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A selection strategy to accommodate genotype-by-environment interaction for grain yield of wheat: managed-environments for selection among genotypes

Abstract Selection for grain yield among wheat lines is complicated by large line-by-environment (L × E) interactions in Queensland, Australia. Early generation selection is based on an evaluation of many lines in a few environments. The small sample of environments, together with the large L × E interaction, reduces the realised response to selection. Definition of a series of managed-environments which provides discrimination among lines, which is relevant to the target production-environments, and can be repeated over years, would facilitate early generation selection. Two series of managed-environments were conducted. Eighteen managed-environments were generated in Series-1 by manipulating nitrogen and water availability, together with the sowing date, at three locations. Nine managed-environments based on those from Series-1 were generated in Series-2. Line discrimination for grain yield in the managed-environments was compared to that in a series of 16 random production-environments. The genetic correlation between line discrimination in the managed-environments and that in the production-environments was influenced by the number and combination of managed-environments. Two managed-environment selection regimes, which gave a high genetic correlation in both Series-1 and 2, were identified. The first used three managed-environments, a high input (low water and nitrogen stress) environment with early sowing at three locations. The second used six managed-environments, a combination of a high input (low water and nitrogen stress) and medium input (water and nitrogen stress) with early sowing at three locations. The opportunities for using managed-environments to provide more reliable selection among lines in the Queensland wheat breeding programme and its potential limitations are discussed.

Introduction

The primary objective for establishing a multi-environment testing regime as part of a breeding program is to accomodate the effects of genotype-by-environment (G × E) interactions in selection and therefore maximise response to selection. Selection is practised in a sample of environments with the objective of maximising indirect response to selection in future environments within in the same geographical region. G × E interactions are expressed as a change in the relative performance of genotypes when they are evaluated in different environments. Where these interactions are large they complicate selection and reduce the indirect response to selection in future environments. The estimation of the size of these interactions (Comstock and Moll 1963), their nature (Finlay and Wilkinson 1963; Byth et al. 1976; Baker 1988), and the opportunity to exploit them (Byth 1981; Baker 1988; Eisemann et al. 1990; Cooper et al. 1993), have each been widely discussed in the literature. A strong focus on defining an appropriate multi-environment selection regime (Roy and Murty 1970; Allen et al. 1978; Brennan et al. 1981; Rosielle and Hamblin 1981; Atlin and Frey 1989, 1990) is a consequence of the presence of G × E interactions and their impact on realised response to selection. Testing regimes may ignore, avoid, or exploit G × E interaction (Eisemann et al. 1990). Where G × E interactions are large, regional

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testing strategies are commonly structured to accommodate these by either avoiding or exploiting them. This study draws on the results from a series of research programmes and the regional testing programme at the Queensland Wheat Research Institute. The objective is to assess the scope for managing environmental conditions at a restricted number of sites to provide discrimination among wheat lines for grain yield which matches that in target production-environments.

The influence of choice of test environment on the attainment of selection objectives has been widely studied (Frey 1964; Roy and Murty 1970; Brennan et al. 1981; Atlin and Frey 1989, 1990; Eisemann et al. 1990; Bramel-Cox et al. 1991). However, there is no consensus on the definition of an optimal selection regime. To assist such a definition, the concept of a target population of environments was considered by Comstock (1977), Allen et al. (1978), Fox and Rosielle (1982), Hallauer (1988), Nyquist (1991) and Cooper et al. (1993). To accomodate G × E interactions, the value of any test environment for selection may be assessed by the similarity between genotypic discrimination within that environment and that in the target environment(s) (Allen et al. 1978; Fox and Rosielle 1982; Cooper et al. 1993). Environments with decreasing similarity have decreasing relevance as a test environment.

A strategy to exploit G × E interactions for the yield of wheat in Queensland

For grain yield of wheat in Queensland, G × E interactions are large relative to differences in genotypic effects across environments (Brennan and Byth 1979; Brennan et al. 1981). This complicates selection for grain yield in early generations where many lines are evaluated for yield in a limited number of environments. Presently, all introduced lines and F_4 bulked lines from the pedigree programme are tested for yield and quality at three locations in 1 year in single replicate experiments. Lines selected from these tests are re-evaluated at the same three locations in the following year. While this strategy has been effective in identifying superior lines, further testing of material suggests many failures are also selected and scope exists to improve the effectiveness of this early generation seleciton. An understanding of the causes of G × E interactions in these regional trials may allow selection for differences in adaptation reflected in the G × E components of variation as well as the average genotypic effects. Response to selection could be improved by identifying the set of selection environments most relevant to the future production-environments. If these test environments can be repeated from year to year, confidence in predicting response in future environments would be increased.

Selection for broad adaptation to a target geographical area implicitly assumes that there is one target population of environments. Recent consideration of the cause of G × E interactions for yield of wheat in Queensland (Cooper et al. 1990; Eisemann et al. 1990) suggests that an alternative model of the geographical target, in which the geographical area may be viewed as a mixture of target populations of environments, may be more useful. This explicity recognises that there is more than one adaptation target. The specific forms of target Eisemann et al. (1990) proposed to investigate were defined by levels of water and nitrogen stress. As pointed out by Matheson and Cotterill (1990), matching genotypes to an environmental target requires that environments are well defined and repeatable. Where the nature of the environmental challenges encountered within a geographical region is poorly understood, the scope for definition of appropriate target environments is limited and a random sampling of locations and years would be the appropriate strategy.

The process of developing a selection regime matched to the target environments is equivalent to replacing a random sampling strategy with a stratified sampling procedure. This can proceed where there is an a priori understanding of the structure of the population to which the sample statistics are to apply. Developing the optimal combination of managed-environments is a long-term process and depends on the quality of the underlying research which characterises the basis of plant adaptation. Following the discussions of Cooper et al. (1990) and Eisemann et al. (1990) this can be approached in two steps. The first is to define the average target of the production-system and attempt selection for this. This is the subject of the current paper. The second is identify what scope exists for resolving the average target into a mixture of underlying target populations. This is to be the subject of a subsequent paper.

