Heritability and Expression of Selected Mixograph Parameters in Progeny of Parents Varying for Mixing Time

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The mixograph performs certain rheological measurements during dough mixing and is a good predictor of wheat end-use quality. The aim of this study was to determine the expression and the heritability of mixing characteristics measured with Mixsmart® software and some quality characteristics in hard red spring wheat parents and their F_1 progeny. Six parents varying in midline peak time and envelope peak time were crossed in a half diallel design. Parents and progeny were planted in three different environments. General combining ability (GCA) was a significant source of variation for the measured characteristics, and parents differed widely in terms of GCA effects. Midline-development time, -peak integral and -peak time showed high narrow sense heritability. Envelope peak-integral and -tail width displayed high narrow sense heritability for some, but not all locations. High GCA:SCA (specific combining ability) ratios indicated the prevalence of additive gene effects for midline-development time, -peak integral and -peak time, indicating that these characteristics are largely genetically determined, and that selection for them should lead to genetic gain.

Keywords: diallel, inheritance, Mixsmart, wheat quality

Introduction

Wheat breeding produces a large amount of cross combinations from potential parents, therefore a multistage selection process is used. The first stage entails the selection of parental lines by evaluation of their performance; in the second stage parental lines are selected based on their GCA (Longin et al. 2009). GCA and large GCA:SCA ratios indicate the presence of additive gene effects, which could be used in breeding due to additive gene effects being retained in progeny, while SCA and small GCA:SCA ratios are an indication of dominance and epistasis (Ahmed et al. 1991). Narrow sense heritability is an indication of phenotypic variance due to additive genetic variability. Parameters with high heritability are beneficial in the selection of new cultivars (Barnard et al. 2002; Neacşu et al. 2009).

The mixograph performs certain rheological measurements during dough mixing and is a good predictor of end-use quality (Bordes et al. 2008). Rate of dough development is

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the most used measurement of a mixograph (Barnard et al. 2002). Peak time is an indication of time that is needed for dough to reach maximum consistency or first indication of dough weakening. Strong doughs tend to have long mixing times, high peak values and band widths and low resistance to breakdown (Mao et al. 2013). Quality and quantity of protein in wheat can increase absorption, thus influencing peak time and mixograph peak value. Different genotypes can all have 12% flour protein content, but differ for mixing properties. This is due to the quality of protein (Finney et al. 1987). Variations in dough rheological properties have been found to be influenced by genotype but also by environment (Li et al. 2013). Bergman et al. (1998) found peak time and flour protein content to have high heritability, but this was contradicted by the findings of Barnard et al. (2002) and Morojele and Labuschagne (2013) who found mixing development time to be a parameter with low narrow sense heritability. The aim of this study was to determine the expression and heritability of mixograph parameters and some quality characteristics in F_1 progeny of parents with varying midline and envelope peak time values in three different locations.

Materials and Methods

Plant material

Six South African spring wheat genotypes with varying midline and envelope peak time values (Table 1) were obtained from PANNAR®. The mixing time data came from the previous two production seasons, but only the averages are shown. As the information on parents is confidential, all parents and progeny were coded. The parents were crossed in the glasshouse in a half diallel mating design, excluding reciprocals, to produce 15 F_1 crosses.

Table 1. Localities and fertiliser used for F_1 trials and parental material used with their mixing characteristics

Location	Province	Latitude	Longitude	Elevation (m)	Fertiliser
Petrusburg	Free State	29°7'18.912"S	25°24'49.388"E	1247	180N:40P:20K
Orania	Northern Cape	29°49'25.82"S	24°24'48.056"E	1126	260N:173P:86K
Magogong	North West	27°39'25.28"S	24°48'44.052"E	1175	180N:40P:20K
Genotype	Midline peak time (min)	Envelope peak time (min)			
Parent 1	2.23	1.93			
Parent 2	2.26	2.06			
Parent 3	2.39	2.10			
Parent 4	2.48	2.26			
Parent 5	2.27	1.82			
Parent 6	2.82	2.12			

S = South, E = East, N = Nitrogen, P = Phosphorus, K = Potassium

Field trials

Field trials were conducted in irrigated locations in three different provinces in South Africa (Table 1). The F_1 hybrids together with the parents were planted in June/July 2012 and harvested in November/December 2012. Experimental plots were planted one row per cultivar (1 m long, with a 30 cm inter row spacing) using a randomized complete block design with three replications. The plot size was small due to limited seed. Fertiliser mixtures, nitrogen (N): phosphorus (P): potassium (K), were applied (Table 1), which is optimal for each production area. Irrigation was applied to create optimal production conditions.

