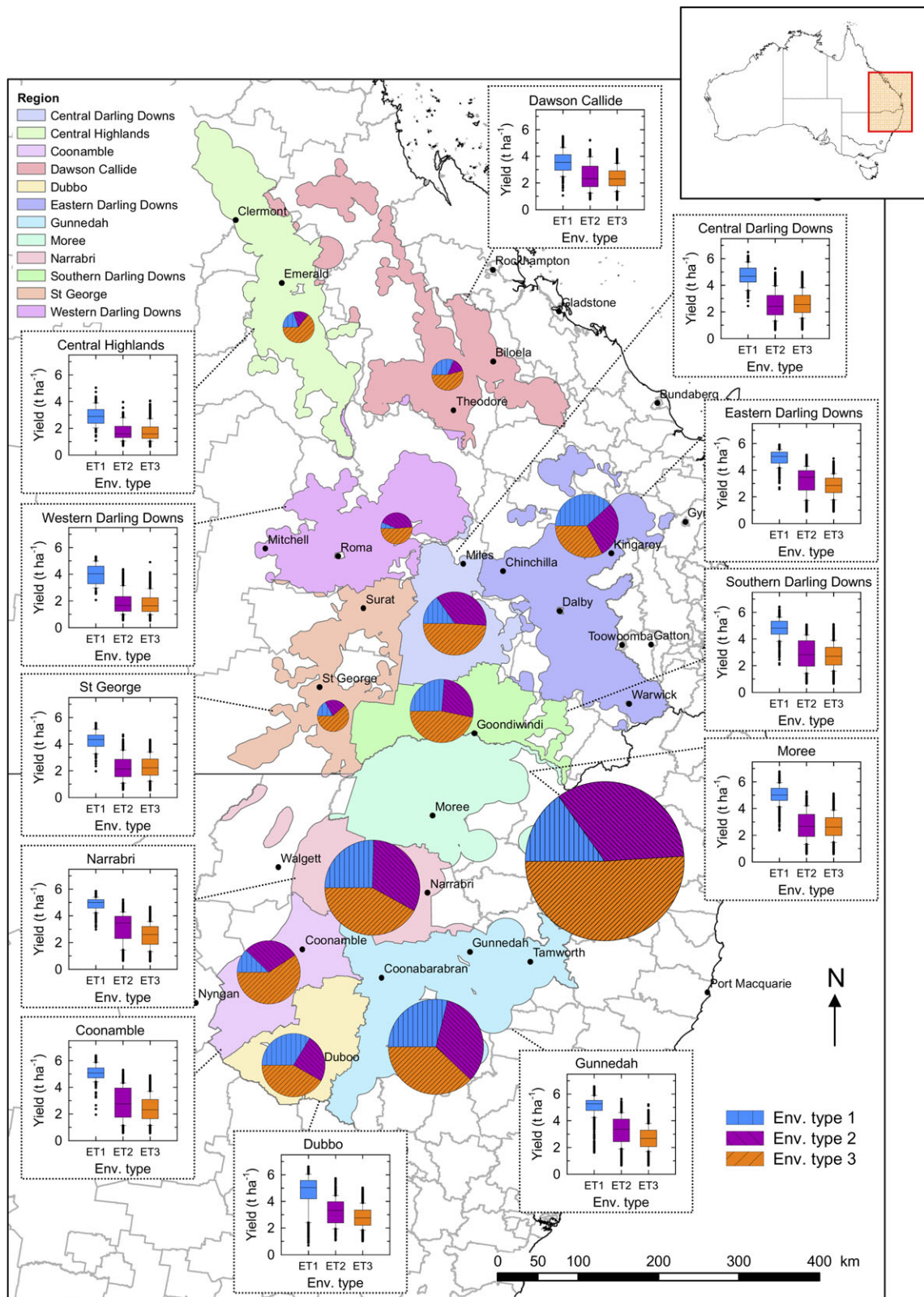


Fig. 3. Map of the frequencies of each environment type (pie charts) and simulated yield distribution of cv. Hartog within each environment type (box plots), for the different regions of the north-eastern wheat-growing area of Australia. Data from simulations over 119 years of historical climate data. The size of the pie charts is proportional to the wheat-planted area in the associated region.

