Providing a biological interpretation of Genotype x environment interactions in bread wheat

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INTRODUCTION

Many soils in the Australian wheat belt have chemical and physical properties that restrict root growth, limit crop water use and grain yield[1]. Tolerance to these stresses among different genotypes contributes to the large Genotype x Environment (GE) interactions that are observed in breeding trials. Faced with this array of constraints, plant breeders need to prioritise their breeding objectives, targeting those traits that will lead to the greatest yield gain. Analysis of the GE interaction provides some guide, but generally analyses in the past have been based only on grain yield, which provide little understanding of the biological bases of adaptation. Interpretation of GE analyses could be enhanced if other characteristics of the varieties that may be important to adaptation were included. The aim of this work is to incorporate phenotypic data on varietal responses to important nutritional constraints, tolerance to root disease, physiological and developmental characteristics and genetic information into a large GE analysis. An outcome of this work is to provide a better understanding of the biological basis of GE interactions.

METHODS

Grain yield data was obtained from field trials conducted between 1994 and 2005 in the Australian cereal belt. The complete data set consisted of grain yields of 52 genotypes grown in 233 trials conducted over 68 locations (Fig. 1). The data set is heavily weighted to environments in the southern and western cereal belt as most of the experiments were in South Australia (113), Western Australia (65) and Victoria (27) with only 23 sites in NSW and Queensland. Each experiment was spatially designed with 4 replicates. Plot sizes were most commonly 6 rows wide and 5 m long. A plant population of 150-200 plants/m^2 was used and standard fertiliser and weed management practices were used as appropriate to the rainfall environment in which the trials were grown. Most trials were done in farmers' fields rather than on research stations.

Phenotyping

The 52 varieties were characterised for a number of traits: tolerance to high levels of boron, tolerance to high pH, zinc efficiency, manganese efficiency, salt tolerance, aluminium tolerance, root penetration ability, C isotope discrimination, leaf chlorophyll content, and resistance to *P. neglectus*. This paper presents a preliminary analysis based on tolerance to high boron, high pH, zinc efficiency and C isotope discrimination

Figure 1. Location of the trial sites used in the analysis

The measurements were made in experiments conducted in the glasshouse or growth room. Tolerance to boron was based on the relative root length at low (0.015 mMB) and high (10 mM B) boron nutrient solutions. Sensitivity to high pH was assessed in nutrient solutions maintained at low (6.5) or high (9.0) pH using bicarbonate buffers[2]. Tolerance to low soil zinc was evaluated by growing plants in a zinc-deficient soil at two levels of zinc[3]. Zinc efficiency was calculated as the ratio of whole shoot dry matter at low and high levels of soil zinc. Carbon isotope discrimination[4] was measured on whole shoots from field grown plants sampled at Zadok's growth stage 31. Salt tolerance was based on relative shoot growth of plants grown at 0 and 100 mM NaCl in supported hydroponics for 20 days[5].

Data analysis

As not all varieties were grown in each Environment (Site x Year combination) the data was unbalanced. For this reason, as well as the large scale nature of the data, an initial two-stage REML mixed modelling procedure was considered appropriate. The first stage accounted for spatial variation as well as estimated Genotype means for each environment independently. The mean yields, with appropriate weights, were then used to fit a 2-Factor Analytic model to describe the GE interaction.

Each of the controlled phenotypic experiments were analysed individually using simple mixed models which, where appropriate, accounted for additional sources of variation such as the glasshouse or growth room design of the experiment as well as genetic replication of the indicator genotypes. For experiments containing low and high levels of a particular treatment, relative root length (boron, high pH) and Zn efficiency scores were calculated from an appropriate conditional predictive distribution of the genotypes at the high treatment level given the genotypes at the low treatment level.

To gain a preliminary understanding of the contribution of a phenotypic traits to the GE interaction the predicted scores for each of the traits was merged with the large scale mean yield data used at the second stage of the initial analysis and incorporated as additional random effects in the 2-Factor Analytic model. For simplicity each trait was analysed separately and, to ease the computational burden, only the traits contribution to the genetic variation at each Environment was assessed. The results of these contributions are given in this paper.

