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Genotype-by-management interactions for grain yield and grain protein concentration of wheat

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Abstract

The magnitude of genotype-by-management (G × M) interactions for grain yield and grain protein concentration was examined in a multi-environment trial (MET) involving a diverse set of 272 advanced breeding lines from the Queensland wheat breeding program. The MET was structured as a series of management-regimes imposed at 3 sites for 2 years. The management-regimes were generated at each site–year as separate trials in which planting time, N fertiliser application rate, cropping history, and irrigation were manipulated. Irrigation was used to simulate different rainfall regimes. From the combined analysis of variance, the G × M interaction variance components were found to be the largest source of G × E interaction variation for both grain yield ($0.117 \pm 0.005\,t^2\,ha^{-2}$; 49% of total G × E $0.238 \pm 0.028\,t^2\,ha^{-2}$) and grain protein concentration ($0.445 \pm 0.020\%^2$; 82% of total G × E $0.546 \pm 0.057\%^2$), and in both cases this source of variation was larger than the genotypic variance component (grain yield $0.068 \pm 0.014\,t^2\,ha^{-2}$ and grain protein $0.203 \pm 0.026\%^2$). The genotypic correlation between the traits varied considerably with management-regime, ranging from −0.98 to −0.31, with an estimate of 0.0 for one trial. Pattern analysis identified advanced breeding lines with improved grain yield and grain protein concentration relative to the cultivars Hartog, Sunco and Meteor. It is likely that a large component of the previously documented G × E interactions for grain yield of wheat in the northern grains region are in part a result of G × M interactions. The implications of the strong influence of G × M interactions for the conduct of wheat breeding METs in the northern region are discussed.

Keywords: Genotype × environment interaction; Broad and specific adaptation; Multi-environment trials

1. Introduction

Grain yield and grain protein concentration are two of the main selection criteria for wheat breeding in the northern grains region of Australia (Fabrizius et al., 1996, 1997). This region includes the state of Queensland and the northern half of the state of New South Wales. An understanding of factors that impact on both the capacity to achieve genetic improvements for these traits and the potential for any genetic improvements to be expressed and realised under on-farm management conditions is critical to the success of the northern region wheat breeding effort. Genotype-by-environment (G × E) interactions and the negative genetic correlation between grain yield and grain

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protein concentration will both impact on the rate of genetic progress. Therefore, in this study an understanding of the influence of both of these factors on genotypic variation for both traits under a range of management-regimes is sought. The management factors manipulated in this study include soil nitrogen, soil water availability and planting date.

G × E interactions have been previously examined for grain yield (Brennan et al., 1981; Brennan and Sheppard, 1985; Cooper et al., 1995, 1997; Sheppard et al., 1999) and to a lesser extent for grain protein concentration of wheat in the northern region (Fabrizius et al., 1997). Fabrizius et al. (1997) found that the G × E interactions were large for both traits and could complicate selection. Generally, grain yield and protein concentration are negatively correlated (e.g. O'Brien and Ronalds, 1984; Stoddard and Marshall, 1990; Fabrizius et al., 1997; Feil, 1997). Stoddard and Marshall (1990), working with a selected set of genetically fixed inbred lines, and Fabrizius et al. (1997) working with random inbred lines sampled from two crosses, observed that the strength of the negative genetic correlation coefficient between these traits varied among test environments in the northern region. Both studies indicated that the negative correlation was likely to be in part a function of the effects of linkage, rather than solely due to pleiotropy, and not of sufficient magnitude to preclude the possibility of improvement of both traits (Feil, 1997).

In the northern grains region the influences of G × E interactions on grain yield and grain protein concentration and their genetic correlation have been studied in plant breeding multi-environment trials (METs) using the site–year cross-classification as a representation of the target population of environments. The analysis of METs in terms of the site–year cross-classification model enables the estimation of genotype-by-site (G × S), genotype-by-year (G × Y) and genotype-by-site-by-year (G × S × Y) interaction components of variance. In these studies the genotypes are usually evaluated under a single management-regime for each site–year combination sampled. However, for any site–year combination a number of different management practices may be applied, depending on the farming system practices that are in use. For example, different tillage practices may be employed, ranging from minimum to conventional tillage, different planting time options may be taken, the cropping history and crop rotation strategies employed by farmers will differ, and the use of fertiliser inputs will change. These management options create different environments and could give rise to G × E interactions, which we refer to here as genotype-by-management (G × M) interactions.

It is often assumed that G × M interactions are large for important commercial traits of wheat in the northern grains region of Australia (Cooper et al., 1996), and for crops in general (presentation given by Reeves et al., 1999). However, the magnitude of these has not been quantified for grain yield or grain protein concentration and compared with other sources of G × E interaction. Since it is rare for different management options to be sampled at each site–year combination in wheat breeding METs, any G × M interactions are usually confounded with the G × S × Y interaction effects estimated from the site–year cross-classification model. Further, it is unlikely that similar management practices would be optimum for different site–year combinations across a target region. Therefore, G × M interactions have not been systematically evaluated in plant breeding METs for comparison with the G × S, G × Y and G × S × Y interaction components of variance and their influence on genotype performance.

Cornish (1987) discussed the significance of G × M interactions in relation to different tillage systems. From his review he concluded, "that breeders should continue to select for wide adaptability" and "It is likely that cultivars developed under one management-regime will be reasonably well suited to another." While this provides some guidance, much of the work on G × M interactions has been conducted using a small number of selected cultivars and/or advanced breeding lines in specific management-regimes at a limited number of sites (often one) across years. Since the germplasm within breeding programs is continually changing and farming practices change with time, it is unclear how generally these conclusions will apply. Therefore, it would be useful to examine the influence of G × M interactions for grain yield and grain protein concentration of wheat in the northern grains region in a way that enables a comparison of the size of these interactions with those for the G × S, G × Y and G × S × Y.

The source of G × M interactions for grain yield that has been most extensively studied in the northern

grains region of Australia is that due to the combined effects of cultivar differences in phenology and management variation introduced by changing crop planting date (Woodruff and Tonks, 1983), referred to here as $G_{PH} \times M_{PD}$. Annual rainfall in the northern grains region is highly variable (Woodruff, 1992) and predominantly in summer. Spring wheat crops are grown during the autumn, winter and spring months. These crops rely heavily on stored soil moisture from the preceding summer (Donald and Puckridge, 1975). Planting dates in the northern grains region commonly range from early April to late July. This large range is due to the need for a significant rainfall event to enable planting and the variable and unpredictable rainfall distribution across the region. To accommodate the effects of this source of environmental variation, farmers select cultivars to match developmental patterns, particularly the timing of flowering, with expected water availability and the likelihood of significant abiotic-stress events that can reduce grain yield and grain quality. Farmers typically select cultivars at the start of a growing season based on the timing of the first significant rainfall event and the likelihood of a yield damaging frost event coinciding with flowering. The latter depends on both latitude and aspects of local topography on the farm. The risk of a damaging frost later in the season decreases with more northern latitudes and with field positions located higher on the slopes of the local landscape. With earlier rainfall and planting options, slower flowering cultivars are preferred to ensure flowering is delayed to avoid the chance that this critical yield determining stage coincides with periods of high incidence of frost. With later rainfall events, quicker flowering cultivars are used. These are still selected to reduce the chance of flowering coinciding with periods of high frost risk but also to avoid later flowering that coincides with periods of high temperature and an increased risk of the crop maturing during a period of higher likelihood of significant rainfall, which can result in pre-harvest sprouting damage to the grain.

Within wheat breeding METs, it is known that $G_{PH} \times M_{PD}$ interactions can have a large influence on the observed genotypic variation for grain yield (e.g. Cooper et al., 1996). Therefore, to avoid this source of $G \times E$ interaction for traits measured in the METs, genotypes are stratified into ''maturity-groups'' so that only genotypes with comparable phenology are included in a trial. In some years trials based on different maturity-groups are planted at the same site. Ideally the trials based on the slower flowering genotypes would be planted earlier so that both trials reach flowering time around the same calendar day. Alternatively, if the genotypes included within a trial vary for genetic control of timing of flowering it is useful to adjust yield variation for the variation in time from planting to flowering to examine genotypic variation after the known effects of flowering time are taken into consideration (e.g. Fabrizius et al., 1997). This latter strategy was adopted in the current study.

In the presence of strong evidence for $G \times M$ interactions, after adjusting for the known effects of genotypic variation for flowering time, an important question becomes, how to incorporate the effects of $G \times M$ interactions into the models of genotype performance within a target population of environments and how to accommodate their effects in evaluation and selection of genotypes within the operation of the breeding program? Two analytical positions are considered in this paper. In the first it is assumed that the breeder is interested in the scope for selecting for broad adaptation across the range of site–year and management combinations encountered. This is the most common selection approach used to improve grain yield of wheat for the northern grains region. The second considers the other extreme, where the breeder seeks to examine the detail of all of the $G \times M$ interactions to consider the scope for exploiting aspects of specific adaptation to particular management conditions. While there is interest in exploiting such specific adaptations, the detail of the causes of any $G \times M$ interactions for grain yield and grain protein concentration have only been pursued previously on an ad hoc basis. This study is the first attempt to quantify the need to more actively consider this aspect of genotype performance in applied breeding METs. In addition to these extreme statistical analysis positions, many intermediate modelling positions can be adopted. These intermediate models would include a restricted range of selected (targeted) management variables incorporated into the MET and explicitly employed as factors in the statistical models used to analyse the observed genotypic variation. The scope for considering these options in future wheat

breeding METs and G × M interaction studies is discussed.

