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Combining ability and heterosis for diastatic activity in grain sorghum

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ABSTRACT

Eighty-five sorghum (*Sorghum bicolor* (L.) Moench) entries including 13 restorer-lines (lines), 5 maintainer-lines (testers), 65 F1 hybrids, and two controls, were grown at Muzarabani, Zimbabwe during the rainy seasons of 1986/87 and 1987/88 to study the combining ability and heterosis for diastatic activity. Grain samples were evaluated for diastatic activity, expressed in Sorghum Diastatic Units (SDU) per gram of malt, in 1989. Differences between sorghum lines, testers, hybrids, and total entries were significant for diastatic activity in both seasons. There were large differences in mean diastatic activity values and ranges for entries in both seasons. The mean SDU g⁻¹ malt for hybrids varied from 20.5 to 67.2 for the 1986/87 season and 13.3 to 48.9 for the 1987/88 season. Variation in diastatic activity was primarily due to non-additive gene action. The highest positive general combining ability effects were observed for the line 4HA85S, and tester 120A. Significant positive specific combining ability effects were observed for hybrid 120A x D 38073-2. This was the only cross which had positive high parent heterosis in both seasons, but it was only significant in the 1987/88 season. Most of the crosses had negative high parent heterosis. To improve diastatic activity, recurrent selection procedures for specific combining ability should be used to develop elite parents for hybrids.

Key Words: *Sorghum bicolor*, diastatic unit, heterosis, non-additive gene action

RESUME

Quatre-vingt cinq entrees du sorgho (*Sorghum bicolor* (L.) Moench) dont 13 lignees) restauratrices (lignees), 5 lignees de maintenance (testeurs), 65 hybrides F1, et deux temoins ont ete cultives a Muzarabani, au Zimbabwe pendant les saisons des pluies de 1986/87 et de 1987/88 pour evaluer l' aptitude a la combinaison et l' heterosis pour l' activite diastasique. Les echantillons de grains ont ete evalues pour l' activite diastasique, exprimee en Unite Diastasique du Sorgho (UDS) par gramme de malt, en 1989. Des differences entre les lignees du sorgho, les testeurs, les hybrides, et les entrees totales etaient significatives pour l' activite diastasique pendant les deux saisons. Il y avait de grandes differences dans les valeurs moyennes de l' activite diastasique et les classes pour les entrees en deux saisons. La moyenne de l' UDS g⁻¹ malt pour les hybrides variait de 20,5 a 67,2 pour la saison 1986/87 et de 13,3 a 48,9 pour la saison 1987/88. La variation de l' activite diastasique etait principalement due a l' action non-additive du gene. Les

effets les plus positifs de l' aptitude a la combinaison etaient observes pour la lignee 4HA85S, et le testeur 120 A. Les effets positifs significatifs de l' aptitude specifique a la combinaison etaient observes pour l' hybride 120 A x D 38073-2. Ceci etait le seul croisement qui avait l' heterosis positif des parents superieurs pendant les deux saisons, mais cece etait significatif seulement pendant la saison 1987/88. La plupart des croisements avaient l' heterosis negatif des parents superieurs. Pour ameliorer l' activite diastatique , les procedures de selection recurrente pour l' aptitude specifique a la combinaison doivent etre utilisees pour developper les parents elites pour les hybrides.

Mots Cles: Sorgho, unite diastatique, heterosis, action non-additive du gene

INTRODUCTION

Sorghum (*Sorghum bicolor* (L.) Moench) is a major cereal in the semi-arid regions of the world where it is an important food and feed crop. It is also used as raw material for industry and, if malted, can be processed into malted foods, beverages, and beer (Palmer, 1992). Sorghum yields have substantially increased in areas where hybrids have been adopted; however, breeding for good malting quality has not been emphasised. Novellie (1982) indicated that good traditional malting (but poor-yielding) sorghums have quickly been replaced by high-yielding varieties that have poor malting performance.

Jayatissa *et al.* (1980) and Kulkarni *et al.* (1987) have screened sorghum hybrids and cultivars suitable for malting so that they could replace barley malt, which has become expensive for India and Sri Lanka to import. Malting sorghum is being used in Nigeria to produce lager beer (Okafor and Aniche, 1980).