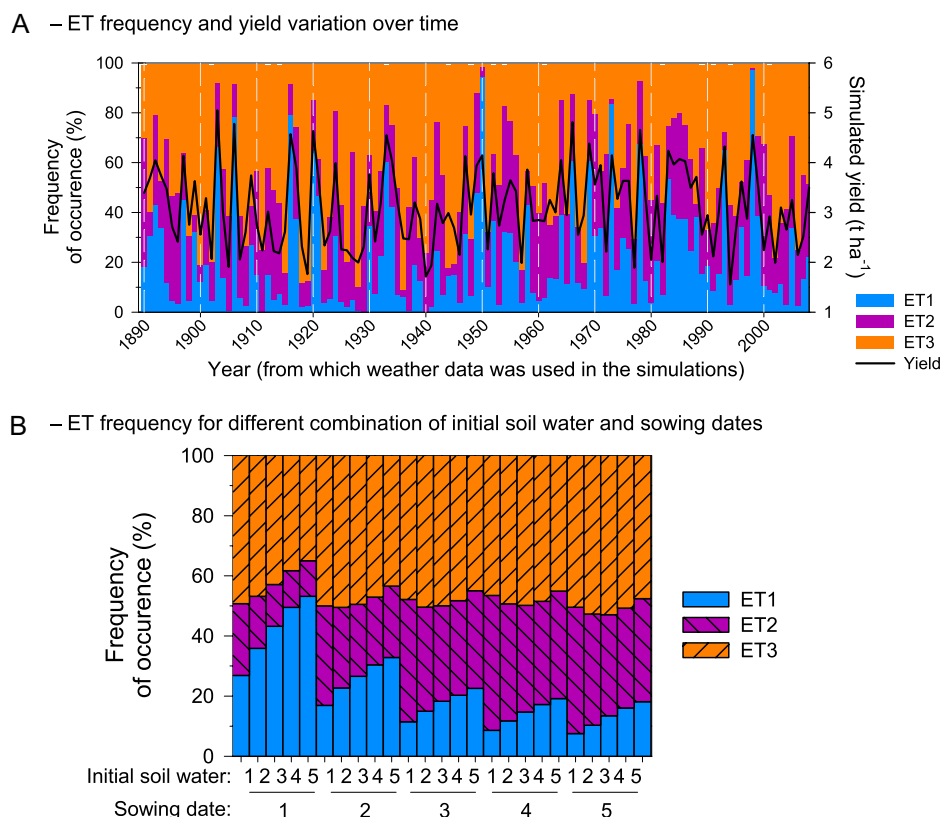


Fig. 4. Frequency of occurrence of the different environment types (A) over 119 years of climatic data in the north-eastern wheat-growing area of Australia, and (B) for each combination of sowing date and initial soil water used in the simulations. (A) Annual yield averaged for the area was superimposed as a line. Note that the yield and environment type simulated here does not correspond to historical yield and drought occurrence, as initial conditions in the simulations were calculated for the entire TPE and not for a particular year (i.e. the same set of sowing dates and initial soil water for each year in the simulations). (B) Sowing dates from the earliest (1) to the latest (5) were separated by 2 week intervals. Initial soil water increased from the lowest (1; most severe conditions) to highest (5), each representing 20% of the initial soil water encountered in the initial round of simulations. Frequency data presented here correspond to all the simulations performed (all sites over 119 years).

were high yielding across most trials (lines 17B30, G6; Seri, G13, and Genaro, G15) but the ranking of the remaining genotypes varied substantially between trials (Fig. 6A).