The objectives of this paper are to examine: (1) the relative sizes of components of variance for G × M, G × S, G × Y and G × S × Y interactions for grain yield and grain protein concentration using a relatively large and diverse sample of 272 advanced breeding lines relevant to the pedigree wheat breeding program at the Leslie Research Centre (LRC) in Queensland; (2) the magnitude of the genetic correlation between grain yield and grain protein concentration and any variation in the genetic correlation among environments represented by management and site–year combinations; and (3) the prospects for improving grain yield and grain protein concentration of wheat cultivars for farming systems in Queensland.

2. Materials and methods

2.1. Germplasm

A total of 272 advanced breeding lines and checks were involved, of which 21 were in every trial. The lines included 17 cultivars that had been released for use in the Australian northern grains region, four cultivars from the southern and western regions, 173 advanced breeding lines from the LRC, 56 advanced lines sampled from the International Bread Wheat Screening Nurseries conducted by CIMMYT, and 22 other lines nominated as special interest lines from a range of crosses. Five reference lines were used in this study. The cultivars Hartog, Sunco and Meteor (a commercial F_1 hybrid) are widely grown in the northern region. The other two are the high-yielding lines Seri M 82 (referred to as Seri) and Genaro T 81 (referred to as Genaro), which are sister lines from the same cross. The 173 advanced lines from LRC included a sample of 35 breeding lines from different stages of testing in the LRC pedigree breeding program and random inbred lines derived from two crosses 11IBWSN50/Vasco (58 lines) and Hartog/Vasco (80 lines). A genetic analysis of grain yield and grain protein concentration for the random inbred lines was reported by Fabrizius et al. (1997) and is not discussed further here. The lines used in this study are considered to represent a random sample of advanced lines relevant to the grain yield and protein improvement objectives of the wheat breeding programs operating in the northern grains region.

2.2. Environments: sites, years and management-regimes

The lines were grown in trials at three sites (Gatton 27°33′S, 152°20′E; Kingsthorpe 27°31′S, 151°47′E; and Emerald 23°31′S, 148°9′E) across 2 years (1988 and 1989). Daily rainfall, maximum and minimum temperature, and daily incident solar radiation were obtained from nearby weather stations (Gatton 27°56′S, 152°28′E; Kingsthorpe 27°25′S, 151°44′E; Emerald 23°57′S, 148°18′E; The SILO Patched Point Dataset (PPD) (www.dnr.qld.gov.au/silo/PPD_frameset.html; The Data Drill, 2000). For temperature and radiation data the daily data were converted to 5-day means and for rainfall data to 5-day totals. These data were used as a characterisation of the weather conditions at each of the six site–year combinations sampled in this study.

Within each site–year combination the management variables planting time, nitrogen fertiliser application and cropping history were manipulated to create a number of different management-regime treatments. Irrigation was used to simulate different rainfall regimes, ranging from low to high rainfall. A total of 23 environments (trials) were included in this study. The combinations of management variables differed among the six site–year combinations sampled (Table 1). Therefore, the different management-regimes were nested within the site–year combinations rather than in a factorial combination with the site–year combinations. This model for examining G × M interactions is considered to be consistent with the applied cropping practice of adopting different locally appropriate management strategies for the varied conditions experienced in the different production areas of the northern grains region. While the types and number of management combinations considered are limited relative to those used for wheat in the northern region, they were considered sufficient to provide preliminary estimates of the magnitude of G × M interactions for comparison with the G × S, G × Y and G × S × Y interaction components for grain yield and grain protein concentration.

In this study a particular combination of management variables at a site–year combination is referred to

Table 1
Management-regimes created at the six site–year combinations by manipulating cropping history, sowing date, nitrogen fertiliser application, cropping history, and irrigation, the input category of the trial, the experimental layout (rows × columns), number of lines tested and the harmonic mean (r_h) of the number of replications of each line

Site	Year	Management-regime (trial)[a]	Input category[b]	Crop history[c]	Sowing date	Nitrogen (kg N ha^{-1})	Irrigation schedule (mm)[d]	Layout	Number of lines	Replication (r_h)	Environmental characterisation hypothesised limiting factor[e]
Emerald	1988	Et1l88	Low	CC	11/5/88	20	25 S	2 × 73	55	1.60	Nitrogen: severe
		Et1m88	Medium	CC	11/5/88	40	25 S, 35 F	2 × 73	55	1.60	Nitrogen: severe
		Et1h88	High	CC	11/5/88	150	25 S, 50 2W	2 × 33	21	2.26	Nitrogen: moderate
		Et2l88	Low	CC	8/6/88	20	25 S	2 × 79	55	1.63	Nitrogen: severe
		Et2m88	Medium	CC	8/6/88	40	25 S, 35 F	2 × 73	55	1.60	Nitrogen: severe
		Et2h88	High	CC	8/6/88	150	25 S, 50 2W	2 × 37	21	2.34	Nitrogen: moderate
	1989	ELFD89	Low	LF	15/6/89	30	0	2 × 160	251	1.03	Nitrogen: moderate
		ELFI89	High	LF	15/6/89	100	4 × 35 E	2 × 160	251	1.03	Nitrogen: moderate
		EDCI89	Medium	DC	15/6/89	100	4 × 35 E	2 × 160	251	1.03	Nitrogen: moderate
Kingsthorpe	1988	Kt1l88	Low	CC	30/6/88	40	12 S	2 × 73	55	1.60	Water: pre-flowering and flowering
		Kt1m88	Medium	CC	30/6/88	70	12 S, 35 F	2 × 79	55	1.63	Water: post-flowering
		Kt1h88	High	CC	30/6/88	150	25 S, 25 2W	1 × 64	21	2.26	Water: post-flowering
		Kt2l88	Low	CC	3/8/88	40	25 S	2 × 73	55	1.54	Water: pre-flowering and high temperature
		Kt2m88	Medium	CC	3/8/88	70	25 S, 35 F	2 × 73	53	1.59	Water: flowering and high temperature
		Kt2h88	High	CC	3/8/88	150	25 S, 25 2W	1 × 64	21	2.26	Water: post-flowering and high temperature
	1989	KLFD89	Low	LF	23/6/89	10	0	2 × 160	251	1.03	Water: pre-flowering
		KLFI89	High	LF	23/6/89	100	4 × 35 E	2 × 160	251	1.03	Low-stress
		KDCD89	Medium	DC	23/6/89	50	0	2 × 160	251	1.03	Water: pre-flowering
		KDCI89	High	DC	23/6/89	100	4 × 35 E	2 × 160	251	1.03	Water: post-flowering
Gatton	1988	Gt1I88	High	LF	25/5/88	150	25 S, 25 2W	2 × 74	55	1.60	Low-stress
		Gt2I88	High	LF	22/6/88	150	25 S, 25 2W	2 × 74	55	1.60	Low-stress
	1989	Ga189	High	LF	22/6/89	110	6 × 35 M	6 × 54	251	1.03	Low-stress
		Ga289	High	LF	22/6/89	110	6 × 35 M	6 × 54	251	1.03	Low-stress: mild nitrogen limitation

[a] Management-regime (trial) acronym was constructed with the first letter identifying the site (E for Emerald, K for Kingsthorpe, G for Gatton), the final two numbers identifying the year (88 for 1988, 89 for 1989), and the letters and numbers in between provide a description of the management regime (t1 and t2 are used to identify the first and second planting date, respectively, at site–year combinations where there was more than one planting date, a1 and a2 are used to distinguish two nitrogen application procedures at the Gatton site in 1989, for some site–year combinations the letters l, m and h are used to distinguish low, medium and high input management-regimes, LF and DC are used to distinguish between long fallow and double crop management-regimes, I and D are used to distinguish irrigated and dryland management-regimes).

[b] Input category is used to distinguish between trials on the basis of whether they were considered to have low, medium or high levels of management inputs. This system of categorising the individual trials was used in previous studies by Cooper et al. (1995, 1997).

[c] Crop history describes the crop management used prior to the establishment of the trial: CC: cover crop which was removed, DC: double cropping, LF: long fallow.

[d] Irrigation schedule describes the irrigation inputs scheduled for the trial (these were modified depending on rainfall): S: single irrigation at sowing, M: irrigation commenced at mid-tillering, E: irrigation commenced at elongation, F: single irrigation at flowering, 2W: every 2 weeks.

[e] Qualitative environmental characterisation based on timing of the plant developmental stage of flowering in relation to weather conditions (Fig. 1) and measurement of soil and plant water and nitrogen status (data not reported).

as a trial. Each trial was identified by an acronym based on a letter for the site (E: Emerald, K: Kingsthorpe, G: Gatton), a descriptor for the management practices and either 88 or 89 to identify the year (Table 1). Each trial was also classified as to whether it represented a low, medium or high-input management-regime. All of the trials at the Gatton site were managed to represent high-input conditions. At Emerald and Kingsthorpe, a range of low, medium and high-input trials were conducted in both years. Additional measurements were taken on soil and plant nitrogen concentration, soil and plant water status (data not shown) to achieve a characterisation of the trials in terms of any major environmental limitation to plant growth and yield accumulation (Table 1). As a secondary objective for this study, the comparison of genotypic performance for grain yield and grain protein concentration between Gatton and the other two sites was of interest as an indicator of the potential to improve these traits for both low-stress conditions (conditions in which the potential yield is likely to be realised), represented by the four trials at Gatton, and a range of rainfed conditions represented by the trials at Emerald and Kingsthorpe.