In southern Africa, opaque beer made from cereals is commonly consumed. The raw materials and processes used in brewing Kaffir beer, a traditional beer in South Africa, were described by Schwartz (1956). Generally, the preparation of sorghum beer requires degradation of starchy endosperm into sugars during malting; the sugars produced then are fermented to produce alcohol. The malting process that generates the fermentable mono- and disaccharides is dependent upon the alpha and beta amylases and the maltose splitting enzyme, maltase, that develop in sorghum during germination (Hulse *et al.*, 1980). The beta-amylase development in some sorghum cultivars is very limited compared to that of barley malt. However, some sorghum cultivars can develop significant levels of this important maltose-producing enzyme (Aniche and Palmer, 1990). The enzyme activity in the malt is determined as the diastatic power which is expressed as Sorghum Diastatic Units per gram of malt (SDU g⁻¹ malt).

Knowledge of the genetic variability, type of gene action, and estimates of heterosis for diastatic activity is essential if sorghum hybrids are to be improved for malt. The purpose of this study was to investigate the combining ability and heterosis for diastatic activity in sorghum.

MATERIALS AND METHODS

Three hundred sorghum inbreds/pure line varieties including maintainer-lines (B-lines) and restorer- lines (R-lines) from the Zimbabwe National Programme, and the Southern African Development Community/International Crops Research Institute for the Semi-Arid Tropics (SADC/ICRISAT) Sorghum and Millet Improvement Programme (SMIP) were selected for analysis of their diastatic activity. The samples were sent to Purdue University, Indiana, where they were analysed for diastatic activity (SDU g⁻¹ malt) using the procedure described by Daiber (1971) during December 1985. This analysis was used to select parents for the development of F1 hybrids. Based on SDU values, five cytoplasmic-genetic male-sterile lines (A-lines) and 13 restorer-lines were randomly selected from three groups, i.e., lines with high, intermediate, and

low SDU values. SDU values ranged from 21 to 97 in the selected parents. The SDU values of the corresponding B-lines were used in selecting A-lines.

At Muzarabani, Zimbabwe during the 1986 winter season, 65 F1 hybrids of five A-lines (testers) and 13 restorer-lines (lines) were generated. A trial of 85 sorghum entries including 5 B-lines, 13 restorer-lines, 65 F1 hybrids and two controls (SV 2 a white-grained open-pollinated cultivar and DC 75, a brown-grained hybrid), was sown at Muzarabani during the 1986/87 and 1987/88 rainy seasons. The experiments were sown on 12 December 1986 and 10 December 1987 in a randomised complete block design with three replications. Each plot consisted of two rows, 75 cm apart and 5 m long. Experiments were hand sown and thinned to a distance of 12 cm between plants 4 weeks after sowing. A fertilizer application of 300 kg ha⁻¹ of compound "D" (8 N:14 P2O5: 7 K2O) was applied at sowing, while 100 kg ha⁻¹ of ammonium nitrate (34.5% N) was side-dressed 6 weeks after sowing.

Muzarabani is located in the Zambezi River Valley in Zimbabwe. The soils are mainly of colluvial origin with some sandstone influence. They vary from medium to heavy textured soils of variable depth and are well-drained. Muzarabani has erratic rainfall averaging 940 mm per annum. Mean temperature during the growing season ranges from a high of 32 C in December to a low of 20 C in March.

At harvest, 20 randomly selected sorghum panicles with similar grain and good seed set were harvested from each plot of every replication. The harvested heads were air-dried and stored at room temperature for a month to bring their grain moisture to equilibrium. The sorghum samples from both the 1986/87 and 1987/88 seasons were analysed for diastatic activity at Matopos, Zimbabwe using the procedure described by Daiber (1971).

The analysis of variance was carried out using PROC ANOVA (SAS Institute, 1985). The chi-square test for homogeneity of error variance for diastatic activity was performed following Bartlett's test (Steel and Torrie, 1980). The variance due to entries was further partitioned into parents, line parents, tester parents, line parents vs. tester parents, hybrids, hybrids vs. parents, controls, controls vs. rest (Table 1). The mean squares for each source of variation were tested against error mean squares.

The combining ability analysis was carried out using the array totals over replications following the procedure of Kempthorne (1957) related to method of Comstock and Robinson (1952). The mean squares due to lines x testers were tested against error mean squares, and the mean squares due to lines and to testers were tested against the mean squares due to lines x testers.