The best phenotypic correlations were found for trials within each environment type, and between trials in ET1 and ET2 (Fig. 6B). Consistently, trials in ET1 and ET2 were grouped together in the principal component analysis (Fig. 6C), although the average yields in ET1 were substantially higher than in ET2 for all lines. Poorer correlations were observed between trials in ET2 and ET3, and between trials in ET1 and ET3. Accordingly, ET3 trials were quite distinct from the ET1–2 group in the principal component analysis (Fig. 6C).

Including the environment characterization in the statistical models assisted in interpreting GEI of the MET (Table 3). In the classical analysis (equation 1), the genotype component was 27% of the GEI component. When considering the different environment types (equation 2), this ratio increased substantially for the trials in ET1 (58%), slightly decreased in ET2 (20%), and remained unchanged in ET3 (27%). This indicated that genotype performance is more predictable in stress-free environments than under drought, although phenotypic correlations within ET1, 2,

and 3 had similar median values (Fig. 6B). Accordingly, heritability was higher for the ET1 trials (h^2 of 0.56) than for the other environment types (h^2 of 0.41–0.47; Table 3).

A consequence of the differences in G and GEI variance components observed across environment types is that the number of trials required to obtain a given level of heritability depends on the environment type to which these trials belong (Fig. 7). For instance, breeders who target a heritability of 0.6, would need to harvest about 3, 9 or 7 trials in ET1, ET2 or ET3 environments, respectively. This interpretation should be valid across the stages of testing in this breeding programme, as the genotypic diversity of the lines is representative of that being evaluated by the breeding programme.

Discussion

The north-eastern wheat-growing area of Australia has a highly variable TPE in terms of drought patterns

Annual wheat production in north-eastern of Australia is highly dependent on rainfall, which varies greatly across years. From 75 000 simulations using historical weather data, three major environment types were identified to

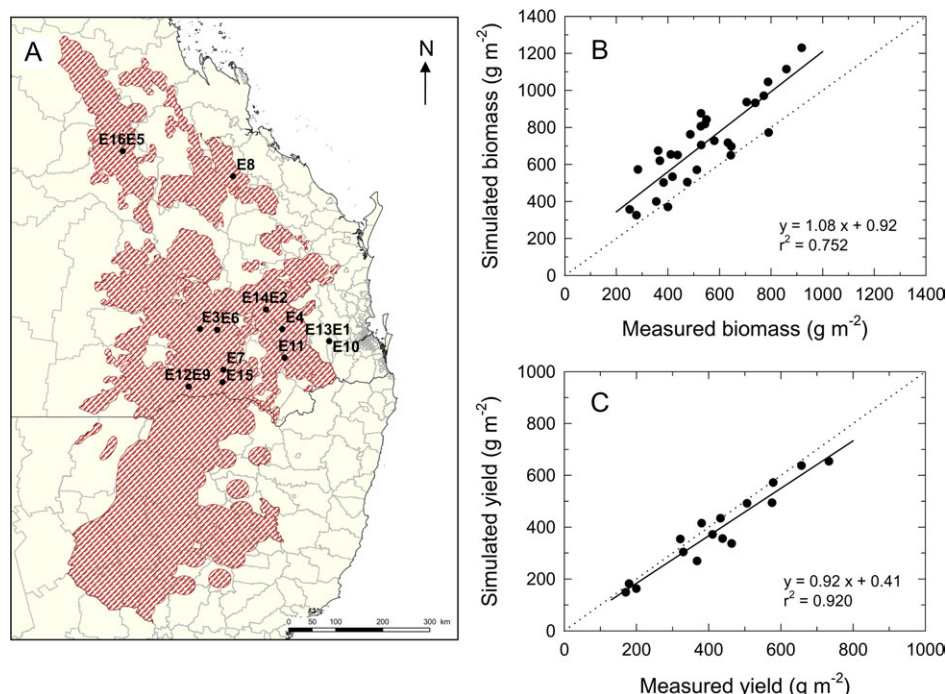


Fig. 5. Map of the 16 wheat trials of the MET, and simulated versus observed biomass (A) and grain yield (B) for the standard cv. Hartog in the MET. Dotted line, 1:1 line; solid line, fitted linear relationship.