Definition of managed-environments for Queensland

In Queensland, water and nitrogen availability have been identified as two major environmental variables which influence the grain yield of wheat (Woodruff and Tonks 1983; Hammer et al. 1987). The availability of both factors at about anthesis ($\pm$ 10 days) has a critical influence on the ability of lines to set a high grain number per unit area (Woodruff 1981 a, b). The performance of genotypes at this critical ontogenetic stage is a major determinant of grain yield of wheat in Queensland. In the present study, both nitrogen and water availability were manipulated, together with sowing date, at three locations, to generate a set of managed-environments. The objective was to generate a range of controlled environmental challenges during the critical flowering period. Discrimination among lines in managed-environments in 1 year was compared to that observed over 4 years in a sample of the regional trials of the Queensland wheat breeding programme. The principles of indirect selection (Falconer 1989; Cooper and DeLacy 1994) were used to quantify the effectiveness of the managed-environment selection strategies.

Materials and methods

Genetic material

Fifteen lines were sampled from the 1985 preliminary yield evaluation trials of the Queensland wheat breeding programme. Three lines were local check cultivars, Hartog, Banks and Kite. The remainder comprised one line from the 11th International Bread Wheat Screening Nursery (11th IBWSN) (entry 50) and 11 lines from the 17th IBWSN (entries 7, 30, 31, 38, 53, 64, 92, 129, 173, 206, Genaro), conducted by the International Maize and Wheat Improvement Center (CIM-MYT). These lines were considered to be a random sample of the lines from the preliminary testing stage of the Queensland programme.

Measurements

Grain yield was measured on all lines using small-plot harvesting equipment. Plot yields were converted to t ha^{-1} at 12% moisture content for most environments. In some cases air-dried yields were used and these were assumed to have an approximately 12% moisture content.

Production-environments

The 15 lines were evaluated in 16 production-environments over 4 years, 1985 to 1988. These were considered to be a random subset of the regional trials used by the Queensland wheat breeding programme (Brennan et al. 1981). The lines were evaluated in either seven (25-cm inter-row spacing)- or nine (18-cm inter-row spacing)-row plots. All rows were harvested to estimate grain yield. The level of replication differed between the production-environments; single replictes for six and three replicates for the other ten. For the pooled analysis of variance the unweighted procedure given by Cochran and Cox (1957, p. 558) was used. The model adopted was

$$p_{ijk} = m + l_i + e_j + (b/e)_{jk} + (le)_{ij} + \varepsilon_{ijk},\qquad(1)$$

where p_{ijk} is the phenotypic observation on line i in the kth block of environment j and $i = 1,..., n_l, j = 1,..., n_e, k = 1,..., n_b$; m is the grand mean of all observations; l_i is the effect of line i, assumed to be distributed as $N(0, \sigma_l^2)$; e_j is the effect of environment j, assumed to be distributed as $N(0, \sigma_e^2)$; $(b/e)_{jk}$ is the effect of block k in environment j, assumed to be distributed as $N(0, \sigma_b^2)$; $(le)_{ij}$ is the interaction effect of line i and environment j, assumed to be distributed as $N(0, \sigma_{le}^2)$; and ε_{ijk} is the experimental error , assumed to be distributed as $N(0, \sigma_\varepsilon^2)$. For each analysis, the variance components for lines (σ_l^2), line by environment ($L \times E$) interaction (σ_{le}^2), and experimental error (σ_ε^2), were estimated by equating the estimated and expected mean squares (Table 1) and solving for the variance components. Heritability on a line mean basis (h^2) was estimated as in Table 1. The average performance of the lines in the 16 production-environments was used to define the average target production-environment. The response to selection from the alternative managed-environment selection regimes was evaluated in this average test environment.

Managed-environments

Two series of managed-environments were conducted. Both involved manipulating the three variables, nitrogen, water availability, and sowing date, at three locations (Cooper et al. 1990; Eisemann et al. 1990). A particular combination of nitrogen, water and sowing date at a location comprised a managed-environment for this study. Series-1 included more environments than Series-2 and was used to investigate the extent of discrimination among lines for grain yield which was generated from managed-environments based on these variables. The discrimination was compared to that observed in the production-environments. Series-2 was used to re-evaluate promising combinations of managed-environments identified in Series-1.

Series-1 managed-environments

Series-1 consisted of 18 managed-environments (Table 2). These were made up of six managed-environments at each of three locations in Queensland; Emerald, Kingsthrope and Gatton. At both Emerald and Kingsthorpe the six managed-environments were conducted in 1988. At Gatton the six managed-environments were conducted over 2 years (1987 and 1988) and involved manipulating irrigation and sowing date. In 16 environments the lines were evaluated in four-row plots with 20- cm inter-row spacing. All four rows were harvested to estimate grain yield. In two of the Gatton environments the lines were evaluated in seven-row plots with 25-cm inter-row spacing. The lines were evaluated in a randomised complete block design with two replicates in each managed-environment. Analyses of variance were based on the linear model given in equation (1). However, in contrast to the production-environments a mixed model was adopted where the lines were considered to be random effects and the managed-environments fixed. The variance components for lines, $L \times E$ interaction, and error, were estimated by equating estimated and expected mean squares and solving for the variance components (Table 1). Heritability was estimated as outlined in Table 1. The estimation of variance components and heritability assumed that the managed-environments could be repeated over years. If these could be repeated then positive aspects of $L \times E$ interaction could be repeatedly selected for and exploited. Therefore, by adopting a mixed model the $L \times E$ interaction component was not partitioned out of the variance component for lines.