The heterosis over higher parent (high parent heterosis) and mid-parent were expressed as percentages. The standard error (difference) for high parent heterosis was calculated as $(2 \text{ EMS}/r)^{1/2}$, and for heterosis as $(3 \text{ EMS}/2 r)^{1/2}$, where EMS = Error Mean Squares, and r = number of replications. If the differences between the F1 value and the higher parent and the F1 value and the mid-parent were greater than the LSD 5% value, the high parent heterosis and heterosis estimates were considered significant.

RESULTS

The pooled analysis was not carried out because the error mean squares for the two seasons were heterogeneous. Differences were significant between entries, line-parents, tester-parents, and hybrids during both the seasons (Table 1). With the exception of lines vs. testers and controls during the 1986/87 season, all other sources of variation were also significant during both seasons (Table 1).

TABLE 1. Analysis of variance for diastatic activity (SDU g⁻¹ malt) at Muzarabani, Zimbabwe for the 1986/87 and 1987/88 rainy seasons

Source	df	Mean squares	
		1986/87	1987/88
Replications	2	584.59**	4.52
Entries	84	5521.30**	236.27**
Parents	17	1005.09**	314.27**
Line parent (L)	12	1029.49**	268.89**
Tester parent (T)	4	1183.31**	420.22**
L vs. T	1	0.37	434.96**
Hybrids	64	306.03**	221.33**
Lines (GCA)	12	494.91*	162.63
Testers (GCA)	4	528.78	239.34
Lines x Testers (SCA)	48	240.24**	234.48**
Parents vs. Hybrids	1	6394.41**	236.34**
Controls	1	48.17	84.37**
Controls vs. rest	1	674.03**	77.90**
Error	168	56.50	8.56
_2GCA	10.06	0	
_2SCA	61.25	75.31	
GCA/SCA	0.16	0	

*,** Significant at 5% and 1% levels of probability, respectively

The sorghum diastatic activity values were higher for the 1986/87 season than for the 1987/88 season for most of the entries. The mean SDU of lines, testers, and controls for 1986/87 and 1987/88 seasons are given in Table 2 and for hybrids in Table 3. The SDU g⁻¹ malt among lines varied from 26.0 to 90.0 in 1986/87 and from 18.5 to 52.7 in 1987/88 season. The diastatic activity for testers ranged from 22.5 to 73.2 SDU g⁻¹ malt for 1986/87 and 14.0 to 42.5 SDU g⁻¹ malt for the 1987/88 season. Among lines, Red Swazi which is the pure line, showed the highest SDU g⁻¹ malt values in both seasons, and was significantly superior to the best control DC 75, while IS 9626 had the lowest SDU in both seasons. The highest SDU values among the testers were shown by ATx 3121 during 1986/87, while 120A gave the highest SDU value for the 1987/88 season. The mean SDU g⁻¹ malt for hybrids varied from 20.5 to 67.2 for the 1986/87 and 13.3 to 48.9 for the 1987/88 season (Table 3). None of the hybrids was superior in diastatic activity to the best parent, Red Swazi.

TABLE 2. Estimates of general combining ability effects and means of lines, testers, and controls for diastatic activity (SDU g⁻¹ malt) at Muzarabani, Zimbabwe, 1986/87 and 1987/88 rainy seasons

Parent	Pedigree	GCA effects		Means	
		1986/87	1987/88	1986/87	1987/88
Lines					
L1	MR 726	7.47**	-2.35*	53.50	25.53