All experimental plots had four rows with a 20 cm inter-row spacing. Prior to planting, seed weight and germination percentage was determined for all genotypes and the quantity of seed per plot was adjusted to achieve a particular target plant population, specified as the number of plants per square-meter. Most plots were sown to achieve a target plant population of 100 plants m^{-2}. A small number of plots at all three sites in 1988 were sown to establish a target plant population of 80 plants m^{-2}, to facilitate comparisons with other experiments outside this study. The effect of the target plant population was not examined in this study and target plant population was used as a factor in the analysis of the trials to adjust for any such effects.

Subsets of the 272 lines were evaluated in each trial (Table 1). A core set of 21 lines was present in all trials. The level of replication of the lines differed within and among the trials (Table 1). The advanced breeding lines, including those from the two crosses, were unreplicated within trials, while the other lines were replicated. A single check line Genaro was used as a grid-plot in 1988, with five plots between each grid within rows. In 1989 both Genaro and Hartog were used as grid-plots, with alternating Hartog and Genaro grid-plots and five plots between each grid-plot within rows. Different randomisations were used for the experimental plots for each trial and the row–column arrangement of the plots was recorded for use in spatial analysis of experimental data (Gilmour et al., 1997), discussed further below.

Flowering time, grain yield and grain nitrogen percentage (N%) data were collected for each plot. Flowering time was recorded as days from planting to when 50% of the plants in a plot had reached anthesis (days-to-flower). Before final harvest, plots were end-trimmed and plot lengths were measured. All four rows of the plots were harvested with a small plot combine and plot-yields were adjusted to a standard plot size. Grain moisture percentage of each plot was measured and yields were converted to tons per hectare at 12% moisture content. A grain sample from each plot was ground and the ground material was digested using a semi-micro Kjeldahl procedure. The N content of each digestion was measured by automated continuous flow methods, slightly modified from the Technicon (1976, 1977) procedure. A multiplier of 5.7 (Tkachuk, 1969) was used to convert the N concentration to protein concentration.

The complex structure of the data set collected from this study, in combination with its relatively large size, complicated its analysis using conventional statistical analysis software packages. Recent advances in statistical analysis software and the availability of faster computers have made the analyses reported in the paper feasible, though still time consuming.

2.3. Single trial analyses

All trials were analysed using the approach suggested by Gilmour et al. (1997) for analysing field experiments using the spatial models proposed by Cullis and Gleeson (1991). This approach attempts to identify large-scale variation (global trend), extraneous variation and small-scale variation (local or natural trend) in field experiments. These sources of variation have been found to be common features of data from small-plot field experiments. Gilmour et al. (1997) advocate using polynomials and spline smoothers (Verbyla et al., 1999) to model global trend and to include design effects, such as rows

and columns, to account for extraneous trend. To account for the local variation, the separable autoregressive process (AR1 × AR1) proposed by Cullis and Gleeson (1991) was used. Since the target plant population was lower (80 vs. 100 plants m^{-2}) for some experimental plots in the 1988 experiments, this was included as a factor in the relevant single trial models. The variable days-to-flower was used as a covariate in the analyses of grain yield and grain protein to adjust for the known effects of time of flowering of lines in relation to environmental conditions (Woodruff and Tonks, 1983; Fabrizius et al., 1997). Non-linear associations between days-to-flower and both grain yield and grain protein concentration were accommodated where necessary by fitting splines to represent the associations. The selected single trial model, from among all of the options considered, is referred to as the preferred model.

Each trial was analysed using a bivariate analysis to estimate the genotypic correlation (r_g) and error correlation (r_e) between grain yield and grain protein concentration. The bivariate analysis fitted different models for each trait, including different autoregressive processes to model the different local variation responses of each trait. The genotypic correlation was estimated as the ratio of the genotypic covariance component over the square root of the product of the genotypic components of variance for the two traits. Similarly the error correlation was estimated as the ratio of the error covariance component over the square root of the product of the error components of variance for the two traits. Estimates of the phenotypic correlation (r_p) between the traits were obtained in two ways: (1) by product moment correlation of the original plot data without any spatial adjustment; and (2) by product moment correlation of the best linear unbiased estimates (BLUEs) of the trait values for the lines after the adjustments for the spatial models had been applied. The two estimation procedures were compared to obtain some assessment of the impact of the preferred single trial model on the estimates of the phenotypic correlation coefficients obtained for these experiments.

Line-mean heritability (h^2) was estimated for grain yield and grain protein concentration for each trial as the ratio of the genotypic component of variance over the phenotypic variance on a line-mean basis using the equation

$$h^2 = \frac{\sigma^2_{g(t)}}{\sigma^2_{g(t)} + (\sigma^2_{\varepsilon(t)}/r_{h(t)})} \quad (1)$$

where $\sigma^2_{g(t)} \sim N(0, \sigma^2_{g(t)})$ is the genotypic component of variance for an individual trial after spatial analysis, $\sigma^2_{\varepsilon(t)} \sim N(0, \sigma^2_{\varepsilon(t)})$ is the environmental (error) component of variance for an individual trial after spatial analysis and $r_{h(t)}$ is the harmonic mean of the number of replicate plots of each line (Table 1).

2.4. Multi-environment trial analysis

Due to the complexity of the single trial analyses, the combined analysis of the MET data was conducted following a two-stage approach. The adjusted BLUEs obtained from applying the preferred model to each of the single trials (stage 1) were used as inputs for the combined analysis across environments (stage 2). To accommodate the effects of heterogeneous errors among trials the predicted means of the line effects (BLUEs) from each trial, for each trait, were used in a weighted analysis to estimate the variance components for the random terms in the combined analysis model, discussed below. The weights were proportional to the inverse of the error variance at that trial. For the MET analysis of each trait a mixed model was specified. Sites and years were defined as fixed effects, predominantly because of their restricted sample sizes (2 years and 3 sites) and the difficulty of reliably estimating variance components for variables with such limited degrees of freedom. Further, the three sites were selected to represent different production conditions within the target region. A larger MET with more extensive samples of sites and years would justify treating these variables as random effects in the model. Trials (management-regimes) were considered to be more adequately sampled than sites and years and were treated as random effects nested within the site–year combinations. The lines were defined as random effects and therefore all G × E interaction terms in the model were defined as random effects. Given the above considerations, the phenotypic performance ($Y_{ijkm(n)}$) of the mean of line i (based on n (Table 1) spatially adjusted plot observations obtained from the single trial analyses, as described in Table 2),

Table 2

The preferred spatial model for analysis of grain yield and grain protein concentration for each trial, trial mean, and line-mean heritability (h^2) for grain yield and grain protein concentration, and the genotypic (r_g), environmental (r_e) and phenotypic (r_p: Raw: phenotypic correlation on unadjusted raw data; BLUE: phenotypic correlation on BLUE of line values after spatial adjustment) correlation coefficients between grain yield and grain protein concentration for each trial

