Journal of Agricultural Science, Cambridge (1999), **133**, 371–377. *Printed in the United Kingdom*

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Combining ability for aluminium tolerance in triticale

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(*Revised MS received 18 August 1999*)

SUMMARY

Root re-growth, following aluminium (Al) stress, has been used as an indicator of Al stress tolerance. Genetic variation in root re-growth characteristics among eight triticale genotypes was investigated by a diallel analysis. Highly significant variation due to both general combining ability (GCA) effects and specific combining ability (SCA) effects indicated that both additive effects and non-additive effects were important in explaining the genetic variation for Al tolerance. The high estimates of heritability and the predictability ratio for root re-growth revealed the preponderance of additive genetic variance in the inheritance of Al tolerance. Differences in patterns of GCA effects and SCA effects among the parents provided strong evidence that the genetic control of variation for Al tolerance as assessed by root re-growth was a complex polygenic system. Three Al-tolerant genotypes, Tahara, Abacus, and 19th ITSN 70–4, were found to be the best general combiners for larger root re-growth, and they could be used in hybridization programmes to improve Al stress tolerance by following a simple pedigree method of selective breeding.

INTRODUCTION

Wider recognition of aluminium (Al) toxicity as the predominant growth-limiting factor in acid soils has prompted extensive studies of Al stress tolerance in crop species (Foy 1988; Scott & Fisher 1989; Carver & Ownby 1995; Jessop 1996). Although attempts have been made to understand the inheritance of some agronomic and morpho-physiological traits for Al tolerance, quantitative genetic studies of the inheritance of root re-growth relevant to Al tolerance in triticale and other cereal crops are limited (Camargo *et al.* 1980; Aniol & Gustafson 1984; Manyowa & Miller 1991; Carver & Ownby 1995). The broad range of, and variability in Al tolerance responses have been taken to indicate that this trait may be controlled by a complex multigenic system (Camargo 1981; Aniol 1991; Taylor 1991). The nature of the genetic mechanisms involved in Al tolerance can be revealed through the application and analysis of suitable genetic designs.

Diallel analysis has been widely used by plant breeders to quantify the genetic variation and relative merits of specific parents from a defined reference population (Mather & Jinks 1982; Basnayake *et al.* 1994; Sughroue & Hallauer 1997). In many circumstances, plant breeders are interested in quantifying the breeding value of a specific selected set of parents. Estimates of breeding values of parents can be obtained from combining ability analysis in a diallel crossing system (Hayman 1954; Gilbert 1958; Wright 1985). This genetic design is also useful since it allows a genetic analysis to be carried out after one generation and serves as a basis for predicting and selecting promising pure lines in breeding programmes.

Table 1. *Eight triticale genotypes used as parents in a diallel crossing system*

Parents	Al tolerance response*	Origin
P1, Tahara	Tolerant	Australia
P2, Empat	Sensitive	Australia
P3, Abacus	Tolerant	Australia
P4, 19th ITSN 70–4	Tolerant	South Africa
P5, 23rd ITYN 27	Sensitive	South Africa
P6, 24th ITYN 29	Sensitive	South Africa
P7, 23rd ITYN 14	Moderately tolerant	South Africa
P8, 20th ITSN 30–1	Moderately tolerant	South Africa

* Based on results tested in nutrient solutions in 1995–96. Entries with an average of root re-growth $\leqslant 0.6$ cm are considered Al-sensitive while entries with a mean root re-growth > 1.0 cm are considered Al-tolerant by the standard testing technique (Aniol 1983).

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https://doi.org/10.1017/S0021859699007194 Published online by Cambridge University Press

A diallel analysis has been made recently in studies of combining ability effects of acid soil tolerance and Al tolerance in sorghum and white clover (Caradus *et al*. 1991; Flores *et al*. 1991); diallel crossing and a similar mating system have also been employed in studies of inheritance of Al or low soil pH tolerance in wheat and barley (Reid 1970; Stølen & Andersen 1978; Camargo *et al*. 1980; Campbell & Lafever 1981) although with very limited genetic analysis of these experimental data. Little information is available for triticale in relation to combining ability variation for tolerance responses to Al stress. The objectives of this study were (i) to estimate combining ability variation and genetic parameters for root re-growth characteristics relevant to Al tolerance in a diallel analysis, and (ii) to assess and identify desirable germplasm for the improvement of Al stress tolerance.