The number and combination of managed-environments required to discriminate among lines in a way similar to average performance in the production-environments was investigated by analysis of variance and indirect selection theory (Cooper and De-Lacy 1994). Sample sizes of 1–9 managed-environments were considered. For a sample size of one, each managed-environment was analysed separately. For sample sizes between two and nine managed-environments, many combinations could be considered. Specific combinations were of interest. However, whether these were optimal selection regimes was unknown. Therefore, in addition to the specific combinations, 30 random combinations of the managed-environments were analysed. This provided a measure of the range and distribution of discrimination among lines for different numbers of managed-environments. Including the single-environment and

Table 1 Expected mean squares[a] for the analysis of the series of managed- and production-environments and estimates of heritability

Source of variation	Multi-environment trials series	
	Production-environments	Managed-environments
Lines	$\sigma_\varepsilon^2 + n_r \sigma_{le}^2 + n_r n_e \sigma_l^2$	$\sigma_\varepsilon^2 + n_r n_e \sigma_{l'}^2$
L × E interaction	$\sigma_\varepsilon^2 + n_r \sigma_{le}^2$	$\sigma_\varepsilon^2 + n_r \sigma_{le}^2$
Error	σ_ε^2	σ_ε^2
Heritability	$h_L^2 = \dfrac{\sigma_l^2}{\sigma_l^2 + \dfrac{\sigma_{le}^2}{n_e} + \dfrac{\sigma_\varepsilon^2}{n_e n_r}}$	$h_{L'}^2 = \dfrac{\sigma_{l'}^2}{\sigma_{l'}^2 + \dfrac{\sigma_\varepsilon^2}{n_e n_r}}$

[a] Expected mean squares were constructed following the guidelines given in Steel and Torrie (1981, p. 357)

Table 2 Controlled inputs for Series-1 and -2 managed-environments and definition of the low, medium and high input characterisation of the managed-environments

Location	Input category	Sowing date	Nitrogen (kg N ha^{-1})	Irrigation schedule[a] (mm)
Series-1				
1. Emerald	Low	11/5/88	20	25 S
2. Emerald	Medium	11/5/88	40	25 S, 35 F
3. Emerald	High	11/5/88	150	25 S, 50 2W
4. Emerald	Low	8/6/88	20	25 S
5. Emerald	Medium	8/6/88	40	25 S, 35 F
6. Emerald	High	8/6/88	150	25 S, 50 2W
7. Kingsthorpe	Low	30/6/88	40	12 S
8. Kingsthorpe	Medium	30/6/88	70	12 S/35 F
9. Kingsthorpe	High	30/6/88	150	25 S/25 2W
10. Kingsthorpe	Low	3/8/88	40	25 S
11. Kingsthorpe	Medium	3/8/88	70	25 S/35 F
12. Kingsthorpe	High	3/8/88	150	25 S/25 2W
13. Gatton	High	29/5/87	150	25 2W
14. Gatton	Medium	29/5/87	150	0
15. Gatton	High	25/5/88	150	25 S/25 2W
16. Gatton	High	22/6/88	150	25 S/25 2W
17. Gatton	High	3/8/88	150	25 S/25 2W
18. Gatton	Medium	3/8/88	150	25 S
Series-2				
19. Emerald	Low	15/6/89	30 (LF)[b]	0
20. Emerald	High	15/6/89	100 (LF)	4 × 35 E
21. Emerald	Medium	15/6/89	100 (DC)	4 × 35 E
22. Kingsthorpe	Medium	23/6/89	90 (DC)	0
23. Kingsthorpe	High	23/6/89	90 (DC)	4 × 35 E
24. Kingsthorpe	Medium	23/6/89	10 (LF)	4 × 35 E
25. Kingsthorpe	Low	23/6/89	10 (LF)	0
26. Gatton	High	22/6/89	150	6 × 35 M
27. Gatton	High	22/6/89	150	6 × 35 M

[a] Irrigation schedule: Series-1; S = sowing, F = flowering, 2W = every 2 weeks Series-2; E = irrigation commenced at elongation, M = irrigation commenced at mid-tillering
[b] Prior management; LF = long fallow, DC = double cropped

multi-environment analyses, a total of 258 analyses of variance were conducted for sample sizes covering 1–9 managed-environments. Specific combinations of the managed-environments were investigated as possible managed-environment selection regimes. These were compared to the distributions generated by the random combinations.

Series-2 Managed-environments.

Series-2 consisted of a reduced set of nine managed-environments conducted in 1989 (Table 2). The reduced set was selected after examining the results of the Series-1 trials. These were conducted at the same locations as Series-1. At Emerald three environments were established at one sowing date, while at Kingsthorpe there were four environments at one sowing date, and at Gatton two environments at one sowing date. The Series-2 managed-environments (Table 2) were used to assess the repeatability of the selection parameters estimated from the Series-1 managed-environments. Therefore, combinations of the Series-2 environments were used to represent the specific managed-environment selection regimes examined in Series-1. In Series-2, the managed-environments were conducted as single replicate experiments. Eight of the fifteen lines were replicated. These replicated lines were used to provide an estimate of experimental error. All lines were evaluated in four-row plots as described for the Series-1 experiments.

Evaluation of managed-environment selection strategies

A managed-environment selection strategy is defined as an evaluation of line-yield performance in a specific combination of one or more of the managed-environments. The success of each strategy was evaluated in terms of the principles of indirect selection (Falconer 1989; Cooper and DeLacy 1994). A successful strategy was defined as one which gave a high indirect response to selection for average yield over the production-environments. This was quantified by the genetic correlation which measured the similarity of line discrimination between the managed-environment selection regime and that for average performance in the production-environments. The genetic correlation was calculated using the equations of Burdon (1977). Managed-environment selection strategies from the Series-1 analysis, with a high genetic correlation to the production-environments, were re-evaluated in the Series-2 managed-environments.

Results

Series-1 managed-environments

The mean yield of the Series-1 managed-environments ranged from 0.68 to 4.98 t ha^{-1}. There was significant ($P < 0.05$) line variation and L × E interaction in Series-1. The L × E interaction component was 1.3-times that for lines and line mean-heritability over the 18 environments was high (Table 3).