RESULTS

Genotype x Environment interactions

Site mean grain yields ranged from 0.24 t/ha (Walpeup Vic, 2004) to 6.93 t/ha (Kojunup WA, 2003). The biplot in Fig 1 illustrates the GE response. Varieties such as WI22100, Correll, Yitpi and Wyalkatchem have yielded well across a range of environments, whereas Sunstate, Hartog, Oxley and Baxter have yielded poorly across environments. Varieties to the left (eg Aroona, Schomburgk and Westonia) and to the right of the scatter (eg Matong, Ruby, Axe (syn RAC1262)) show a narrower range in adaptation.

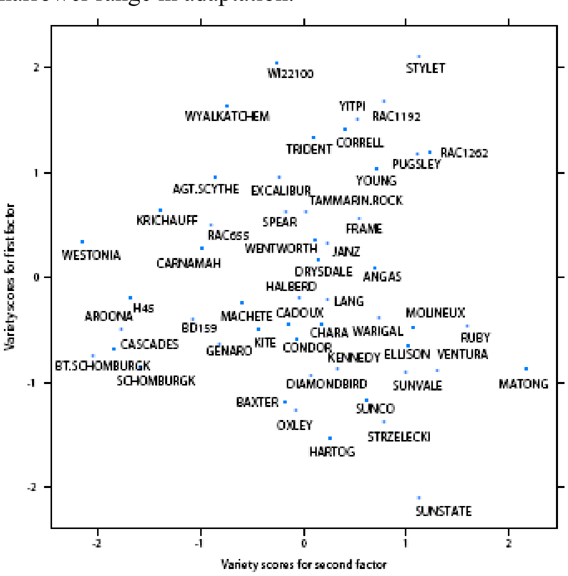

Figure 1 Biplot of the Variety scores for the first and second factors. Varieties that perform well across environments have vertical positive vectors, varieties that perform poorly across environments have vertical negative vectors, while varieties with vectors to the left of right show greater instability in yield.

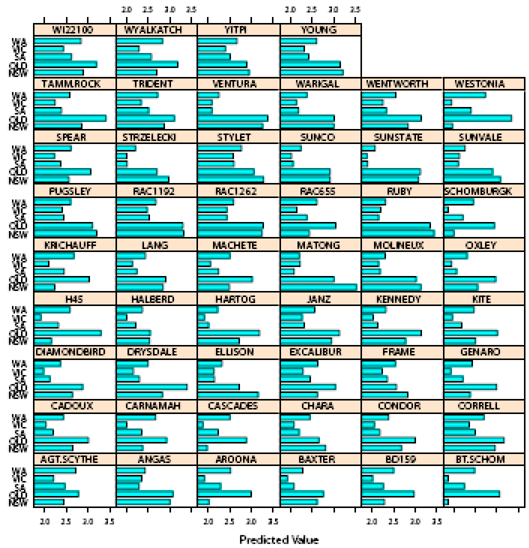

Figure 2. The predicted yields of each of the 52 varieties in each state. Yields are the average of the trials in each state over the 12-year period of yield trials.

The relative performance of the 52 lines in the different states is illustrated in Fig. 2. Data for Queensland should be interpreted with some caution because the means are based on a very small number of experiments. Nevertheless, the broad adaptation of varieties such as Yitpi, Correll and Wyalkatchem identified in Fig 1 is clearly evident, as are the more variable yields of varieties such as Matong and Westonia. There is evidence of regional adaptation among some varieties. Sunstate and Strezlecki, for example yielded poorly in Western Australia, South Australia and Victoria, but well in NSW. In contrast, Cascades, Aroona and Schomburgk yielded well in Western Australia and South Australia but poorly in NSW.

Contribution from individual traits.

There was either a weak correlation or no correlation among the varieties for the traits used in this analysis (Fig 3). Among all the sites, tolerance to high boron and zinc efficiency contributed to yield variation at the greatest proportion of sites, followed by salinity tolerance (Table 1). Carbon isotope discrimination was the least influential trait.