Laboratory methods

Laboratory analysis was done at the Small Grain Institute (Bethlehem). All the grain samples were evaluated for grain characteristics, after which they were conditioned and milled. Tests were done according to the American Association of Cereal Chemists (AACC) standards (AACC, 2000) and included conditioning (AACC procedure 26-95), mixograph analyses (AACC method 54-40A), flour protein content (AACC Method 39-11.01), Sodium Dodecyl Sulphate (SDS) sedimentation volume (AACC 56-70) and falling number (AACC method 56-81B). Using Mixsmart® software, 44 parameters can be measured on a single mixogram curve (Pon et al. 1989). These parameters result from measurements made at different heights, widths and slopes as well as areas on the mixogram curve (Walker and Walker 1992). In this study the 17 most repeatable Mixsmart parameters with acceptable coefficients of variation were included.

Diallel analysis

Analysis of GCA and SCA for the characteristics were done using Agrobase 2nd Generation Software (Agronomix 2014). The relative magnitude of mean squares of GCA and SCA were determined using the GCA:SCA ratios. Heritability of characteristics was estimated as

$$h_n^2 = 2\sigma^2GCA/(2\sigma^2GCA + \sigma^2SCA + \sigma^2E) .$$

LSD for GCA and SCA was estimated as $\sqrt{\sigma^2(gi-gj)} \times tp$ (use of two sided table at p = 0.05) and $\sqrt{\sigma^2(sij)} \times tp$ (*t* table), respectively, where *gi* and *gj* are GCA effects of parents and *sij* is SCA effects of crosses (Dabholkar 1999).

Results

Combining ability effects of parents

Only GCA was discussed as SCA was not relevant in the context of this study, except for determining GCS:SCA ratios. Parent 1 was the best combiner for envelope peak time, midline peak value, SDS sedimentation volume, envelope left value and flour protein

Table 2. Orania general combining ability effects of parents for mixograph parameters and selected quality characteristics

Character	LSD GCA (0.05)	GCA effect Parent					
		1	2	3	4	5	6
ELV	8.61	**3.67**	0.21	2.96	–2.75	–1.50	–2.60
ELW	6.43	–0.29	–0.64	**4.10**	–2.34	–0.11	–0.72
MDT	0.17	–0.07	–0.07	0.04	–0.03	–0.07	**0.21**
MPI	10.51	–0.16	–3.06	–4.53	–0.44	–3.28	**11.48**
MPT	0.24	–0.02	–0.08	–0.13	–0.01	–0.1	**0.33**
MPV	1.35	**0.68**	0.17	–0.45	0.07	0.35	–0.83
MTI	6.53	0.60	–2.14	–0.31	–0.39	**2.05**	–0.80
MTV	0.97	0.01	–0.45	–0.50	0.21	0.10	**0.63**
EPI	11.79	–2.07	–3.07	1.98	–0.06	–0.13	**3.35**
EPT	0.52	**0.09**	–0.12	–0.12	0.08	–0.01	0.08
EPV	3.43	–1.11	1.01	**1.62**	–1.04	0.54	–1.02
EPW	9.13	–4.29	1.82	**4.11**	–2.16	0.02	0.54
ERI	16.16	–2.85	–3.21	3.19	–2.21	1.57	**3.51**
ERT	0.85	**0.19**	–0.18	–0.17	0.06	0.03	0.07
ERV	4.35	–1.22	0.33	**1.09**	–0.33	0.00	0.13
ETV	1.30	–0.22	–0.95	–0.17	**0.16**	0.13	1.04
ETW	1.60	–0.41	–0.84	0.65	–0.11	–0.05	**0.73**
FLN	85.89	–18.65	–12.11	8.64	–24.49	**45.26**	1.35
FPC	0.40	**0.38**	–0.16	–0.05	–0.10	–0.01	0.06
SDSVOL	4.73	**8.04**	–0.88	–2.38	–3.42	–1.08	–0.29