L2	6HA85S	4.67	-0.17	72.00	39.73
L3	Red Swazi	2.67	1.51	90.00	52.67
L4	1HA85S	-3.70	0.52	44.00	27.33
L5	IS 2390	0.93	-1.94	39.83	42.23
L6	14/90	4.37	2.17*	49.53	26.77
L7	TGR 61	-5.55*	-0.57	51.50	34.17
L8	IS 2412	-8.60**	2.18*	40.17	20.50
L9	IS 9626	0.20	2.37*	26.00	18.50
L10	MR 852	-9.83**	-4.31**	36.33	26.03
L11	4HA85S	8.67**	3.18**	74.67	35.60
L12	M 39335	-0.97	-7.21**	74.50	27.30
L13	D 38073-2	-0.27	4.70**	48.00	34.30
	LSD (5%)	5.38	2.09	-	-
	LSD (1%)	7.07	2.75	-	-
Testers					
T1	120A	5.53**	2.55**	59.00	42.47
T2	ATx 3048	-3.07	0.65	48.67	26.03
T3	ATx 3042	-2.68	-2.66**	22.50	29.43
T4	ATx 3121	1.99	-2.53**	73.17	13.97
T5	68K328A	-1.75	2.02**	66.83	14.37
	LSD (5%)	3.34	1.30	-	-
	LSD (1%)	4.39	1.71	-	-
Controls					
	DC 75	57.83	33.50		
	SV 1	52.17	26.00		
Mean (85 entries)				44.52	28.02
LSD (5%)				12.03	4.68
CV (%)				16.88	10.44

*,** Significant at 5% and 1% levels of probability, respectively

The variance due to general combining ability (GCA) of the lines was only significant in 1986/87, and the variances due to specific combining ability (SCA) were highly significant in both seasons (Table 1). These results suggest that non-additive type of gene action is primarily involved in determining diastatic activity. The ratio between GCA and SCA was less than one, indicating that non-additive gene action was more important than additive gene action in governing this trait (Table 1).

Estimates for GCA effects for diastatic activity are presented in Table 2. The line 4HA85S had a significant positive GCA effect, whereas the line MR 852 had a significant negative GCA effect in both seasons. Only one tester 120A, had significant positive GCA effect in both seasons. GCA effects of some of the lines and testers during two seasons were not in agreement. For example, the line MR 726 had significant positive GCA effect in the 1986/87 season and a significant negative GCA effect in the 1987/88 season. Similarly, line IS 2412 had a significant negative GCA effect in the 1986/87 season and a significant positive GCA effect in the 1987/88 season. Among testers, significant negative GCA effects were found for ATx 3042 and ATx 3121, and a positive GCA effect for 68K328A was observed during the 1987/88 season. GCA effects for these testers were not significant during the 1986/87 season.

The SCA effects for diastatic activity are presented in Table 3. The hybrid 120A x D 38073-2 had a significant positive SCA effect, whereas the hybrid ATx 3042 x D 38073-2 had a significant negative SCA effect in both seasons. Five hybrids had positive SCA effects in both seasons, however, these effects were only significant in one season. In six hybrids, SCA effects were significant and positive in one season, and significant and negative in the other season.

TABLE 3. Mean performance of crosses, estimates of SCA effects, and heterosis over mid-parent (MP) and higher parent (HP) for diastatic activity (SDU g⁻¹ malt) at Muzarabani, Zimbabwe, 1986/87 and 1987/88 rainy seasons

Cross no.^1	Mean		SCA effects		Heterosis (%)			
	1986/87	1987/88	1986/87	1987/88	1986/87		1987/88	
					MP	HP	MP	HP
T1/L1	61.00	20.87	6.41	-6.79**	8.44	3.39	-38.62**	
	50.86**							
T2/L1	41.50	15.93	-4.49	-9.81**	-18.76	-22.43	-38.21**	-
	38.80**							
T3/L1	49.50	30.70	3.11	8.25**	30.26*	-7.48	11.72	
	4.32							
T4/L1	37.83	33.53	-13.22*	10.97**	-40.27**	-48.30**	69.77**	
	31.34**							
T5/L1	55.50	24.50	8.19	-2.62	-7.75	-16.95	22.81*	-
	4.03							
T1/L2	36.00	31.70	-15.79**	1.87	-45.04**	-50.00**	-22.87**	-
	25.36**							
T2/L2	42.50	22.30	-0.69	-5.63*	-29.56**	-40.97**	-32.17**	-
	43.87**							
T3/L2	47.00	34.97	3.41	10.34**	-0.53	-34.72**	1.13	-
	11.98*							
T4/L2	62.50	19.27	14.24*	-5.48*	-13.89	-14.58	-28.23**	-
	51.50**							
T5/L2	43.33	28.20	-1.18	-1.10	-37.58**	-39.82**	4.25	-
	29.02**							
T1/L3	36.00	45.97	-13.79*	14.45**	-51.68**	-60.00**	-3.36	-
	12.72**							
T2/L3	49.00	41.40	7.81	11.79**	-29.33**	-45.56**	5.21	-
	21.40**							
T3/L3	34.83	13.30	-6.75	-13.01**	-38.08**	-61.30**	-67.60**	-
	74.75**							
T4/L3	49.00	28.60	2.74	2.17	-39.94**	-45.56**	-14.17*	-
	45.70**							
T5/L3	52.50	15.60	9.99	-15.39**	-33.05**	-41.67**	-53.46**	-
	70.38**							
T1/L4	54.00	31.30	10.58	0.77	4.85	-8.47	-10.32	-
	26.30**							