classify the water-deficit patterns occurring in this cropping area. Despite their classification by the main limiting factor (drought), high variability in yield remained within each environment type (Fig. 3), for two major reasons. Firstly, classifying environments of such a broad TPE inevitably led to a broad range of stresses being included in the same smoothed and averaged environment type. Secondly, only stresses related to water were characterized here, meaning that limitation due to extreme temperatures or other environmental factors were only included in the environment classification through their effect on the water-deficit index, regardless of their additional effects on yield.

Given the high variability in rainfall patterns in the studied TPE, none of the environment types clearly dominated within any of the regions. Specific adaptation to a single environment type would thus be risky in such a TPE, unless rainfall could be forecast long enough before the sowing date and the environment type of the season predicted. In practice, farmers of this region target varieties that provide high yield (income) in good years, and sufficient yield to cover more than production costs in poor years. Broad adaptation to drought for this complex TPE thus appears as an appropriate strategy from a breeding viewpoint.

Environment characterization as a direct aid to selection

As frequently observed in dry-land wheat trials (Brennan *et al.*, 1981; van Ginkel *et al.* 1998; Rebetzke *et al.*, 2002; Mathews *et al.*, 2002; Dreccer *et al.*, 2007), the effect of GEI in the MET contributed a greater fraction of the variance for yield than did the direct genotypic effect (Table 3). To increase our understanding of GEI, climatic or soil varia-

bles, such as average rainfall, can be incorporated in the data analysis via mixed models or structural equation models (Malosetti *et al.*, 2004; Vargas *et al.*, 2007). However, these statistical approaches do not account for the interactions between the plants and their environment (e.g. the feedback of plant growth on soil water depletion). To resolve this issue, the environment characterization in this study integrated the water-deficit patterns that plants experience over time, and aimed to assist breeders to deal with large GEI, as detailed below. In addition, the analysis was performed here for breeding trials classified against the TPE, i.e. against a central reference independent from the specific scenarios of breeding trials.

Including the environment types into the statistical analysis assisted in interpretation of the GEI. Here, the G/GEI ratio in the MET (Table 3A) doubled when only considering the generally stress-free ET1 trials (Table 3B), meaning that a greater proportion of the genotypic effect was explained when considering the ET1 trials. In a previous study, when defining the environment types within a set of wheat trials (i.e. without consideration of the TPE), more than 30% of GEI for yield in these trials was associated with genotypic interactions across environment types (Chapman, 2008). For maize in the USA, Löffler *et al.* (2005) also demonstrated the benefit of environmental characterization. There, environment types were defined by mega-environments mainly based on temperature and photoperiod, and enabled up to 30% of the GEI variance observed in large-scale trials (18 hybrids tested in 90 environments) to be explained.

Knowledge about the main environment types of the TPE can help breeders choose trial locations and design