GCA = General combining ability, LSD = Least significant difference, ELV = Envelope left value, ELW = Envelope left width, MDT = Midline development time, MPI = Midline peak integral, MPT = Midline peak time, MPV = Midline peak value, MTI = Midline tail integral, MTV = Midline tail value, EPI = Envelope peak integral, EPT = Envelope peak time, EPV = Envelope peak value, EPW = Envelope peak width, ERI = Envelope right integral, ERT = Envelope right time, ERV = Envelope right value, ETV = Envelope tail value, ETW = Envelope tail width, FLN = Falling number, FPC = Flour protein content, SDSVOL= Sodium Dodecyl Sulphate sedimentation volume, highest GCA effects indicated in bold.

content in Orania (Table 2). It was also the best combiner for flour protein content in Petrusburg as well as for envelope left value and envelope right time in Magogong (Tables 3 and 4). Parent 2 was the best combiner only for envelope left value in Petrusburg (Table 3). Parent 3 was the best combiner for falling number in Petrusburg and Magogong as well as for flour protein content in Magogong. Parent 3 was also the best combiner for envelope-left width, -peak value, -peak width and -tail value at Orania (Tables 2–4). Parent 4 was the best combiner in Magogong for envelope-left width, -midline tail value, -envelope peak time, -peak value and -tail integral as well as for envelope-peak width and -right value in Petrusburg. It was also the best combiner for envelope tail

Table 3. Petrusburg general combining ability effects of parents for mixograph parameters and selected quality characteristics

Character	LSD GCA	GCA effect Parent					
	(0.05)	1	2	3	4	5	6
ELV	9.64	2.36	**5.39**	−1.99	−3.51	0.41	−2.66
ELW	3.81	0.59	1.71	−0.39	−1.36	**0.63**	−1.18
MDT	0.14	−0.15	−0.01	0.06	−0.01	−0.12	**0.23**
MPI	6.85	−4.51	−1.97	3.74	−1.27	−2.98	**7.00**
MPT	0.17	−0.13	−0.03	0.08	−0.03	−0.11	**0.23**
MPV	1.61	0.30	−0.53	0.20	−0.21	**1.00**	−0.77
MTI	8.76	−0.57	−1.45	1.05	0.10	**3.70**	−2.83
MTV	3.61	0.30	−0.14	−0.43	−0.13	**0.96**	−0.55
EPI	4.57	−5.01	−0.31	1.40	1.16	−1.84	**4.60**
EPT	0.16	−0.17	−0.04	0.07	0.00	−0.11	**0.25**
EPV	2.33	−0.35	−0.18	0.03	0.72	**0.73**	−0.95
EPW	3.60	−0.75	0.79	−0.34	**1.58**	−0.62	−0.67
ERI	6.89	−6.17	0.03	3.34	0.92	−2.26	**4.14**
ERT	0.33	−0.16	−0.05	0.22	−0.11	−0.15	**0.25**
ERV	4.01	−1.11	0.71	−1.20	**1.71**	0.78	−0.89
ETV	4.71	−0.09	−0.07	−0.60	0.06	**1.60**	−0.90
ETW	2.68	−0.89	0.05	−0.14	0.27	**1.07**	−0.35
FLN	37.26	3.42	−9.54	**15.58**	9.16	−4.67	−13.96
FPC	0.39	**0.26**	−0.09	−0.11	−0.07	0.17	−0.16
SDSVOL	5.92	1.40	−3.43	1.69	−2.01	−0.47	**2.82**

GCA = General combining ability, LSD = Least significant difference, ELV = Envelope left value, ELW = Envelope left width, MDT = Midline development time, MPI = Midline peak integral, MPT = Midline peak time, MPV = Midline peak value, MTI = Midline tail integral, MTV = Midline tail value, EPI = Envelope peak integral, EPT = Envelope peak time, EPV = Envelope peak value, EPW = Envelope peak width, ERI = Envelope right integral, ERT = Envelope right time, ERV = Envelope right value, ETV = Envelope tail value, ETW = Envelope tail width, FLN = Falling number, FPC = Flour protein content, SDSVOL= Sodium Dodecyl Sulphate sedimentation volume, highest GCA effects indicated in bold.

value in Orania (Table 2). Parent 5 was the best combiner for midline tail integral and falling number in Orania as well as for envelope left width and midline-peak value, -tail integral and -tail value, and envelope-peak value, -tail value and -tail width in Petrusburg. It was also the best combiner for SDS sedimentation volume in Magogong (Table 4).