Line variation was significant ($P < 0.05$) in 13 of the 18 managed-environments (Table 4). For the 258 analyses of variance conducted on the Series-1 managed-environments, 97.3% identified significant ($P < 0.05$)

Table 3 Variance components for lines (σ_l^2), line-by-environment interaction (σ_{le}^2) and experimental error (σ_e^2) and line mean-heritability (h^2) for grain yield of 15 wheat lines evaluated in three series of multi-environment experiments and the genetic correlation (r_g) between average line performance in the Series-1 and -2 managed-environments and that in the production-environments

Environments	Genetic parameter				
	σ_l^2	σ_{le}^2	σ_ε^2	h^2	r_g
Series-1	0.082 ± 0.030	0.110 ± 0.015	0.099 ± 0.009	0.968	0.724
Series-2	0.100 ± 0.041	0.064 ± 0.034	0.200 ± 0.033	0.900	0.787
Production	0.042 ± 0.019	0.092 ± 0.017	0.127 ± 0.007	0.803	–

Table 4 Number of analyses of variance in which line main-effects and L × E interaction for grain yield were identified as significant ($P < 0.05$) from the evaluation of 15 wheat lines in 18 individual managed-environments (Series-1) and 30 random combinations of 2–9 of these managed-environments

Number of environments over which lines were evaluated	Source of variation			
	Line main-effects		L × E interaction	
	Significant	Not significant	Significant	Not significant
1	13	5	–[a]	—
2	28	2	23	7
3	30	.0	28	2
4	30	0	30	0
5	30	0	30	0
6	30	0	30	0
7	30	0	30	0
8	30	0	30	0
9	30	0	30	0
Category total	251	7	231	9
Total analyses	258	258	240	240
Percentage of total	97.3	2.7	96.25	3.75

[a] Lines evaluated in one environment, therefore L × E interaction cannot be tested

differences among lines (Table 4). For the 240 multi-environment analyses conducted for 2–9 managed-environments, 96.25% identified significant ($P < 0.05$) L × E interaction. There was a large range in the estimates of the variance components for lines, L × E interaction, and experimental error, from the different combinations of the managed-environments (Fig. 1). Therefore, the nature of discrimination among lines changed with the combination of managed-environments.

The range for the experimental-error component from individual environments (Fig. 1c), indicated heterogeneity of error variance. This was not unexpected for this diverse set of environments and may have contributed to an overestimation of the number of analyses with significant L × E interaction in the multi-environment analyses of variance. Working with transformed data may reduce this complication. However, for the purposes of this study it was considered appropriate to work on untransformed data, because the emphasis lay on interpreting patterns of interaction rather than testing inferences about the occurrence of interactions. Therefore, results for significance tests given above must be interpreted with caution.

The range and variability of the variance components decreased with an increasing number of managed-environments, reflecting an influence of sample size and sampling variation (Fig. 1). For both L × E interaction and experimental error the means of the random samples from 2–9 managed-environments (Fig. 1b, c) were similar to the corresponding variance components from the analysis based on the 18 managed-environments (Table 3). The mean of the line variance component was higher than that based on all managed-environments where only one or two environments were sampled (Fig. 1a), but after five environments were sampled the mean of the samples was similar to that based on all environments (Table 3). However, individual samples could still have an estimate much greater than that derived from all 18 environments.

There was a large range in the estimate of line mean-heritability (Fig. 1d) for individual environments. The heritability in three individual managed-environments was low, indicating they were of limited value as managed-environments. Line mean-heritability generally increased with the number of managed-environments and approached that for the complete set of managed-environments (Table 3), while the variabilty of the estimates decreased.

Relationship between Series-1 managed-environments and production-environments

The mean yield of the production-environments ranged from 1.9 to 5.3 t ha^{-1} and there was significant ($P < 0.05$) line and L × E interaction variation (Table 3).
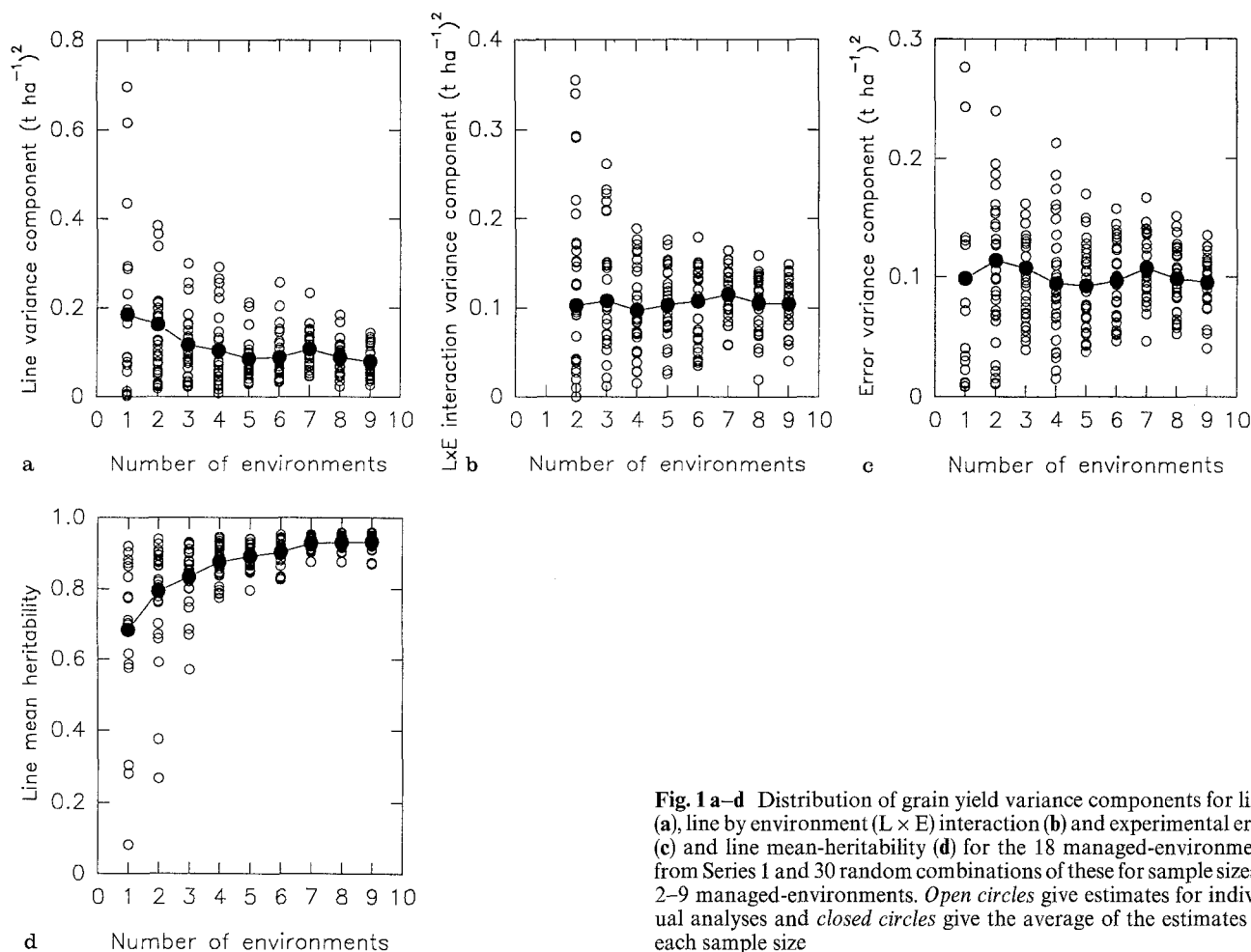
Fig. 1 a–d Distribution of grain yield variance components for lines (a), line by environment (L × E) interaction (b) and experimental error (c) and line mean-heritability (d) for the 18 managed-environments from Series 1 and 30 random combinations of these for sample sizes of 2–9 managed-environments. *Open circles* give estimates for individual analyses and *closed circles* give the average of the estimates for each sample size