Trial	Trait						Trait correlation			
	Grain yield			Grain protein concentration			r_g	r_e	r_p	
	Preferred model[a]	Mean (t ha^{-1})	h^2	Preferred model[a]	Mean (%)	h^2			Raw	BLUE
Et1l88	P + AR1 × AR1	0.99	0.11	$P + l(\text{col}) + s(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	8.7	0.80	−0.98	−0.17	0.00	−0.34
Et1m88				$F + \text{row}/l(\text{col}) + \text{row}/s(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	1.24	0.17				
				$F + \text{row}/l(\text{col}) + \text{row}/s(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	9.2	0.73	−0.54	0.18	0.01	−0.19
Et1h88	$P + l(\text{col}) + s(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	3.90	0.88	$P + l(\text{col}) + s(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	11.1	0.75	−0.66	−0.18	−0.40	−0.58
Et2l88	$\text{row}/l(\text{col}) + \text{row}/s(\text{col}) + \text{AR1} \times \text{AR1}$	1.10	0.32	$F + l(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	8.9	0.73	−0.62	0.02	−0.35	−0.29
Et2m88	$\text{row}/l(\text{col}) + \text{row}/s(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	1.39	0.61	$F + \text{frow} + \text{AR1} \times \text{AR1}$	8.5	0.77	−0.59	0.06	−0.37	−0.33
Et2h88	$F + l(\text{col}) + \text{AR1} \times \text{AR1}$	4.37	0.79	$F + s(\text{F}) + \text{row}/l(\text{col}) + s(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	9.7	0.91	−0.36	−0.23	−0.33	−0.04
ELFD89	F + AR1 × AR1	2.22	0.41	F + AR1 × AR1	10.9	0.36	−0.82	0.15	−0.33	−0.49
ELFI89	$F + s(F)$ + AR1 × AR1	3.23	0.40	$F + s(F)$ + AR1 × AR1	11.4	0.62	−0.81	0.04	−0.54	−0.53
EDCI89	$F + s(F) + l(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	2.49	0.62	$F + s(F) + l(\text{col}) + s(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	9.6	0.58	−0.31	0.00	−0.14	−0.12
Kt1l88	$F + l(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	2.29	0.74	$F + s(F) + l(\text{col}) + s(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	16.4	0.73	−0.64	−0.15	−0.59	−0.67
Kt1m88	$P + l(\text{col}) + s(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	4.70	0.63	$F + s(F) + \text{row}/l(\text{col}) + \text{row}/s(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	12.9	0.32	−0.60	0.01	−0.22	−0.42
Kt1h88	$F + s(F) + l(\text{col}) + \text{rep} + \text{AR1}$	4.04	0.53	$F + s(\text{F}) + l(\text{col}) + s(\text{col}) + \text{AR1}$	13.5	0.73	−0.37	−0.18	−0.44	−0.40
Kt2l88	$F + P + l(\text{col}) + s(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	1.21	0.72	$F + P + l(\text{col}) + \text{frow} + \text{AR1} \times \text{AR1}$	18.6	0.58	−0.32	−0.26	−0.53	−0.36
Kt2m88	$F + P + l(\text{col}) + \text{AR1} \times \text{AR1}$	2.85	0.19	$F + P + \text{frow} + \text{AR1} \times \text{AR1}$	15.2	0.69	−0.54	0.11	−0.45	−0.43
Kt2h88	$F + P + \text{fodds} + \text{AR1}$	3.23	0.57	$F + P + l(\text{col}) + \text{AR1}$	14.7	0.74	0.00	−0.37	−0.48	−0.41
KLFD89	$l(\text{col}) + s(\text{col})$	0.73	0.69	$l(\text{col}) + s(\text{col})$	14.5	0.51	−0.34	−0.26	−0.33	−0.28
KLFI89	$F + s(F) + l(\text{row}) + l(\text{col}) + \text{AR1} \times \text{AR1}$	5.40	0.55	$F + s(F) + \text{AR1} \times \text{AR1}$	13.6	0.27	−0.75	0.05	−0.26	−0.31
KDCD89	$l(\text{col}) + s(\text{col}) + \text{frow} + \text{fodds} + \text{AR1} \times \text{AR1}$	1.33	0.40	$l(\text{col}) + \text{AR1} \times \text{AR1}$	15.3	0.48	−0.42	−0.15	−0.35	−0.29
KDCI89	$F + l(\text{row}) + l(\text{col}) + s(\text{col}) + \text{AR1} \times \text{AR1}$	3.42	0.43	$F + l(\text{row}) + l(\text{col}) + s(\text{col}) + \text{AR1} \times \text{AR1}$	13.8	0.63	−0.82	0.10	−0.43	−0.33
Gt1I88	$F + s(F) + \text{AR1} \times \text{AR1}$	4.67	0.59	$F + s(F) + \text{AR1} \times \text{AR1}$	13.6	0.76	−0.69	−0.30	−0.52	−0.52
Gt2I88	$F + s(F) + P + \text{AR1} \times \text{AR1}$	4.62	0.78	$F + \text{frow} + \text{AR1} \times \text{AR1}$	13.8	0.78	−0.48	−0.48	−0.56	−0.55
Ga1I89	$F + s(F) + \text{AR1} \times \text{AR1}$	5.37	0.48	$F + s(F) + \text{AR1} \times \text{AR1}$	13.3	0.48	−0.47	−0.35	−0.44	−0.49
Ga2I89	$F + \text{row} + \text{AR1} \times \text{AR1}$	4.70	0.52	$F + \text{row} + \text{AR1} \times \text{AR1}$	13.1	0.34	−0.57	−0.23	−0.38	−0.22

[a] l(col) and l(row) represent the linear regression of the variate on the column index and row index, respectively; F is a covariate representing maturity; P represents a factor based on the target planting population; s(col) and $s(F)$ represent the random spline components for column and maturity, respectively; frow represents a fixed factor based on the row index; rep represents a factor based on the replicate index; fodds represents a two level fixed factor defined for the odd and even column indices; row and col represent random factors based on the row and column indices; AR1 represents a first-order autoregressive error model; and AR1 × AR1 represents a first-order separable autoregressive error model; a/b represents factor b nested within factor a.

in trial m in year k at site j was modelled as

$$Y_{ijkm(n)} = \mu + s_j + y_k + (sy)_{jk} + (m|sy)_{mjk} + g_i + (gs)_{ij} + (gy)_{ik} + (gsy)_{ijk} + (gm|sy)_{ijkm} + \varepsilon_{ijkm(n)} \quad (2)$$

where μ is the grand mean, s_j the effect of site j, $j = 1, \ldots, 3$; y_k the effect of year k, $k = 1, \ldots, 2$; $(sy)_{jk}$ the effect of the interaction between site j and year k; $(m|sy)_{mjk} \sim N(0, \sigma_m^2)$ the effect of trial m (management-regime) within site–year combination jk, $m = 1, \ldots, n_m$; $g_i \sim N(0, \sigma_g^2)$ the effect of line i, $i = 1, \ldots, 272$; $(gs)_{ij} \sim N(0, \sigma_{gs}^2)$ the effect of the interaction between line i and site j; $(gy)_{ik} \sim N(0, \sigma_{gy}^2)$ the effect of the interaction between line i and year k; $(gsy)_{ijk} \sim N(0, \sigma_{gsy}^2)$ the effect of the interaction between line i site j and year k; $(gm|sy)_{imjk} \sim N(0, \sigma_{gm}^2)$ the effect of the interaction between line i and management m within site–year combination jk; and $\varepsilon_{ijkm(n)} \sim N(0, \sigma_\varepsilon^2)$ the residual effect for line i, expressed on a line-mean basis across n observations, within trial m at site j in year k. REML (Patterson and Thompson, 1971) estimates of variance components were obtained using the average information algorithm (Gilmour et al., 1995). The estimates of error variance from each trial were used to compute a pooled estimate of error variance, which was treated as fixed in the MET analysis.

2.5. Pattern analysis of the site–year cross-classification

Pattern analysis (Williams, 1976) was used to investigate the genotypic variation, G × Y, G × S and G × S × Y interactions for the site–year cross-classification structure of the MET for grain yield and grain protein concentration following the procedures used by Basford et al. (1996). In this analysis the six site–year combinations were treated as six environments. The best linear unbiased predictions (BLUPs) for the genotypes from the combined analysis were used to construct a 272 × 6 × 2, three-mode, three-way (Carroll and Arabie, 1983) genotype× environment × attribute table of BLUPs. The three-mode three-way methodology is needed as each data value represents a measurement on a certain attribute on a particular genotype in a given environment and these data are not condensed or modified by re-expressing them as proximity measures (such as correlation coefficients or dissimilarity distances).

The three-way mixture method of clustering (Basford and McLachlan, 1985) enables the 272 genotypes (lines) to be grouped based on the BLUPs for grain yield and grain protein concentration simultaneously. Mean grain yield and grain protein concentration, and their standard errors, were computed for the genotype groups. The group-means (±1.5 standard error, Tukey, 1991) were displayed graphically as group-mean performance profiles across the six environments. If the error bars do not overlap, there is confidence about the direction of the difference of the group-means.

A three-mode principal component analysis (Kroonenberg, 1983) was conducted on the grain yield and grain protein BLUPs using the program TUCKALS3 (Kroonenberg, 1994). This procedure enables a small number of components to be determined for each of the three modes (genotypes, environments and attributes) to explain much of the variation in the data. A $P \times Q \times R$ solution has P genotype components, Q environment components and R attribute components. Prior to principal component analysis, the BLUPs for grain yield and grain protein concentration were centred and scaled (Basford et al., 1996) using the standardisation recommended by Fox and Rosielle (1982) and Cooper and DeLacy (1994). Joint-plots (Kroonenberg, 1983; a three-way variant of Gabriel's (1971) biplot) were constructed to portray the relationships between the genotypes and attributes for the first environment component and the relationships between the genotypes and environments for each attribute component. The latter were obtained by rotating the attribute components to represent grain yield and grain protein concentration independently. The joint-plots were used to identify genotypes that had desirable grain yield and protein concentration characteristics.

2.6. Pattern analysis of the G × M interactions

For the pattern analysis of the G × M interactions the objective was not to consider the grain yield–grain protein correlation, as above, but to consider the influence of management on each trait independently.

Because of the unbalanced nature of the MET data set it was considered inappropriate to use pattern analysis to examine the G × M interactions based on the BLUPs for the complete set of 272 lines. A balanced subset, based on the 21 common lines included in all 23 trials, was extracted from the full data set and used to investigate the G × M interactions for grain yield and grain protein concentration. Since the balanced subset of 21 lines represented a selected set of lines the BLUEs from the single trial analyses were used to construct the two-way (21 × 23) genotype-by-management data sets for pattern analysis. A two-mode principal component analysis was conducted separately for the standardised (Fox and Rosielle, 1982) grain yield and grain protein concentration data sets and a biplot (Gabriel, 1971) was constructed for both traits, using the GEBEI software (Watson et al., 1996). The biplot graphical display was chosen in preference to a three-mode analysis as the intention was to investigate the G × M interaction for each trait independently.

Rules for interpretation of biplots have been discussed elsewhere (DeLacy et al., 1996). In this paper the nature of the G × M interactions was examined by interpretation of the spatial positioning of the genotype (line) and trial (management-regime) scores on the biplots. The biplots were constructed with the 21 genotypes represented as points, each defined by the genotype's scores on the principal component axes, and the 23 trials were represented by vectors that extended from the origin to the trial's scores on the principal component axes. The angles between the trial vectors were used to infer the level of correlation of genotype performance between pairs of environments; a small angle indicates a positive correlation, an angle of 90° indicates that there is independence of performance, and an angle greater than 90° and approaching 180° indicates a negative correlation. Thus, the angles among the trial vectors on the biplot can be used as a graphical tool to consider the impact of G × M interactions on genotype performance in terms of the genetic correlation framework suggested by Falconer (1952), as discussed for pattern analysis by Cooper and DeLacy (1994). The predicted performance of a genotype in a particular trial, on the basis of the information presented in the biplot, is determined by projecting a perpendicular line from the genotype's score to the trial's vector.