MATERIALS AND METHODS

Parents and F_1 hybrids

Eight triticale genotypes, of Australian and South African origin, were chosen from experiments previously screened in nutrient solutions (Zhang & Jessop 1998). They represented Al-tolerant, moderately Al-tolerant and Al-sensitive types (Table 1). A full diallel crossing programme was made among the eight parents during the spring (September–October) of 1996 in a glasshouse of the University of New England, Armidale. The resulting 64 genotypes (composed of 8 parents and 56 F_1 hybrids) were tested for root re-growth characteristics in April 1997.

Procedures for testing Al tolerance response in nutrient solution

Al tolerance response was determined by the modified Al pulse method (Aniol 1983) and has been described previously by Zhang & Jessop (1998). The test was conducted in nutrient solutions under controlled conditions in a growth cabinet. Procedures included seedling culture in an Al-free nutrient solution for 4 days, treatment of seedlings in an Al solution of 10 mg/l Al (as $AlCl_3{\cdot}6H_2O$) for 24 h, and seedling re-culture in a fresh nutrient solution (without Al) for 2 days. Solutions were maintained at pH 4·5 with daily pH adjustment. Roots were then stained with 1·5 g/l aqueous solution of *Eryochrome cyanine R* for 8 min, and the excess dye after staining was removed by rinsing in running tap water. A three-replicate randomized complete block design was utilized with root length, re-growth root length, and total root length (cm) being measured on ten seedlings of each replicate; the total root length is simply made up of the other two length values.

The Al tolerance response of genotypes in this experiment was quantitatively assessed from the extent of root extension during the 2-day re-culturing period following the imposition of Al stress. Staining defines the position of the root meristem at the time of Al stress applied. Root length distal to the stained section was measured to indicate re-growth root length. Typical Al-tolerant genotypes have a narrow stained section and more extensive root re-growth whilst Al-sensitive types have more extensively stained root tips and limited root re-growth.

Genetic analysis

A combining ability analysis was performed on the 64 genotypes following method 1 of Griffing (1956) assuming a fixed effects model (Model I). General combining ability (GCA) effects and specific combining ability (SCA) effects, together with reciprocal effects, were estimated for re-growth root length and two other root characters on a plot mean basis. To determine the relative contribution of genetic components, a random effects model (i.e. Griffing's Model II) was used to obtain estimates of GCA variance (σ^2_{gca}), SCA variance (σ^2_{sca}), and reciprocal variance (σ^2_r) for each character. Variances for these estimated components were calculated as outlined by Ma (1982). Additive variance (V_a) and dominance variance (V_d) were estimated as $V_a = 2\sigma^2_{gca}$ and $V_d = \sigma^2_{sca}$, which give rise to estimates of genetic variance (V_g) and phenotypic variance (V_p). Heritabilities in both broad sense (h^2_b) and narrow sense (h^2_n) were calculated from those estimated components of variance as: $h^2_b = V_g/V_p$ and $h^2_n = V_a/V_p$, respectively. The relative sizes of variance due to GCA and SCA were compared following Baker's predictability ratio (PR): $2\sigma^2_{gca}/(2\sigma^2_{gca} + \sigma^2_{sca})$ (Baker 1978). The closer this ratio is to unity, the greater is the predictability of F_1 progeny performance based on the general combining ability effects alone. Estimation of the degree of average dominance $\sqrt{(H/D)} = \sqrt{(\sigma^2_{sca}/\sigma^2_{gca})}$ was made following Ma (1982).

RESULTS

Mean performance of parents and their F_1 progenies

Re-growth root length ranged from 0·33 cm (23rd ITYN 27) to 1·93 cm (Abacus and 19th ITSN 70–4) for parents and from 0·37 cm (Empat/23rd ITYN 27 and 23rd ITYN 27/Empat) to 2·27 cm (Abacus/Tahara) for F_1 progenies (Table 2). Overall mean value of re-growth root length in F_1 progenies (x_{F_1}) was 1·22 cm while the mean value of the eight parents (x_p) was 1·08 cm, suggesting that dominance was predominantly in the direction of longer re-growth root length in the F_1 hybrids. Mean re-growth root length over F_1 progenies generated from each female parent was also found to be linearly associated with that measured directly on the female parent ($r = 0{\cdot}97$; $P < 0{\cdot}01$); this was also true for the male parents ($r = 0{\cdot}99$; $P < 0{\cdot}01$).