Parent 6 was the best overall combiner as it was the best combiner for midline-development time, -peak integral, -peak time, -tail value, and envelope-peak integral, -right integral and -tail width in Orania as well as for midline-development time, -peak integral, -peak time and envelope-peak integral, -peak time, -right integral and -right time and SDS sedimentation volume in Petrusburg. It was also the best combiner for midline-develop-

ment time, -peak integral, -peak time and envelope-peak integral, -peak value, -peak width, -right integral, -right value, -tail value and -tail width in Magogong (Tables 2–4).

GCA mean squares, GCA:SCA mean square ratios and heritability of mixograph parameters and quality characteristics

The number of characteristics with significant GCA mean square values by far exceeded those with significant SCA mean squares (Table S1*). Orania had seven charac-

Table 4. Magogong general combining ability effects of parents for mixograph parameters and selected quality characteristics

Character	LSD GCA	GCA effect Parent					
	(0.05)	1	2	3	4	5	6
ELV	10.56	**1.81**	0.39	−1.67	1.02	−2.31	0.77
ELW	4.77	0.22	−0.43	0.36	**0.77**	−1.30	0.38
MDT	0.19	−0.06	−0.09	−0.13	0.07	−0.05	**0.25**
MPI	11.35	−1.21	−3.46	−1.32	4.18	−7.21	**9.01**
MPT	0.19	−0.06	−0.10	−0.08	0.07	−0.05	**0.21**
MPV	1.95	−0.04	−0.12	0.22	**0.80**	−0.51	−0.35
MTI	23.64	1.82	0.63	2.45	**6.12**	−15.44	4.43
MTV	3.12	−0.84	0.20	−1.50	**1.49**	−0.37	1.02
EPI	9.04	−2.31	−1.27	−1.73	3.39	−3.03	**4.96**
EPT	0.34	−0.03	0.02	−0.07	**0.16**	−0.19	0.11
EPV	2.96	−0.72	−0.44	0.06	0.42	−1.06	**1.74**
EPW	4.65	−1.56	−1.08	−0.03	−1.09	−0.83	**4.59**
ERI	11.43	0.31	−2.07	−1.7	2.63	−5.19	**6.02**
ERT	0.54	**0.19**	0.00	−0.06	0.18	−0.32	0.01
ERV	4.38	−1.08	−0.80	0.75	−0.09	−1.06	**2.28**
ETV	3.73	−0.67	0.11	−1.83	1.35	−0.55	**1.60**
ETW	1.17	0.41	−3.57	−0.43	−0.34	−0.40	**1.12**
FLN	8.22	0.94	−1.68	**3.38**	−1.24	1.92	−3.33
FPC	0.41	0.09	−0.11	**0.12**	0.08	−0.01	−0.17
SDSVOL	5.59	2.43	−3.61	−0.86	−1.36	**3.14**	0.26

GCA = General combining ability, LSD = Least significant difference, ELV = Envelope left value, ELW = Envelope left width, MDT = Midline development time, MPI = Midline peak integral, MPT = Midline peak time, MPV = Midline peak value, MTI = Midline tail integral, MTV = Midline tail value, EPI = Envelope peak integral, EPT = Envelope peak time, EPV = Envelope peak value, EPW = Envelope peak width, ERI = Envelope right integral, ERT = Envelope right time, ERV = Envelope right value, ETV = Envelope tail value, ETW = Envelope tail width, FLN = Falling number, FPC = Flour protein content, SDSVOL= Sodium Dodecyl Sulphate sedimentation volume, highest GCA effects indicated in bold.