^1 Pedigrees for testers and lines involved in crosses are given in Table 2

*, ** Significant at 5% and 1% levels of probability, respectively

Heterosis for diastatic activity ranged from -63.7 to 54.0% and high parent heterosis from -69.3 to 39.1% during the 1986/87 season, whereas during the 1987/88 season heterosis ranged from -67.6 to 100.8%, and high parent heterosis from -74.8 to 78.4% (Table 3). The hybrid 120A x D 38073- 2 had positive significant heterosis in both seasons and was the only hybrid with positive high parent heterosis, but it was only significant in the 1987/88 season. The other hybrids with positive heterosis in both seasons were AT x 3042 x MR 726, AT x 3042 x 14/99, AT x 3042 x IS 2412, AT x 3048 x IS 9626, and AT x 3042 x IS 9626 (Table 3). The majority of the hybrids showed significant negative heterosis during 1986/87 (36 vs. 4) and 1987/88 (29 vs. 18) seasons.

DISCUSSION

The differences observed in mean performance for diastatic activity for different entries between the two seasons were high. During these two seasons, it was observed that rainfall patterns were different (337 mm for the 1986/87, and 898 mm for the 1987/88 seasons); and the number of rainy days were different (15 days during 1986/87, and 36 days during 1987/88). Correspondingly, grain size was smaller during the drier year, but SDU was higher. This is supported by significant negative genetic correlations for SDU with 1000-grain weight and test weight (Mushonga *et al.*, 1993).

In order to improve SDU in sorghum, good moisture management is essential. The phenomenon of small grain size association with high SDU values as a consequence of low rainfall is an interesting observation that deserves further investigation.

Variation among genotypes is an important tool by which the breeder can fully exploit the diversity in a population to the maximum advantage in parental selection for hybrids. In such a programme, knowledge of the combining ability of parents becomes necessary. The information on the inheritance, and the combining ability of parents, for diastatic activity is not available in sorghum.

This study has indicated the importance of non-additive type of gene action for diastatic activity. Significant positive and negative GCA effects were generally found for both line and tester parents for SDU (Table 2). The magnitude of the variation in GCA effects among the parents suggest that it may be possible to select those with superior SDU values.

Both GCA and SCA effects are important in the selection of hybrid combinations. On this basis, the hybrid 120A x D 38073-3 is of interest to plant breeders. This hybrid had the highest per se performance, high SCA effects, and was the only hybrid with positive high parent heterosis for SDU in both seasons. However, the high parent heterosis was only significant during the 1986/87 season. Both parents involved in this hybrid had high GCA effects. The parent 120A was the best general combiner among the testers. The second parent D 38073-2 had a significant positive GCA effect during the 1987/88 season. This hybrid had higher SDU than the best control in the trial; however, the differences were only significant during the 1987/88 season.

Generally, the majority of the hybrid combinations were of no interest to plant breeders as they had diastatic activities that were lower than those of the higher parent or even of the mid-parental value. This might be due to the presence of partially dominant genes for low diastatic activity. The

involvement of dominant gene action for the expression of SDU is in line with the findings of Ellis *et al.* (1986) who reported the presence of dominant gene action in barley diastatic activity.

GCA and SCA effects differed between two seasons for some entries (Tables 2 and 3). Such variation in the type of gene action controlling the same trait may be attributed to the low heritability of the trait and to genotype x environment interactions. Since SDU is primarily non-additive, a recurrent selection programme to improve primarily specific combining ability should be an appropriate method by which to breed parents with good malting quality for hybrid development. More research is required to estimate the heritability of SDU and the factors that affect its expression.

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