https://doi.org/10.1017/S0021859699007194 Published online by Cambridge University Press

Table 2. *Mean value of re-growth root length* (*cm*) *over three replications in 64 genotypes and mean value of eight parents*

	Male (P)*								
Female (P)*	1	2	3	4	5	6	7	8	Mean
1	1·83	1·33	1·87	1·93	1·33	1·43	1·57	1·50	1·60
2	1·37	0·57	1·30	1·37	0·37	0·60	0·70	0·67	0·87
3	2·27	1·73	1·93	2·10	1·70	1·93	1·63	1·60	1·87
4	1·87	1·30	1·77	1·93	1·50	1·63	1·43	1·47	1·61
5	1·13	0·37	1·23	1·27	0·33	0·67	0·57	0·53	0·76
6	1·33	0·67	1·83	1·50	0·73	0·60	0·87	0·80	1·04
7	1·40	0·83	1·27	1·37	0·77	0·77	0·83	0·70	0·99
8	1·10	0·63	1·40	1·23	0·53	0·63	0·73	0·63	0·86
Mean	1·54	0·93	1·58	1·59	0·91	1·03	1·04	0·99	1·20

* The numbers correspond with the parents given in Table 1.

Table 3. *ANOVA for three characters* (*with only MS values shown*)

Source	*df*	Re-growth root length	Root length	Total root length
Genotypes	63	0·774**	0·469**	1·769**
Replications	2	0·106**	0·838**	1·212**
Error	126	0·030	0·059	0·102

** Significant at 1% level of probability.

Table 4. *Analysis of components of combining ability variance. Mean square* (*MS*) *values were shown together with expected mean square* (*EMS*) *following Model II of Griffing* (*1956*)

Source	*df*	Re-growth root length	Root length	Total root length	EMS‡
GCA	7	2·113**	0·822**	31·150**	$\sigma_e^2+\frac{2(p-1)}{p}\sigma_{sca}^2+2p\sigma_{gca}^2$
SCA	28	0·028**	0·078**	2·413**	$\sigma_e^2+\frac{2(p^2-p+1)}{p^2}\sigma_{sca}^2$
Reciprocal	28	0·024**	0·069**	3·561**	$\sigma_e^2+2\sigma_r^2$
Error†	126	0·010	0·020	0·034	σ_e^2

† *MS* values due to error were calculated as the error *MS* in Table 3 divided by number of replications ($r = 3$); ‡ $P = 8$; ** Significant at 1% level of probability.

The three Al-tolerant genotypes (Tahara, Abacus, and 19th ITSN 70–4) produced progenies with larger root re-growth and root growth (including root length and total root length; data not shown) when they were used as either female or male parents; while Al-sensitive genotypes (Empat, 23rd ITYN 27) produced progenies with a much smaller root re-growth. The only exception was the Al-sensitive genotype 24th ITYN 29, which showed a similar response to the two moderately Al-tolerant genotypes (23rd ITYN 14, 20th ITSN 30–1) in their corresponding female and male groups. Combinations made from any two Al-sensitive parents generally had smaller root re-growth.

Combining ability variance

There was highly significant variation for root re-growth and root growth characters among the 64 genotypes (Table 3). Based on the data, highly significant variation was identified for GCA, SCA, and reciprocal effects (Table 4). This clearly indicated the importance of both additive and non-additive

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Table 5. *GCA effects of eight parents for three characters*

Parents	Re-growth root length	Root length	Total root length
P1, Tahara	0·37	0·03	0·39
P2, Empat	−0·30	−0·43	−0·73
P3, Abacus	0·52	0·33	0·85
P4, 19th ITSN 70−4	0·40	0·02	0·42
P5, 23rd ITYN 27	−0·36	−0·12	−0·49
P6, 24th ITYN 29	−0·16	0·03	−0·12
P7, 23rd ITYN 14	−0·18	0·22	0·04
P8, 20th ITSN 30−1	−0·28	−0·08	−0·34
SE_{gca}	0·013	0·018	0·023

genetic variance in the inheritance of Al tolerance. The genetic variance due to the non-additive component may involve both dominance and epistasis.