*Further details about the Electronic Supplementary Material (ESM) can be found at the end of the article.

teristics with significant mean squares for GCA (flour protein content, midline- development time, -peak integral, -peak time, -tail value and envelope-tail value and -tail width) and one highly significant GCA mean square for SDS sedimentation volume. Petrusburg had four significant GCA mean squares (midline peak integral, and envelope-peak integral, -right integral and -right time) and three highly significant GCA mean squares (midline-development and -peak time and envelope peak time). Magogong showed six significant GCA mean squares (midline-development time and -peak time, -integral and envelope-peak width and -tail width and SDS sedimentation volume). High GCA:SCA mean square ratios were found for most of the characteristics for all three locations. Envelope peak time had high narrow sense heritability only in Petrusburg while midline development time and midline peak time showed high narrow sense heritability for all three locations.

Discussion

In order to improve the mixograph parameters and selected quality characteristics, parents with high GCA effects should be used as parental lines (Barnard et al. 2002). The South African quality standard SST 806 has a peak time ranging from 1.8 min to 3.8 min with an average of 2.4 min. Thus a cultivar may not deviate from these values by more than 35% or less than 10% (SAGL, 2013). A predominance of GCA compared to SCA effects was reported by Gowda et al. (2012). As this was also seen in this study, the importance of additive genetic variances in the inheritance of characteristics in this set of material was emphasised. High GCA:SCA mean square ratios indicate high heritability and low influence of the environment (Barnard et al. 2002). Midline-development and -peak time and envelope peak time, SDS sedimentation volume and flour protein content (except for Magogong) had GCA:SCA mean square ratios above one, this is in accordance with the findings of Barnard et al. (2002) except for SDS sedimentation volume in their study which had a GCA:SCA mean square ratio below one. This is an indication of additive gene action and supports the high GCA values found for mixograph parameters and quality characteristics. This is important as peak time values are used for quality selection in breeding programmes (Neacşu et al. 2009). GCA:SCA mean square ratios below one are indicative of non-additive and dominant gene actions as was the case for envelope peak value for all the locations. These results are in accordance with Barnard et al. (2002) where GCA mean squares were significant for flour protein content, and both GCA and SCA were significant for mixograph development time. They found no significant GCA or SCA for SDS sedimentation volume contrary to what was found in this study.

Parameters with high heritability can be used by breeders and is beneficial in the selection of new cultivars (Neacşu et al. 2009). In the study of Gras and O'Brien (1992) it was found that mixing time had a medium to high heritability, this corresponded with the findings of this study. Miles et al. (2013) found genotype to be the largest contributor of variation for mixograph peak time, indicating a small environmental effect. This contradicts the findings of Barnard et al. (2002) and Morojele and Labuschagne (2013) where mixo-

graph development time had low narrow sense heritability. They also found flour protein content and SDS sedimentation volume to have a low narrow sense heritability which contradicted the findings of Gras and O'Brien (1992) where flour protein content had a medium heritability. This could be due to different parents and locations used in this study compared to other studies, as flour protein content and SDS sedimentation volume are known to be influenced by environmental conditions (Labuschagne et al. 2009; Miles et al. 2014).

To conclude, this study showed that GCA was a significant source of variation for the characteristics studied. Midline-development time, -peak integral and -peak time showed very high narrow sense heritability. This is an indication that environment had little to no effect on these characteristics. In contrast to this, envelope-peak integral and tail-width displayed high narrow sense heritability for some, but not all locations. This indicates that environment influenced inheritance of these characteristics. High GCA:SCA ratios indicated the prevalence of additive gene effects for midline-development time, -peak integral and -peak time, indicating strong genetic effects for these characteristics, and that selection for them should lead to genetic gain. When making crosses, parents with good GCA can be used to obtain progeny with desired mixing characteristics. In order to improve the mixograph parameters and selected quality characteristics, parents with high GCA effects should be used as parental lines (Barnard et al. 2002).

Acknowledgement

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Electronic Supplementary Material (ESM)

Electronic Supplementary Material (ESM) associated with this article can be found at the website of CRC at http://www.akademiai.com/content/120427/

Electronic Supplementary *Table S1*. Heritability and GCA:SCA ratios for mixograph parameters and selected quality characteristics