Table 1. The total number of sites and the proportion of the 233 trial locations at which an individual trait made a significant contribution to the variation in yield in field trials from 1994 to 2005.

Trait	No sites	%
Boron tolerance	95	41
High pH	70	30
Zinc efficiency	88	38
Salinity tolerance	75	32
C isotope discrimination	48	21

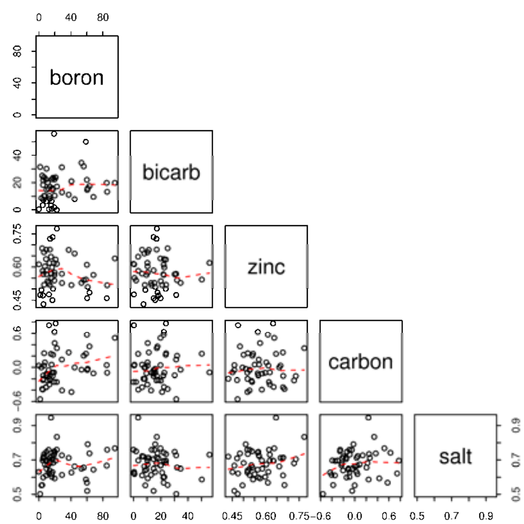

Figure 3. Correlation plots among the 52 genotypes of the indicator trial series for tolerance to high boron, high pH (bicarbonate), zinc efficiency, carbon isotope discrimination and salt tolerance

Similar trends were evident in Western Australia and South Australia, with boron tolerance and zinc efficiency contributing most to the GE interaction (Table 2). Salinity tolerance was relatively more important in the Victorian and NSW trials and tolerance to low zinc was greatest in Victoria.

Table 2. The total number of trials and the proportion in each state in which an individual trait has made a significant contribution to the variation in grain yield. B = tolerance to high boron; pH = tolerance to high pH; CID = carbon isotope discrimination.

State	Trials	Proportion of trials (%)				
		B	pH	Zinc	Salinity	CID
W. Aust.	65	40	32	37	34	18
S. Aust	113	41	27	37	28	23
Vic.	27	33	33	52	41	26
NSW	21	57	43	29	48	14
Qld	2	50	0	100	0	0

DISCUSSION

This paper presents a preliminary analysis of the contribution of a small number of traits to the GE interaction. It is recognised that there are other potential yield limitations that have not yet been included in the analysis. For example, on calcareous soils under high pH there is evidence that aluminium may become toxic to plants[8] and tolerance to aluminium toxicity may be a factor on some alkaline soils. Screening for aluminium tolerance indicates that Schomburgk is sensitive to high aluminium and the boron tolerant line BT Schomburgk is tolerant. The aluminium tolerance of BT Schomburgk appears to be derived from Halberd. Thus while BT Schomburgk and Halberd have been used as indicators of boron tolerance, their yield on highly alkaline soils may also reflect their tolerance to aluminium. It may also be helpful on acidic soils where aluminium toxicity is a problem.

Assessing the contribution of individual traits to the GE interaction assumes the relative performance of varieties in the field when a particular stress is prominent reflects the phenotypic variation in tolerance assessed in the screening tests. However, at more than half the sites the selected traits did not contribute to yield variation, indicating there were other characteristics not included in the analysis that may be important. Future analysis using a wider range of phenotypic data will be done and it is expected the relative importance of the different traits will change and the ability to explain the GE interaction will improve. This preliminary analysis indicates tolerance to boron, zinc and salinity are the most important traits influencing GE interactions in the southern and western cereal belt, and salinity tolerance is relatively more important at Victorian and NSW sites.

The importance of zinc efficiency in the analysis is unexpected. While it has been long recognised that zinc deficiency is a problem in parts of the region, it has been routinely rejected as a major breeding objective as farmers regularly apply zinc fertiliser. The data suggests that variation in Zn efficiency has contributed significantly to adaptation in the region.

ACKNOWLEDGEMENT

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