3. Results

3.1. Environmental characterisation: site–year combinations and management-regimes

There were substantial differences in the temporal patterns of the weather variables rainfall, maximum and minimum temperature and incident solar radiation among the six site–year combinations (Fig. 1). There were differences among the three sites (Gatton, Fig. 1a and b; Kingsthorpe, Fig. 1c and d; Emerald, Fig. 1e and f) in the quantity of rainfall and temporal patterns of the weather variables that were consistent across the 2 years. However, there was no major contrast between the 2 years (1988 and 1989) in the quantity or temporal patterns of rainfall, temperature or incident solar radiation that was consistent across the three sites.

Gatton tended to have a higher total rainfall than the other two sites in both years, with large rainfall events occurring early in the experimental periods (Fig. 1a and b). In the first planting date at Gatton in 1988 (T1), the flowering developmental phase (Fb to Fe, Fig. 1a) of most lines occurred during a period of relatively low temperatures and low incident solar radiation. For the second planting date (T2), the temperatures and incident solar radiation during the flowering period were higher and generally increasing. In 1989 at Gatton, flowering of lines for the single planting date coincided with a period of higher temperatures and incident radiation (Fig. 1b) in comparison to the conditions for both planting dates in 1988 (Fig. 1a).

In both years at Kingsthorpe, daily maximum and minimum temperatures were generally lower for much of the season (Fig. 1c and d) than at the other two sites. Because there was a higher risk of a damaging frost coinciding with flowering of lines at Kingsthorpe, all trials were planted later here than at the other two sites. In 1988, flowering of all lines in all management-regimes coincided with a period of high temperatures and incident solar radiation and low rainfall (Fig. 1c). In 1989, flowering coincided with a period of relatively lower temperatures (Fig. 1d) than were encountered at Kingsthorpe in 1988 (Fig. 1c).

At the northernmost site Emerald, temperatures and incident solar radiation were generally higher and rainfall lower than at the other two sites (Fig. 1e and f). Because of the higher temperatures at Emerald,

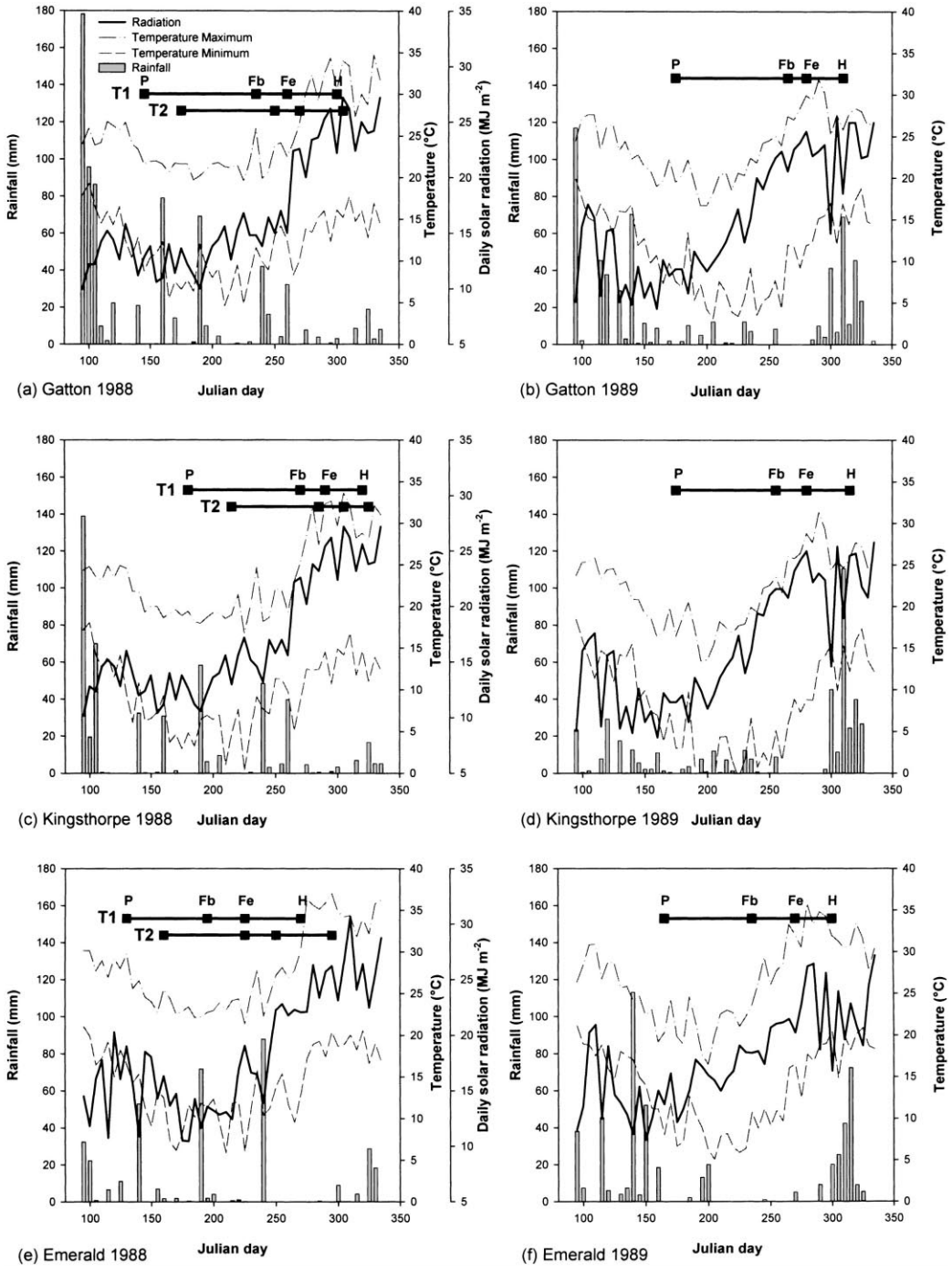

Fig. 1. Maximum and minimum temperatures (5-day mean), daily solar radiation (5-day mean), and 5-day total rainfall for (a) Gatton 1988; (b) Gatton 1989; (c) Kingsthorpe 1988; (d) Kingsthorpe 1989; (e) Emerald 1988; and (f) Emerald 1989. Timing of planting (P), beginning of the flowering period (Fb) and end of the flowering period (Fe), and final grain harvest (H) for the first (T1) and second (T2) planting dates in 1988 and the single planting date in 1989.

and associated lower risk of frost damage, the trials were generally planted earlier than at the other two sites. While total rainfall at Emerald in 1988 (Fig. 1e) was lower than that in 1989 (Fig. 1f), three substantial rainfall events occurred during the first half of the growing season and two of these events coincided with the flowering periods of most lines (Fig. 1e). Therefore, while there was low total rainfall at Emerald in 1988, the distribution of the rainfall in relation to the timing of flowering was such that water was not a major limitation to plant growth and yield accumulation in all trials at this site–year combination. In contrast to the conditions in 1988 at Emerald, in 1989 at the same site much of the rainfall was distributed early and late in the season and all lines in all trials flowered during a period of low rainfall and increasing temperatures (Fig. 1f).

All four trials at Gatton were generally free of major limitations due to lack of water or nitrogen (Table 1). All of the trials at Emerald were considered to have experienced some degree of nitrogen limitation. The trials at Kingsthorpe generally experienced some degree of water limitation and in some cases this was combined with the effects of damaging high temperatures during the flowering and grain filling periods.

3.2. Single trial analyses

The mean grain yield and grain protein concentration for the various management-regimes are shown in Table 2. Manipulation of soil water and nitrogen availability across planting dates and site–year combinations had a strong influence on mean grain yield and grain protein concentration. The high-input conditions at Gatton resulted in high mean grain yields ranging from 4.62 to 5.37 t ha^{-1} and mean grain protein ranging from 13.1 to 13.8%. The management-regimes applied at Emerald and Kingsthorpe generally resulted in mean grain yields lower than those at Gatton. However, three of these trials had mean grain yields similar to those obtained at Gatton, namely the high-input trial Et2h88 at Emerald, and the medium-input Kt1m88 and high-input KLFI89 trials at Kingsthorpe. The mean grain protein concentration at Emerald was generally low, ranging from 8.5 to 11.4%. At Kingsthorpe the grain protein concentration was generally higher than at Emerald, ranging from 12.9 to 18.6%. The highest mean grain protein concentrations at Kingsthorpe were associated with those trials that were most strongly affected by the high temperatures during flowering and grain filling in 1988 (Fig. 1c, Table 1; i.e. Kt1l88, Kt2l88 and Kt2m88).

The preferred spatial models differed among the trials for each trait and also between the two traits for individual trials (Table 2). Most of the trials had only a few rows and many columns (e.g. 2 rows and 73 columns for six of the trials) and contained a majority of unreplicated advanced breeding lines. Therefore, in many cases no extraneous trend was identified. However, for seven of the grain yield models and twelve of the grain protein concentration models, a fixed row effect was fitted to model the differences between rows. More obvious was the presence of large-scale (global) trends. In fifteen of the grain yield models and fourteen of the grain protein concentration models, either a linear regression or smoothing spline on the column indices was fitted. For all but one trial (KLFD89) a separable autoregressive process was fitted to account for small-scale or local trend. For this one trial the lag 1 autocorrelations of residuals were small enough to be ignored and the AR1 × AR1 term was dropped from the preferred model. It should be noted that as trials Kt1h88 and Kt2h88 had only one row, a one-dimensional autoregressive term (AR1) was fitted. Days-to-flower was identified as an important covariate for both grain yield (16 trials) and grain protein concentration (19 trials) in the majority of the 23 trials. For some trials a linear association between days-to-flower and both grain yield and grain protein was detected (e.g. Et1m88, Kt2m88, Ga2I89), while for other trials a non-linear association was detected (e.g. ELFI89, Kt1h88, Gt1I88). Target plant population was identified to have a significant effect on both grain yield (7 out of 14 trials) and grain protein (5 out of 14 trials) in some of the 1988 trials.