The variance component for L × E interaction was 2.2-times that for line main-effects. This ratio was larger than that observed for the Series-1 managed-environments. The increase in this ratio was associated with a decrease in the magnitude of the line component of variance for the production-environments. The increase in the relative importance of L × E interaction was not unexpected as the variables manipulated in the managed-environments are only components of the total challenge profile expected in the production-environments. Heritability on a line mean basis over the 16 environments was high, but lower than that achieved in the managed-environments (Table 3).

Average line performance for yield in the Series-1 managed-environments was linearly associated ($P < 0.05$) with that in the production-environments (Fig. 2a). Lines which were higher yielding than the check cultivars were identified in both the managed and production-environments and the relative performance of the three check cultivars was similar in both. The newer cultivar, Hartog, gave a higher yield than both the older cultivars, Banks and Kite. While there was a positive association between the managed- and production-environments, there were lines which performed

well in the managed-environments that performed poorly in the production-environments.

There was a large range in the genetic correlation between line performance in the managed-environments and that in the production-environments, for the sample sizes evaluated (Fig. 3). On average, the genetic correlation was lowest when single managed-environments were related to the production-environments. For samples sizes of 2–9, the average genetic correlation gradually increased and approached that based on all 18 managed-environments (Table 3). The variability of the genetic correlation decreased with an increasing number of managed-environments (Fig. 3). For each sample size, there were combinations of managed-environments which gave a high genetic correlation with line performance in the production-environments.

Specific managed-environment selection strategies

There was considerable variation for the genetic correlation between line performance in the managed-environments and that in the production-environments among the alternative managed-environment selection stra-
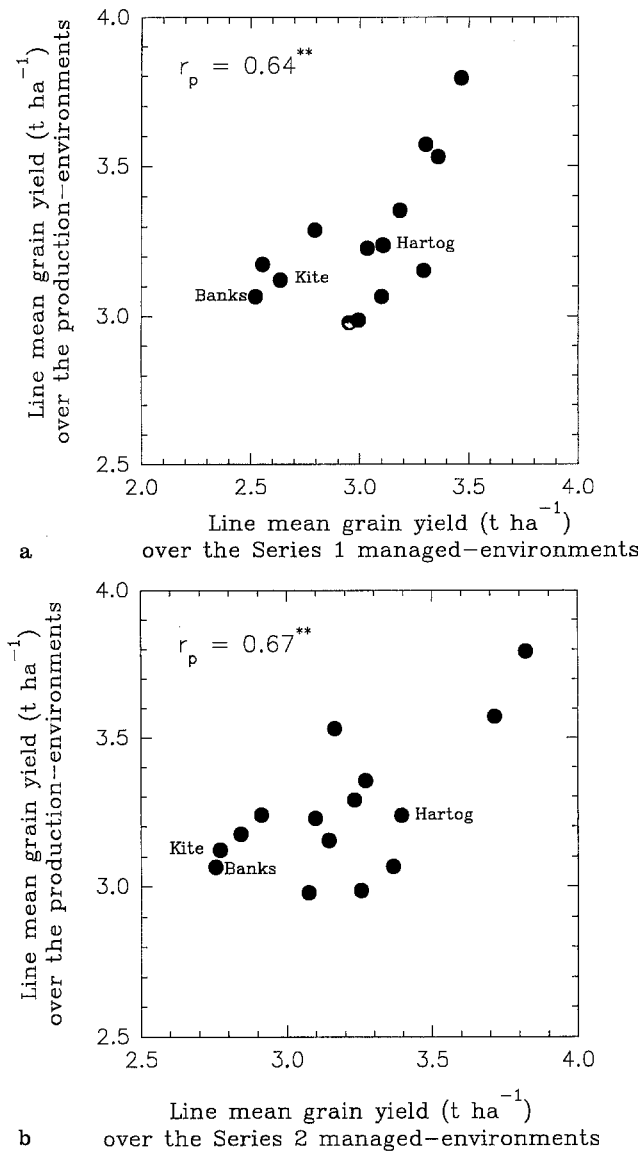
Fig. 2 a, b Association between average line grain yield in the Series-1 (a) and Series-2 (b) managed-environments and in the production-environments