GCA effects and SCA effects

Highly significant differences in GCA effects were detected among the eight parents (Table 5). Al-tolerant Tahara, Abacus, and 19th ITSN 70–4 showed positive GCA effects for re-growth root length and total root length while Abacus and 23rd ITYN 14 showed positive GCA effects for root length. The moderately Al-tolerant parents (23rd ITYN 14, 20th ITSN 30–1) and the Al-sensitive parents (Empat, 23rd ITYN 27, and 24th ITYN 29) exhibited negative GCA effects for re-growth root length. Thus, the three Al-tolerant parents were also the best general combiners for Al tolerance.

SCA effects for re-growth root length were estimated for each hybrid combination (Table 6). There appeared some contrasting patterns of SCA effects for the eight parents. Combinations with high positive SCA effects ($\geqslant 0{\cdot}1$ cm) included Tahara/23rd ITYN 14, Empat/Abacus, Abacus/23rd ITYN 27, Abacus/24th ITYN 29, 19th ITSN 70–4/23rd ITYN 27 and 19th ITSN 70–4/24th ITYN 29, and their corresponding reciprocals. All these crosses involved one good and one poor general combiner for Al tolerance. Combinations which showed negative SCA effects ($\leqslant -0{\cdot}1$ cm) were Empat/23rd ITYN 27, Empat/24th ITYN 29 and Abacus/19th ITSN 70–4, and their corresponding reciprocals. These crosses involved either two poor general combiners or two good general combiners. The various patterns of SCA effects indicated the presence of genic interactions, either allelic or non-allelic.

Reciprocal effects

Reciprocal effects on root re-growth were also detected (Table 7). Abacus, when used as a female parent, exhibited uniformly positive effects in all its combinations (compared with the effects when used as a male parent). Both Tahara and 19th ITSN 70–4, when used as females, showed positive effects in their combinations with 23rd ITYN 27, 24th ITYN 29, 23rd ITYN 14, or 20th ITSN 30–1. Moderately Al-tolerant genotypes (23rd ITYN 14, 20th ITSN 30–1) and Al-sensitive genotypes (Empat, 23rd ITYN 27, and 24th ITYN 29) however showed various patterns of reciprocal effects. These results suggest that although small, cytoplasmic effects, or maternal or paternal effects, may be involved in the inheritance of Al tolerance.

Estimates of genetic parameters

The estimates of combining ability variance and genetic parameters given in Table 8 indicated that genotypic variability accounted for most of the total variability for re-growth root length and the other two characters. The greater magnitude of GCA variances (σ^2_{gca}) in comparison with SCA variances (σ^2_{sca}) suggested that additive variability was of greater importance. Variance due to reciprocal effects (σ^2_r) was found (with some exceptions) to be of the same magnitude as that due to the SCA effects. High

Table 6. *SCA effects of eight parents in each combination for re-growth root length*

	Male (P)*							
Female (P)*	1	2	3	4	5	6	7	8
1	−0·11	0·08	−0·02	−0·07	0·03	−0·03	0·10	0·01
2		−0·03	0·10	0·04	−0·16	−0·10	0·05	0·03
3			−0·31	−0·18	0·11	0·32	−0·09	0·06
4				−0·07	0·15	0·13	−0·02	0·03
5					−0·14	0·03	0·02	−0·03
6						−0·27	−0·03	−0·05
7							0	−0·03
8								−0·02

* The numbers correspond with the parents given in Table 1.

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Table 7. *Reciprocal effects (R) of eight parents in each combination for re-growth root length*

	Male (P)							
Female (P)*	1	2	3	4	5	6	7	8
1	–	−0·02	−0·20	0·03	0·10	0·05	0·09	0·20
2		–	−0·22	0·04	0	−0·04	−0·07	0·02
3			–	0·17	0·24	0·05	0·18	0·10
4				–	0·12	0·07	0·03	0·12
5					–	−0·03	−0·10	0
6						–	0·05	0·09
7							–	−0·02
8								–

* The numbers correspond with the parents given in Table 1. $R_{ij} = -R_{ji}$ ($i, j = 1, 2, \ldots 8$; $i \neq j$).