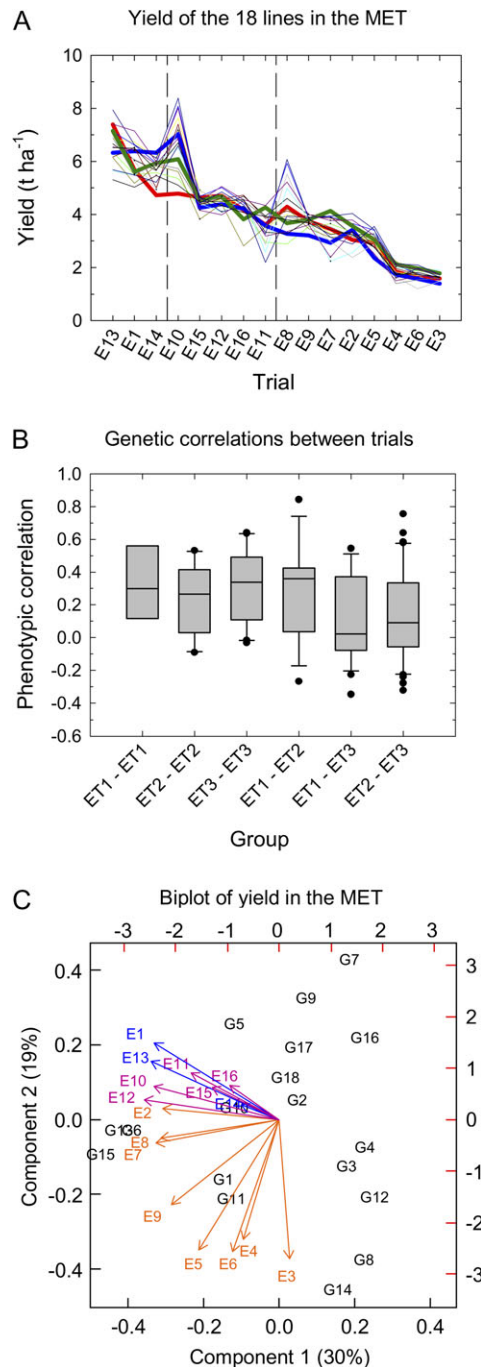


Fig. 6. Genotype–environment interactions for yield in the MET (18 lines in the 16 trials). (A) Yield of the lines in each trial. Trials of each environment type were ordered from high to low average yield among the genotypes. Three lines are in bold in order to highlight the genotype–environment interactions within and across environment types. (B) Distribution of the genetic correlations between trials and within and across environment types. (C) Biplot of the principal component analysis for the different trials (coloured by environment type) and genotypes.

experiments to focus on genetic variability in the environment type(s) of interest. In the studied TPE, ET1 was the least-frequent environment type (Figs 3, 4) but was associated with a high heritability (Table 3; Fig. 7). Furthermore,

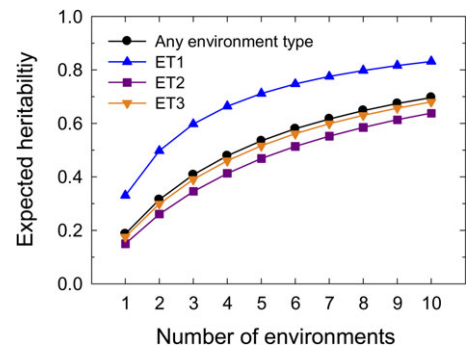


Fig. 7. Expected heritability (h^2) for 1–10 environments, given the variance estimates for genotype (G), genotype–environment interaction (GEI), and residual error observed in the MET (Table 3B, C). Heritability was calculated for environment of any type (i.e. random environment) and for environments of each environment type. Estimates assume two replicates per trial.

ET1 also had good phenotypic correlation with ET2 trials in the MET (Fig. 6B), meaning that relatively few ET1 trials (3–5) should suffice to select for adaptation to both of these environment types (at least for the genotypic diversity represented by the lines studied here). This finding quantitatively supports the argument of Cooper *et al.* (1997) who argued that including irrigated nurseries would improve the selection response for broad adaptation in this region, especially during commonly occurring years when most or all of the on-farm breeding trials would experience only drought conditions (Fig. 4A). To ensure broad adaptation of the genotypes, breeders could then attempt to select in ET3 environments by growing trials in places where ET3 environments are more common, for example, in the more northern and western areas, especially on shallow soils.

An extension of these uses of environment characterization is to weight genotype performance by the representativeness of their growing environment with respect to the TPE. Brennan and Sheppard (1985) proposed that environments could be weighted based on proximity to a hypothetical most frequently encountered environment. Analysis of breeding-system simulations has demonstrated advantages of such a weighted selection strategy in variable environments, especially when GEI are high (Cooper and Podlich, 1998; Podlich *et al.*, 1999).