Fig. 3 Distribution of genetic correlation coefficients between average line yield in the production-environments (*PE*) and the 18 managed-environments (*ME*) from Series 1 and 30 random combinations of these for sample sizes of 2–9 managed-environments. *Open circles* give estimates for individual analyses and *closed circles* give the average of the estimates for each sample size

tegies investigated in Series-1 (Table 5). For strategies based on three managed-environments, selection strategies T1-ser1, T3-ser1 and T7-ser1 each gave a high genetic correlation. Comparison of the genetic correlation for these managed-environment selection strategies with those for the 30 random samples of the managed-environments (Fig. 3), indicated these genetic correlations were high relative to those from most of the random combinations of managed-environments.

The genetic correlation coefficients for the early sown managed-environment combinations at Emerald (T3-ser1) and Kingsthorpe (T5-ser1) were higher than those for the later sown combinations of the same treatments (T4-ser1, T6-ser1, respectively) (Table 5). The low genetic correlation for the late sown T6-ser1 combination at Kingsthorpe was attributed to a severe heatwave, which
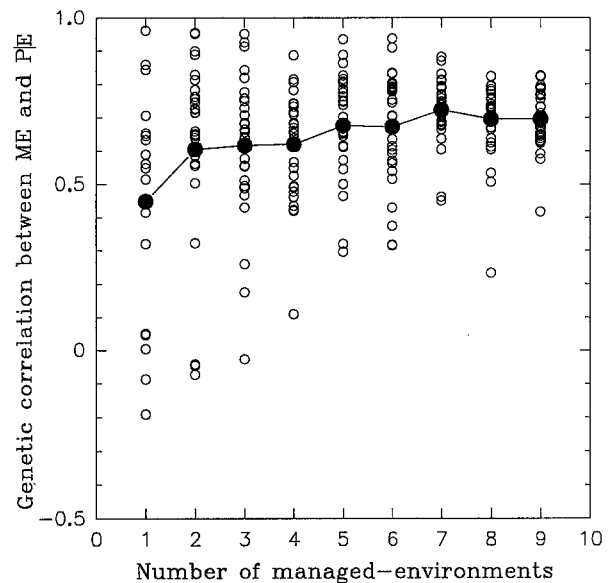
coincided with flowering and grain filling in these environments. This was considered to be an atypical event and did not occur at any of the production-environments sampled. At Gatton the high input environments at three sowing dates in 1988 (T7-ser1) had a higher genetic correlation than the lower input environments at Gatton (T8-ser1).

For selection strategies based on six managed-environments, strategies S1-ser1 (high input at two sowing dates at each location), S2-ser1 (six trials at Emerald) and S5-ser1 (high plus medium input at the early sowing date from three locations) each gave high genetic correlations. These were high in comparison to the distributions for the 30 random combinations for six managed-environments (Fig. 3). Selection based on all six trials at one location gave variable results (Table 5). The genetic correlation for Emerald (S2-ser1) was high, but was intermediate for Kingsthorpe (S3-ser1) and Gatton (S4-ser1). Strategies T1-ser1 and S5-ser1 were re-evaluated in the Series-2 managed-environments.

Series-2 managed-environments

The mean yield of the Series-2 managed-environments ranged from 1.1 to 5.3 t ha^{-1} and there was significant ($P < 0.05$) line and L × E interaction variation. The L × E interaction component of variance was 0.6-times that of the component for lines (Table 3). This ratio was less than that for both the Series-1 managed-environments and the production-environments. The magni-

Table 5 Line mean-heritability within managed-environment selection strategies evaluated in Series-1 and -2 and their phenotypic and genetic correlation with average line performance over the 16 production-environments. (*Significant at $P < 0.05$, **Significant at $P < 0.01$)

Selection strategy[a]	Combination of managed-environments used for selection strategy	Genetic parameter		
		Heritability	Phenotypic correlation	Genetic correlation
	Series-1			
T1-Ser1	High input, sowing data 1 at Emerald, Kingsthorpe and Gatton (3 environments)	0.912	0.792**	0.926
T2-Ser1	High input, sowing date 2 at Emerald, Kingsthorpe and Gatton (3 environments)	0.821	0.439	0.541
T3-Ser1	Low, medium and high input, sowing date 1 at Emerald (3 environments)	0.889	0.786**	0.930
T4-Ser1	Low, medium and high input, sowing date 2 at Emerald (3 environments)	0.754	0.340	0.437
T5-Ser1	Low, medium and high input, sowing date 1 at Kingsthorpe (3 environments)	0.948	0.636*	0.730
T6-Ser1	Low, medium and high input, sowing date 2 at Kingsthorpe (3 environments)	0.807	−0.046	−0.057
T7-Ser1	Gatton irrigated (1988), early, medium and late sowing (3 environments)	0.889	0.693**	0.821
T8-Ser1	Gatton irrigated and dryland (1987) early sowing and dryland (1988) late sowing (3 environments)	0.881	0.463	0.550
S1-Ser1	High input, sowing date 1 and 2 at Enerald, Kingsthorpe and Gatton (6 environments)	0.928	0.714**	0.827
S2-Ser1	Low, medium and high input, sowing date 1 and 2 at Emerald (6 environments)	0.877	0.738**	0.879
S3-Ser1	Low, medium and high input, sowing date 1 and 2 at Kingsthorpe (6 environments)	0.944	0.451	0.518
S4-Ser1	Gatton irrigated and dryland in 1987 and 1988, early medium and late sowing (6 environments)	0.938	0.600*	0.691
S5-Ser1	High and medium input, sowing date 1 at Emerald, Kingsthorpe and Gatton (6 environments)	0.951	0.754**	0.863
S6-Ser1	High and medium input, sowing date 2 at Emerald, Kingsthorpe and Gatton (6 environments)	0.890	0.424	0.502
	Series-2			
T1-Ser2	High input, sowing date 1 at Emerald, Kingsthorpe and gatton (3 environments)	0.725	0.770**	1.010
T3-Ser2	Low, medium and high input, sowing date 1 at Emerald (3 environments)	0.777	0.166	0.210
T5-Ser2	Low, medium and high input, sowing date 1 at Kingsthorpe (4 environments)	0.900	0.675**	0.795
T7-Ser2	Gatton irrigated (1988), medium sowing (2 environments)	0.768	0.670**	0.854
S5-Ser2	High and medium input, sowing date 1 at Emerald, Kingsthorpe and Gatton (6 environments)	0.855	0.668**	0.806