The line-mean heritability for grain yield ranged from the low value of 0.11 (Et1l88) to 0.88 (Et1h88) and for grain protein concentration it ranged from 0.27 (KLFI89) to 0.91 (Et2h88) (Table 2). The genotypic correlation between grain yield and grain protein concentration was negative for all but one trial (Kt2h88), where it was estimated to be zero. The negative genotypic correlations ranged from the strong negative correlation of −0.98 (Et1l88) to

the relatively weak negative correlation of −0.31 for EDCI89. The environmental correlations were variable, ranging from −0.48 (Gt2I88) to +0.18 (Et1m88). At Emerald and Kingsthorpe the environmental correlations were generally weak, with a number of estimates close to or equal to zero. At Gatton the four estimates of the environmental correlation were negative. The estimates of the phenotypic correlation coefficient were predominantly negative. Some differences between the estimates of the phenotypic correlation coefficient based on the raw data and the spatially adjusted BLUEs were noted (e.g. Et1l88, Et2h88, Kt1m88). Therefore, in some of these trials adjusting the grain yield and grain protein concentration data for spatial environmental effects had some influence on the estimates of the phenotypic correlation coefficients between these traits.

3.3. Multi-environment trial analyses

Significant genotypic variation for average performance across environments was identified for both grain yield and grain protein concentration (Table 3). For grain yield, the G × S and G × S × Y interaction components of variance were comparable in size to the genotypic component, but there was no G × Y interaction detected. The G × M interaction component was the largest source of G × E interaction and was approximately twice the size of the genotypic component of variance. The residual component of variance was the largest source of variance. For grain protein concentration, small G × S and G × S × Y interaction components of variance were detected and these were approximately a quarter of the size of the genotypic component of variance. As in the case of grain yield, there was no G × Y interaction detected. The G × M interaction component was again the largest source of G × E interaction and was approximately twice the size of the genotypic component of variance. The residual variance for grain protein concentration was slightly smaller than the G × M interaction component of variance. The BLUPs for grain yield and grain protein concentration were computed for the 272 genotypes at each site–year combination, based on the results of the multi-environment trial analyses. These BLUPs were considered to represent an assessment of the genotypic performance for the site–year combinations that takes into consideration the available information on the influences that the different management-regimes may have on the performance of the genotypes. These BLUPs were then used as the focus for the pattern analysis component of the site–year cross-classification study.

Table 3
Estimates of the genotypic (G), genotype-by-site (G × S), genotype-by-year (G × Y), genotype-by-site-by-year (G × S × Y) and genotype-by-management (G × M) interaction components of variance and their standard errors for the combined analysis of variance for grain yield (t ha^{-1}) and grain protein concentration (%) for 272 lines tested under various management-regimes at three sites (Emerald, Kingsthorpe and Gatton) across 2 years (1988 and 1989) in Queensland

Source	Trait	
	Grain yield	Grain protein
G	0.068 ± 0.014	0.203 ± 0.026
G × S	0.064 ± 0.018	0.044 ± 0.032
G × Y	0.001 ± 0.010	0.000[a]
G × S × Y	0.056 ± 0.017	0.057 ± 0.031
G × M	0.117 ± 0.005	0.445 ± 0.020
Residual	0.175	0.371

[a] The standard error of the G × Y interaction component was much larger than the component such that the ratio of the component to the standard error was effectively zero. Therefore, this component is reported as zero.

3.4. Pattern analysis of the site–year cross-classification (broad adaptation)

A five-group summary identified by the three-way cluster analysis of the 272 genotypes was selected as a satisfactory representation of major features of the genotypic and G × E (G × S, G × Y and G × S × Y) interaction variation for grain yield and grain protein concentration (Fig. 2). The genotype groups varied in size, ranging from 12 members for group 3–83 members for group 5. The negative correlation between grain yield and grain protein concentration was evident in the group mean response profiles. Generally the genotype groups with high grain yield BLUPs (Fig. 2a) had lower grain protein BLUPs (Fig. 2b). Two groups were identified to have consistently higher grain yield across the six site–year combinations; group 1 with 41 members and group 4 with 76 members (Fig. 2a). The mean grain yield BLUPs for groups 1 and 4 were similar for Emerald and

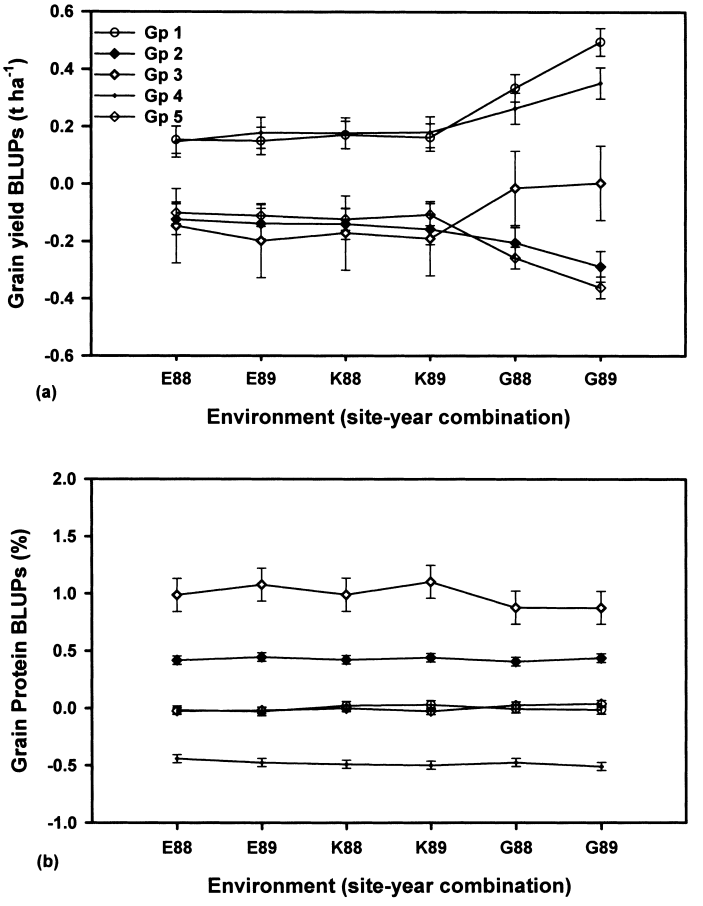

Fig. 2. Group mean (±1.5 standard error) Best Linear Unbiased Predictions (BLUPs), for the five genotype groups identified by cluster analysis, for (a) grain yield and (b) grain protein concentration across the six site–year combinations sampled in the multi-environment trial; E88 and E89 are Emerald 1988 and 1989, respectively, K88 and K89 are Kingsthorpe 1988 and 1989, respectively, and G88 and G89 are Gatton 1988 and 1989, respectively.

Kingsthorpe in both years but differed for Gatton, particularly in 1989 (G89). The three remaining groups (groups 2, 3 and 5) had lower mean grain yield BLUPs, with group 3 showing higher mean yield than groups 2 and 5 at Gatton in both years. There was no evidence of crossover interactions for grain yield on a group-mean basis between the two high-yielding genotype groups (groups 1 and 4) and the three low-yielding groups (groups 2, 3 and 5). There was some evidence of crossover interactions among the three low-yielding groups, with group 3 having the lowest mean yield for site–year combinations E88, E89, K88 and K89 and higher yield than genotype groups 2 and 5 for G88 and G89. Genotype group 5 which had the lowest mean yield for G88 and G89 had a higher mean yield than genotype groups 2 and 3 for E88, E89, K88 and K89. There was no evidence of crossover interactions on a group-mean basis for grain protein concentration (Fig. 2b). The two high-yielding genotype groups, 1 and 4 (Fig. 2a), both had relatively low group-mean grain protein BLUPs (Fig. 2b). However, group 1 had a consistently higher group-mean grain protein concentration than group 4. This indicates that there is some scope to select for higher grain protein concentration among the higher-yielding genotypes of groups 1 and 4.

Comparison of the genotype group-mean grain yield (Fig. 2a) and grain protein concentration

(Fig. 2b) BLUPs between the high-input site–year combinations generated at Gatton (G88 and G89) and the other four site–year combinations (E88, E89, K88 and K89), suggested that there is scope to select lines that have a degree of broad adaptation for yield and protein across both high-input (potential yield) conditions and the water and nitrogen limited environments generated at Emerald and Kingsthorpe.