Characterization of the environment types could also be useful to test specific physiological and breeding hypothesis, for example, concerning the identification of key adaptive traits. In the present study similarity, was observed in the genotype rankings in the relatively stress-free ET1 environments and in the stress-around-flowering ET2 environments (Fig. 6B). This phenotypic similarity in the genotype responses could be due to a lack of genetic diversity for drought-adaptive traits (as only 18 genotypes were studied here); traits associated with tolerance or avoidance of stress at flowering (e.g. limited potential transpiration rate; Condon *et al.*, 2002; Sinclair *et al.*, 2005) would be expected to be advantageous for yield in ET2, but also to introduce

some trade-offs for yield performance in the more favourable ET1. Given the results for the genotypic diversity represented by the set of lines tested, seeking new germplasm with well-adapted traits for ET2 could be an alternative to improve yield in these environments.

Finally, knowledge about the main environment types is also valuable in breeding-simulation studies. In this case, crop models are employed to predict the phenotypes associated with the allelic combinations explored by the breeding programmes (Chapman *et al.*, 2003; Hammer *et al.*, 2005; Chenu *et al.*, 2009; Messina *et al.*, 2009) and are used to assist decision-making about breeding strategies with respect to relevant traits and genomic regions for broad or specific adaptation in the TPE.

Improving environment characterization to increase GEI understanding?

There are several possibilities for improving and broadening the applicability of this approach to characterizing crop growing environments.

Firstly, the environment types presented here only characterized water deficit patterns. Other major stresses affecting trials in the TPE (e.g. frost/heat around flowering) or management factors (e.g. different levels of fertilization) could be included. In order to integrate all the environmental factors (biotic and abiotic), environment characterizations based on crop yield have been proposed (Chauhan *et al.* 2008; Hernandez-Segundo *et al.*, 2009). However, such a level of integration does not necessarily help in the improvement of specific factors, such as for drought tolerance.

Secondly, the MET characterization was performed for a single genotype (Hartog), and could be improved by running simulations for all genotypes studied in the MET, or for groups of these genotypes. Traits such as flowering date or tillering significantly influence the stress pattern, and can improve stress tolerance (via modification of plant leaf area and transpiration), or allow stress avoidance (via early flowering). Accounting for the genotypic variability for such traits in the simulations would allow the different stress patterns that genotypes experienced within trials to be characterized (i.e. for the same climate and soil) and would enhance our capacity to understand GEI (Hammer and Jordan, 2007).

Finally, increasing the number of environment types would allow us to explain better the variation in the stress patterns. However, for a given MET, this would inevitably reduce the number of trials that belong to each environment type, thus increasing the probability of insufficient data to analyse properly the genotypic variability within single environment type(s). In this study, three environment types seemed to be an accurate trade-off, as adding a fourth environment type only explained 3% more of the variability for the TPE water-deficit patterns (Fig. 2, inset).

Conclusion

Understanding a TPE in terms of major environmental conditions that cause genotype discrimination is important for both conventional and molecular selection approaches. Although only water-deficit patterns were characterized in this example for the wheat-growing area of north-eastern Australia, the grouping of MET based on this environmental classification helped to explain the basis for the observed GEI for yield. As discussed in this paper, knowledge of the spatial and temporal distribution of environment types can help to improve the predictability of genotype performance in the TPE, in the design of breeding programmes, and in phenotyping strategies. Furthermore, extending such environmental characterization to other drought-prone regions of the world, and thus facilitating robust comparison of environmental challenges in diverse regions, could aid the exchange of adapted germplasm among breeders.

With climate change, the 10–15 years necessary to develop a new wheat variety conventionally presents a new challenge for breeders. Modelling tools offer an opportunity to consider possible changes in the frequency of different stress patterns, and to prepare for these changes. Integrated modelling approaches used to characterize TPE under a future climate could help breeders, geneticists, and physiologists target genotypes, traits, and genetic regions of specific interest for predicted climates.

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