[a] Abbreviations for managed-environment selection strategies used in the text. Prefix letter identifies T for three environments and S for six environments, the number is an identifier used in the table. The suffix identifies the series of managed-environments, Ser1 for Series-1 and Ser2 for Series-2

tude of the L × E interaction variance component was reduced relative to Series-1 and the line component was increased. Therefore, deletion of a number of the Series-1 managed-environments changed the pattern of challenges to which the lines were exposed. The partially replicated trials for the Series-2 managed-environments were less precise than for Series-1, with a higher error-variance component. However, line mean-heritability, over the nine managed-environments in Series-2 was high (0.900) and of a similar magnitude to that for Series-1 (Table 3).

As for the Series-1 managed-environments (Fig. 2a), there was a linear phenotypic association ($P < 0.05$) (Fig. 2b), and a relatively high genetic correlation (Table 3), between average line performance for yield in the Series-2 managed-environments and that in the production-environments. The nature of the association of lines (Fig. 2b) was changed relative to that for Series-1 (Fig. 2a). The three check cultivars were similarly discriminated, with Hartog experssing a higher yield than Banks and Kite (Fig. 2b). Two lines which were higher yielding than the check cultivars were identified in both the Series-2 managed-environments and the production-environments. These were also identified in the

Series-1 managed-environments (Fig. 2a). However, as for Series-1, there were lines which expressed higher grain yield in the Series-2 managed-environments than in the production-environments (Fig. 2b). Further, one line which expressed relatively high grain yield in the production-environments, and which was identified as such in Series-1, only expressed intermediate grain yield in Series-2.

The linear phenotypic association ($P < 0.05$) between line performance for yield in the T1-Ser1 (Fig. 4a) and S5-Ser1 (Fig. 4b) selection strategies (Table 5) and the production-environments, identified in Series-1, were repeated in the selection strategies T1-Ser2 (Fig. 4c) and S5-Ser2 (Fig. 4d) of Series-2. For both of these managed-environment selection strategies, lines higher yielding than the three check cultivars were identified in the managed-environments and the production-environments. The high genetic correlations for the T1-Ser1 and S5-Ser1 selection strategies, observed in Series-1, were repeated in Series-2 for T1-Ser2 and S5-Ser2 (Table 5). Therefore, the line discrimination for these selection regimes was associated with that observed in the production-environments and could be repeated between successive series of managed-environments.
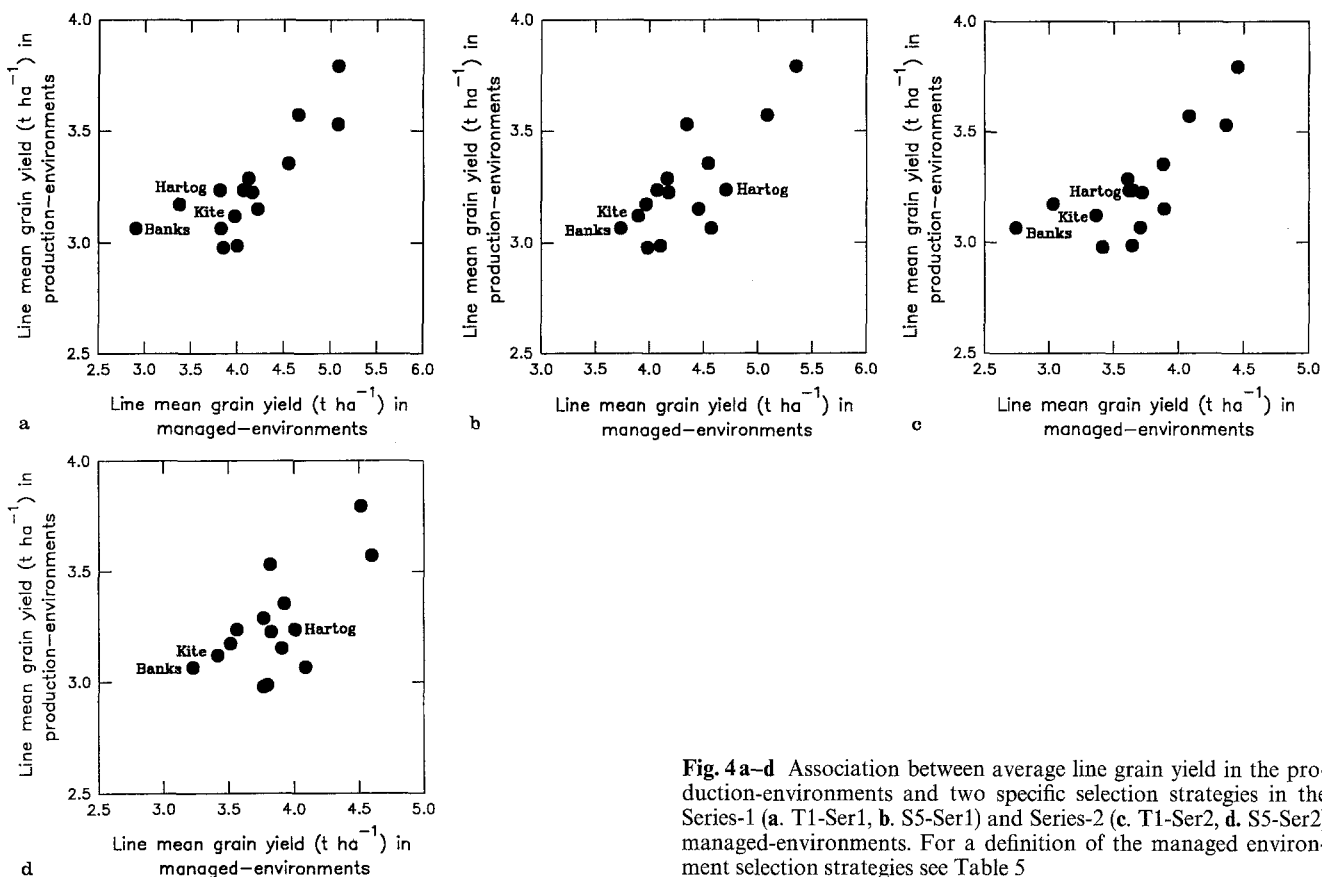
500