A $2 \times 1 \times 2$ (genotype $\times$ environment $\times$ attribute) solution for the three-way principal component analysis was selected. The joint-plot for the genotypes and attributes for the first environment component provided an appropriate representation of the main features of the results of the analysis (Fig. 3). For this joint-plot, 84% (component $1 = 65\%$ and component $2 = 19\%$) of the total variation in the original $272 \times 6 \times 2$ data set was represented. This graphical display allowed consideration of genotype scores for both traits simultaneously for a large proportion of the common information across the six environments (site–year combinations). The negative correlation between grain yield and grain protein concentration

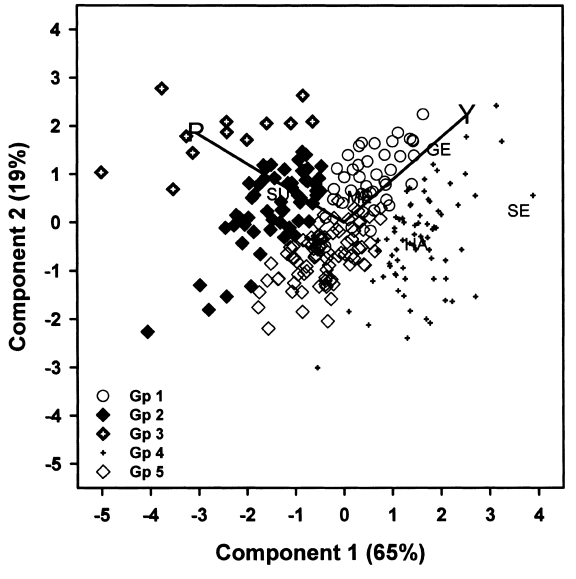

Fig. 3. Joint-plot for genotypes (272) and attributes (2, Y: grain yield and P: grain protein concentration) for the first environment component. The five genotype groups identified by cluster analysis are identified by the same symbols used in Fig. 2. The five check genotypes are identified, SU: Sunco (group 2), HA: Hartog (group 4), SE: Seri (group 4), GE: Genaro (group 4), ME: Meteor (group 5).

was apparent in that the angle between the grain yield and grain protein vectors was greater than 90° but less than 180°. This was consistent with the generally intermediate negative values of genetic correlations between the traits observed for the individual trials (Table 2).

The five groups of genotypes identified by cluster analysis generally occupied different positions on the joint-plot (Fig. 3). At the extremes the highest yielding genotype groups and individual genotypes generally had lower grain protein and those with the highest grain protein concentration generally had lower yield. The high yielding check lines Seri and Genaro had high positive scores for grain yield but low and intermediate scores for grain protein concentration, respectively. However, there were a few genotypes with positive scores on both the grain yield and grain protein vectors. These genotypes came predominantly from the genotype groups 1, 2 and 3. A large proportion of the lines from genotype group 1 had both high grain yield and positive scores for grain protein. Importantly, a large number of the advanced breeding lines that were sampled from the pedigree breeding program had combined grain yield and grain protein scores that were superior to those of the three commercial check cultivars Hartog, Sunco and Meteor.

3.5. Pattern analysis of the G × M interactions (specific adaptation)

A combined analysis of variance for the subset of 21 common genotypes across the 23 trials indicated that there were significant G × M, G × S, G × Y and G × S × Y interactions ($P < 0.01$) for both grain yield and grain protein concentration. The G × M interactions influenced the correlation of the genotype BLUEs between trials within a site. For grain yield the correlation coefficients between trials at Gatton ranged from 0.24 to 0.79 (mean $= 0.45 \pm 0.21$) at Kingsthorpe they ranged from -0.07 to 0.76 (mean $= 0.43 \pm 0.20$), and at Emerald they ranged from -0.21 to 0.68 (mean $= 0.24 \pm 0.21$). For grain protein concentration the correlation coefficients at Gatton ranged from 0.18 to 0.69 (mean $= 0.42 \pm 0.19$), at Kingsthorpe from 0.03 to 0.87 (mean $= 0.42 \pm 0.24$), and at Emerald from -0.58 to 0.89 (mean $= 0.38 \pm 0.44$). The biplots for grain yield (Fig. 4a) and grain protein concentration (Fig. 4b) were used

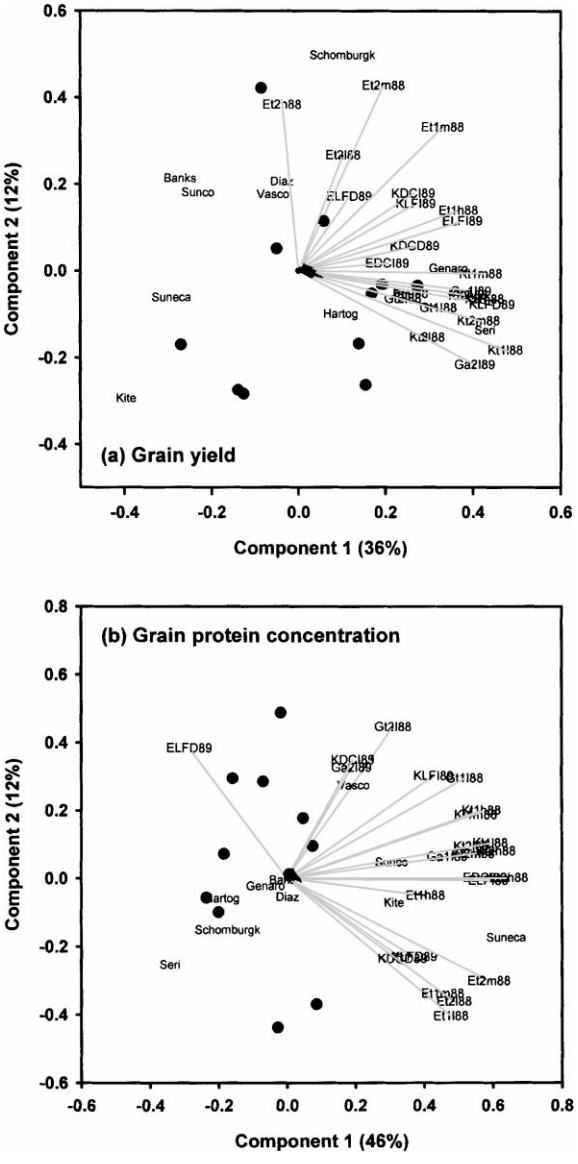

Fig. 4. Biplots for the first two principal components from the analysis of the 21 common genotypes evaluated in all 23 trials (management-regimes) for (a) grain yield and (b) grain protein concentration. For the 21 genotypes, the 10 cultivars are identified by name and the 11 advanced breeding lines are identified by the closed circle symbol. The 23 trials are identified by the trial identifiers listed and defined in Table 1.

to further investigate the form of these correlations among trials.

The first two components of the principal component analysis of the grain yield data accounted for 48% (component 1 = 36% and component 2 = 12%) of the standardised grain yield variation. For grain protein concentration the first two components accounted for 58% (component 1 = 46% and component 2 = 12%). For both traits the genotypic variation at some of the trials was less well represented than others. For these analyses, based on standardised data, the poorer representation is indicated by the trials with the shorter vectors extending from the origin (Fig. 4).

For grain yield, the angles between the trial vectors ranged from small positive values to values that were greater than 90° but less than 180°. The genotypes with positive scores on component 1 (e.g. Seri and Genaro) had greater grain yield in the four high-input management-regimes at Gatton (Ga1I89, Ga2I89, Gt1I88, Gt2I88) and in a number of the management-regimes at the other two sites (e.g. Kt1I88, Kt1m88, Et1h88, ELFI89), but predominantly those at Kingsthorpe (Fig. 4a). A number of the management-regimes at Emerald, where nitrogen was considered to be a major environmental limitation (Table 1), resulted in genotypic performance that was either weakly or not correlated with that observed in the Gatton high-input regimes (i.e. angles between the trial vectors > 45°; e.g. Et1m88, Et2m88, Et2h88, Fig. 4a). In these low nitrogen management-regimes at Emerald, different genotypes showed superior grain yield in comparison to the Gatton management-regimes, e.g. Schomburgk had higher yield than Seri at Et1m88, Et2m88 and Et2h88, but Schomburgk was intermediate at Ga1I89 and Ga2I89 where Seri had the higher yield.

For grain protein concentration (Fig. 4b) most of the angles between the trial vectors ranged from close to 0° (e.g. between Et1I88, Et1m88, Et2I88 and Et2m88) to 90° (e.g. between Gt2I88 and Et2m88). One trial (ELFD89) contrasted with the other trials and the angles between this trial and the others ranged from 90 to 180°.

4. Discussion

The major finding from this study was that genotype-by-management interactions were the largest individual source of G × E interaction variance for both grain yield (49%) and grain protein concentration (82%). For both traits, the G × M interaction

component of variance was larger than the genotypic component. For grain yield, the G × S and G × S × Y interactions were also large and comparable in size with the genotypic component. For grain protein concentration, the G × S and G × S × Y interaction components were small relative to the genotypic component. For both traits, no G × Y interactions were observed. Cullis et al. (1996) reported the G × Y component to be similar in magnitude to the G × S interaction component, and about 40% of the genotypic component, for grain yield of selected wheat varieties in New South Wales. The absence of any G × Y interaction here may reflect the different climatic factors in Queensland, or more specifically the particular patterns of weather variables sampled at the three sites in the 2 years 1988 and 1989, but may also reflect the fact that most genotypes in this study were only evaluated in 1989. Regardless, the large estimates of the G × M interaction components of variance relative to G × S, G × Y and G × S × Y identified in this study suggest that the influence of management practices on genotype performance warrant more explicit consideration in the conduct of wheat breeding METs in the northern grains region. Brennan et al. (1981), Cooper et al. (1996) and Cullis et al. (1996) all found that G × S × Y was the largest interaction component for grain yield of wheat in this region. Much of this is likely to be G × M in nature. Follow-on work from this study should examine the influence of the specific management factors that influence soil nitrogen and water availability at time of planting across a wide range of site–year combinations in order to quantify the relative importance of the management factors in generating G × M interactions for grain yield and grain protein concentration of wheat in the northern grains region. This has not yet been systematically attempted for wheat breeding METs in this region.