Table 8. *Estimates of combining ability variance and genetic parameters for three characters*

Genetic parameters*	Re-growth root length	Root length	Total root length
$\sigma^2_{gca} \pm V(\sigma^2_{gca})$	0·130 ± 0·005	0·047 ± 0·001	1·799 ± 1·084
$\sigma^2_{sca} \pm V(\sigma^2_{sca})$	0·010 ± 0	0·033 ± 0	1·336 ± 0·131
$\sigma^2_r \pm V(\sigma^2_r)$	0·007 ± 0	0·025 ± 0	1·764 ± 0·226
$\sigma^2_e \pm V(\sigma^2_e)$	0·030 ± 0	0·059 ± 0	0·102 ± 0·001
$V_a = 2\sigma^2_{gca}$	0·260	0·094	3·598
$V_d = \sigma^2_{sca}$	0·010	0·033	1·336
$V_g = V_a + V_d$	0·270	0·127	4·934
$V_e = \sigma^2_e$	0·030	0·059	0·102
$V_p = V_g + V_e$	0·300	0·186	5·036
h^2_b (%)	90·0	68·3	98·0
h^2_n (%)	86·7	50·5	71·4
PR	0·96	0·74	0·73
$\sqrt{(H/D)} = \sqrt{(\sigma^2_{sca}/\sigma^2_{gca})}$	0·3	0·7	0·9

* V_a, V_d and V_e are the additive, dominance and environmental components of variance, respectively.

heritability estimates in both broad sense and narrow sense (90·0 and 86·7% respectively) were recorded for re-growth root length, implicating again the greater importance of additive variability in the inheritance of Al stress tolerance. This was also indicated by the high value of the predictability ratio ($PR = 0{\cdot}96$) for re-growth root length.

Estimates of the degree of average dominance [$\sqrt{(H/D)}$] showed the existence of partial dominance for re-growth root length and the preponderance of dominance for the other two characters. Al stress tolerance response as assessed by re-growth root length was therefore mainly controlled by additive gene effects; this was indicative of a polygenic system controlling Al tolerance in the eight genotypes used.

DISCUSSION

The present experiment considered the combining ability of eight triticale parents with contrasting Al tolerance responses as assessed by root re-growth. The highly significant variation due to GCA and SCA effects suggests that both additive effects and non-additive effects were important in explaining the genetic variation for Al tolerance among the F_1 progenies. Similar results have been reported in wheat and sorghum (Campbell & Lafever 1981; Flores *et al.* 1991; Bona *et al.* 1994); additive gene effects for Al tolerance in several triticale F_2 crosses have also been implicated by Pinto Carnide *et al.* (1991). Multigenic control of Al tolerance in triticale has been indicated by previous genomic analyses and gene location studies (Slootmaker 1974; Mugwira *et al.* 1976; Sapra *et al.* 1979). In addition, this study indicated the presence of small cytoplasmic effects (or maternal or paternal effects) on the expression of Al tolerance in F_1 hybrids. Results concerning cytoplasmic inheritance of Al tolerance are limited but Rhue *et al.* (1978) showed no cytoplasmic effects on Al tolerance in maize. This apparent discrepancy may reflect either species or bioassay technique differences.

The relative Al stress tolerance (Table 2) of the eight parental genotypes was in good agreement with previous studies (Zhang & Jessop 1998). The three Al-

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tolerant genotypes, Tahara, Abacus and 19th ITSN 70–4, were found to be the best general combiners for Al tolerance and therefore could be used in hybridization programmes to improve Al stress tolerance. The high estimates of heritability and predictability ratio for re-growth root length (Table 8) in addition to confirming the greater relative importance of general combining ability imply that useful improvement in Al tolerance would be attained following selection in for example a simple pedigree breeding method.

The genetic information generated from this experiment will assist decisions on parental selection for a more extensive study of inheritance of Al tolerance response. Further work might be directed to testing the hypothesis of polygenic inheritance of Al stress tolerance in triticale and to determining whether the various sources of Al tolerance are based on similar or different genes in those genotypes. A better understanding of the genetic mechanisms by which plants tolerate toxic Al will help to develop plant genotypes having greater stress tolerance and hence promote plant production in acid stressed environments.

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