a

b

c

d

Fig. 4 a–d Association between average line grain yield in the production-environments and two specific selection strategies in the Series-1 (a. T1-Ser1, b. S5-Ser1) and Series-2 (c. T1-Ser2, d. S5-Ser2) managed-environments. For a definition of the managed environment selection strategies see Table 5

Discussion

When evaluating response to selection, inference is made from selection-environments to a wider population of target production-environments. The use of managed-environments is an attempt to establish a selection regime which is repeatable over years and provides discrimination among lines relevant to the target production-system. Manipulating nitrogen and water availability together with sowing date at three locations generated considerable L × E interaction for grain yield in two series of managed-environments. L × E interaction had a larger influence on line discrimination in the production-environments than in the managed-environments. However, the line discrimination for yield in both series of managed-environments was positively associated with that in the production-environments. Therefore, in two series of managed-environments average discrimination among the lines similar to that over 4 years of production-environments was observed. This suggests there is considerable scope to rationalise the testing of wheat lines in Queensland.

Since the ratio of L × E interaction on line variation was greater in the production-environments, it is clear that all of the target-environment challenges were not encompassed by these managed-environments. The managed-environment challenges were restricted to a

specific set generated by manipulating nitrogen and water availability. Pathogens avoided in the managed-environments may have been influential in some of the production-environments, with root lesion nematode (*Pratylenchus thornei*) occurring in some of the environments on the Darling Downs, yellow spot (*Pyrenophora tritici-repentis*) in one environment, and crown rot (*Fusarium graminearum*) in another. These additional challenges may be expected to reduce the genetic correlation between performance in the managed- and production-environments.

Examination of the relationship between line performance in managed- and production-environments by investigating random combinations of the Series-1 managed-environments, highlighted the level of confidence which can be placed on the estimates of heritability in the managed-environments and the genetic correlation with performance in the production-environments. In Series-1, small random samples of the managed-environments resulted in highly variable estimates of both heritability and the genetic correlation between managed- and production-environments. Increasing the sample size of managed-environments decreased the variability of the line mean-heritability.

The managed-environments can only be considered as such when the management is well defined and well executed. It is clear from this study that judicious selection of the managed-environments from Series-1 could

increase the reliability of the discrimination among lines for grain yield and its relevance to the production-environments. The managed-environment selection strategies based on the three high input environments (T1-Ser1, T1-Ser2) were generally successful and resulted in a high genetic correlation with the line performance observed in the production-environments. This suggests that line performance in favourable environments is an important component of line-yield adaptation in the production system. The basis of this requires further investigation. The strategy based on six managed-environments, which combined the high input environment with a medium input environment at each of the three locations (S5-Ser1, S5-Ser2), also gave a high genetic correlation with performance in the production-environments. This strategy considers both the impact of the high input environment and a degree of stress at each location. The repeated high genetic correlation for both of these selection strategies in the Series-2 managed-environments indicated that the average line discrimination observed in the production-environments could be reliably generated in one series of managed-environments. These selection strategies require further investigation. Such studies should place emphasis on selection among and within segregating populations. A comparison of the response to selection achieved using the managed-environments and the current procedure for the Queensland wheat breeding programme is the next step in evaluating the managed-environment selection strategies.

The managed-environments may be incorporated into the Queensland wheat breeding programme by using them at the preliminary yield-evaluation stage. A potential limitation of this strategy is the chance of excluding important genes conditioning adaptation to an undefined challenge/stress not sampled in the managed-environments. To accommodate this, advanced yield testing must sample a diverse range of production-environments. If a particular stress is important, and the relevant genes are being rejected by the managed-environments, then an appropriate analysis of advanced regional trials would identify this. Such analyses would be facilitated by the use of probe genotypes (Eisemann et al. 1990) selected as a bioassay for specific environmental challenges.

Linking the managed-environments with the target production-environments could be facilitated by the use of crop-physiological models. Where a model can explain the physiological basis of yield variation among genotypes it may be used to define appropriate managed-environments. Selection among genotypes across a managed-environment regime may be considered as an ideotype approach to plant breeding. This approach differs from the traditional concept of ideotype breeding, which attempts to define specific attributes desirable for adaptation in one target environment. The proposed ideotype strategy focuses on defining the range of target environments, followed by screening germplasm in a mixture of these environ-

ments. Where the managed-environments are repeatable, G × E interactions associated with these are explicitly accommodated in the selection regime. Further, this strategy explicitly recognises the transient nature of germplasm within breeding programmes by providing flexibility to screen a wide range of germplasms in the defined selection regime.

To represent all of the relevant environmental challenges from the production-system in a series of managed-environments is unrealistic. The objective is to establish a stratified sample of the relevant challenges which more consistently represents the target environments than do small random smaples. If this can be achieved, then an increase in the realised response to selection would be expected. Where the nature of the target environments within the production-system can be clearly defined there is scope for taking better aim at these targets. The concept of managed-environments is a step in this direction.

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