The variable nitrogen and water status of the environments sampled in breeding METs is rarely quantified. This greatly complicates the interpretation of the detected genetic variation for grain yield and grain protein concentration. The results of this study suggest that there were strong effects of the environmental variables soil water and soil nitrogen in determining the growth and development patterns and ultimately the grain yield and grain protein concentration of the wheat genotypes. For example, in the trials where soil nitrogen was considered to be a major limiting factor (e.g. Et1l88, Et1m88, Et2l88, Et2m88, ELFD89, ELFI89) there was generally a strong negative genetic correlation between grain yield and grain protein concentration (e.g. −0.98 for Et1l88 and −0.81 for ELFI89). In contrast, in environments where both soil nitrogen and water were considered not to be major limiting factors (e.g. Gt1I88, Gt2I88, Ga1I89, Ga289) there tended to be a weaker negative genetic correlation between grain yield and grain protein concentration (e.g. −0.47 for Ga1I89 and −0.48 for Gt2I88). In other situations it appeared that soil water interacted with the effect of changing planting date (e.g. Kt1l88, Kt1m88 and Kt1h88 cf. Kt2l88, Kt2m88 and Kt2h88) to influence mean grain yield, grain protein concentration and the genetic correlation between them. Future work will focus on quantifying the prevailing environmental conditions and types of management-regimes that are sampled in the wheat breeding METs and the relevance of these to the target population of environments and range of management practices used throughout the northern grains region.

Linear and non-linear influences of genotypic variation for timing of flowering on both grain yield and grain protein concentration were consistently observed. These associations were accommodated in this study by using days-to-flower as a covariate in the individual trial analyses of variance. Thus, it is assumed that the genotypic variation for grain yield and grain protein concentration examined in the combined analyses of variance and pattern analysis components of this study was independent of the recognised strong influences of flowering time on G × E interactions for yield (Woodruff and Tonks, 1983; Cullis et al., 1996; Cooper et al., 1997). This may in part explain the lower levels of crossover types of interaction that were observed for the G × S × Y interaction component of variance for grain yield in this study, in comparison to the high levels of crossover interaction that are frequently observed for grain yield of wheat in experimental and breeding METs conducted in the northern grains region (Cooper et al., 1996). However, it does not provide any obvious explanation for the large G × M interactions observed for grain yield and grain protein concentration.

The conclusion of Cornish (1987), ‘‘It is likely that cultivars developed under one management-regime will be reasonably well suited to another.’’ requires

further investigation when both grain yield and grain protein concentration are considered. The influences of genotypic variation for flowering time require explicit consideration. The contributions of genotypic variation for flowering time and environmental variation for the timing of water-deficit to G × E interactions for yield can often obscure the detection and investigation of other sources of interaction, and therefore must be quantified in any investigation of the impact of G × M interactions on the scope to select for broad and specific adaptations in a target population of environments. The G × M interactions for the balanced subset of 21 genotypes evaluated across all 23 trials in this study indicated that the ranking of the genotypes could change with management regime. A number of the low, medium and high-input management-regimes at Kingsthorpe resulted in a ranking of the 21 genotypes that was similar to that observed for the high-input management-regimes at Gatton. However, in a number of the management-regimes at Emerald, where nitrogen limitation was considered to be a major limiting environmental factor, the ranking of the genotypes contrasted with that at Gatton.

A negative genotypic correlation between grain yield and grain protein concentration was consistently observed across the management-regimes, sites and years sampled in this study. The range of the estimates of the correlation coefficients was similar to previous reports (Stoddard and Marshall, 1990; Fabrizius et al., 1997). Under the high-input management-regimes generated at the Gatton site the genotypic correlation was intermediate, ranging from −0.47 to −0.69, while the estimates of the correlation coefficients varied to a greater extent at the Emerald and Kingsthorpe sites where low, medium and high-input management-regimes were included. Consistent with the conclusions by Feil (1997), the range of these estimates suggest that under some environmental conditions there is scope to select for genotypes that combine higher grain yield and protein concentration, particularly where the available soil nitrogen is not severely limiting, while under others, where available soil nitrogen is the major limitation, there is limited scope.

The three-way pattern analysis of the grain yield and grain protein BLUPs provided a useful summary of the major features of genotypic variation for broad adaptation observed in the MET. The scores of the 272 genotypes on the genotype by attribute joint-plot for the first environment vector gave a representation of the major features of the genotype by attribute relationships that were common across the environments (sites, years and management-regimes). This joint-plot can be used to provide a graphical display of the scope for selection among the advanced lines for improved grain yield and grain protein concentration relative to the three check cultivars Hartog, Sunco and Meteor, that are currently widely used in the northern region, and the high yielding checks Seri and Genaro. The superior grain yield performance of the check lines Seri and Genaro across the management-regimes and site–year combinations indicated that there is scope to increase the yield of wheat cultivars in the northern grains region for the water and nitrogen limited conditions and also under potential conditions when the effects of these production constraints were removed or reduced by high-input management. However, both of these check lines had low to intermediate grain protein concentration scores in the multivariate analysis. This suggests that selection for grain protein concentration would influence the extent to which the superior yield of these lines can be combined with high grain protein concentration and could thus limit the extent to which broad adaptation for grain yield can be improved. Feil (1997) argued that simultaneous genetic improvement of grain yield and grain protein concentration in cereals requires attention to increasing grain protein yield and is most profitably targeted at production systems managed to ensure adequate soil nitrogen is available to the crop. Further work is underway to determine the scope to increase grain protein yield in combination with the Seri and Genaro sources of higher yield, through either enhanced accumulation of nitrogen in plants, enhanced partitioning efficiency, or a combination of both enhanced accumulation and partitioning.

5. Conclusions

While there were large sources of G × E interactions for both grain yield and grain protein concentration and a consistently negative genotypic correlation between these traits across the management-regimes, there was sufficient genotypic variation among the advanced breeding lines generated by the breeding

program to enable identification of lines with higher grain yield and equivalent or superior grain protein concentration relative to the important commercial check cultivars Hartog, Sunco and Meteor. The large source of G × E interaction variation attributed to G × M interactions for both grain yield and grain protein indicates the need for further work to examine the joint influences of genotype and management-practice on both: (1) the potential to select for cultivars with improved levels of broad adaptation for grain yield and grain protein concentration to variation in management and environmental regimes encountered within the northern grains region, and (2) the scope to realise the grain yield and protein potential of the cultivars by matching management and genotype for the range of on-farm management-regimes used within the northern grains region.

While the results of this study suggest that there may be scope to select for specific adaptations associated with G × M interactions, practical considerations in conducting and analysing METs to select for adaptation patterns are critical in the operation of a breeding program. Structuring and analysing METs to enable selection for specific adaptations is resource intensive and time consuming. The simplest approach, and one that is often employed, is to select for broad adaptation. The results of this study indicate that progress for grain yield and grain protein concentration can be expected if this strategy is continued. However, the large G × M interaction component of G × E interaction variance is strongly suggestive of an opportunity to complement selection for broad adaptation by analysing the results of METs to seek out genotypes with specific adaptations to some of the nitrogen management practices used in the northern grains region of Australia.

To extend this result beyond the observational nature of this present study requires assessment of the value of systematically including multiple management-regimes at some of the site–year combinations that are sampled in the METs of the breeding program. To date such augmentation of METs has only been attempted on an ad hoc basis or for specific research investigations (e.g. Cooper et al., 1996). One form of augmentation that is under consideration following this study is that of replacing the current practice of multiple replicates of a single management-regime at each site–year combination with single replicates of two (high and low input) nitrogen fertiliser management-regimes at a number of selected site–year combinations. Where this approach is adopted estimates of experimental error for a site–year combination can be obtained by using repeated check entries distributed within each of the management-regimes.

The present study considered grain yield and grain protein concentration of 272 advanced breeding lines across a range of management-regimes at 3 sites for 2 years. G × M interactions were found to have a large influence on genotypic performance for both traits. Where only one management-regime is considered at a site–year combination G × S × Y and G × M interactions will be confounded in the combined analysis of breeding METs. Therefore, the large G × S × Y interactions that have previously been reported for grain yield of wheat in the northern grains region of Australia (summarised by Cooper et al., 1996) are likely to be in part explicable in terms of the sampled management conditions (e.g. effect of prior cropping history on soil nitrogen status, planting date) as well as the fluctuating environmental conditions sampled across the site–year combinations (e.g. variable rainfall and temperature patterns in relation to the timing of plant development). The costs, potential benefits and practicalities of a comprehensive MET program that explicitly incorporates multiple management-regimes across site–year combinations will be examined further in more extensive METs based on additional years and a wider range of sites.

The appropriate genotype-environment model for studying genotypic adaptation of breeding lines within the complex range of farming systems of the northern grains region of Australia will require detailed consideration. In the current study two extreme modelling approaches were considered: (1) a broad adaptation model, and (2) an unstructured G × M interaction model that enables investigation of patterns of specific adaptation to different management-regimes. While these were useful in exploring the features of this MET data set, both are unlikely to be optimal in practice, particularly if explicit features of the G × M interactions are to be examined and specific adaptations are to be targeted for selection. As the repeatable components of G × M interaction are determined from investigations across studies, specific structured G × M models of genotypic adaptation that are intermediate

between the extreme statistical models considered here are likely to be identified. These models are considered to be intermediate in the sense that they would be structured to incorporate a specific targeted subset of management variables. The detection in this study of a large component of G × M interactions for grain yield and grain protein concentration has stimulated interest in pursuing this avenue of research.

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