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Combining ability and reciprocal effects for physico-chemical grain quality characteristics in maize

J. E. Alika & J. O. Ojomo

Department of Crop Science, Faculty of Agriculture, University of Benin, Benin City, Nigeria

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The gene action involved in the inheritance of four physico-chemical grain characteristics, i.e. starch content, gel spread, gelatinization time and temperature, in maize (*Zea mays*) was studied in a six-parent diallel cross. The experimental material consisted of parents, F1s and reciprocals. Additive and non-additive gene actions were observed to significantly influence the variation of starch content and gel spread with the additive gene action being more pronounced, implicating the effectiveness of selection for increased starch yield through a recurrent selection procedure. The reciprocal effects were equally significant for grain starch content, an indication of the importance of cytoplasmic effects. Variability of specific combining ability was more pronounced for time of gelatinization, whereas reciprocal effect accounted for greater variability in differences due to temperature of gelatinization. Parents BC 63 C2 and TZB-SR-SE expressed more favourable genes for increased grain starch content, limited gel spread and quicker gelatinization. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

Wet or dry starch extracted from cereal grains and, most importantly, from maize is used considerably in the preparation of traditional breakfast and weaning foods in Nigeria. Consumption of soft and stiff porridges from starch preparations has long been a dietary habit of the people and several methods have been proposed to improve the nutrient quality of the products (Akinrele *et al.*, 1970; Adeniji & Potter, 1978; Adeyemi, 1988; Banigo *et al.*, 1974).

Variability in starch yield among existing cultivated maize varieties has been reported (Adeyemi *et al.*, 1987; Alika, 1993). The cultivars commonly planted by farmers were originally selected for grain yield and disease resistance rather than for starch content. Alika (1993) reported that some of the high grain yielding cultivars contain higher proportions of chaff than starch following wet milling and sieving.

In view of the importance of maize starch in food, there is a need for genetic improvement of the trait both quantitatively and qualitatively, as has been reported for other chemical traits such as proteins (Alexander *et al.*, 1967; Dudley *et al.*, 1977; Shenoy *et al.*, 1991; Shingh *et al.*, 1984) and oils (Lee, 1977; Roche *et al.*, 1977; Shingh *et al.*, 1984).

The properties of starch that are of upmost importance are the pasting characteristics and retrogradation tendencies. These are of considerable importance to both processors and consumers. Limited information on the gene action influencing the pasting characteristics of starch and flours in maize has been reported. Non-additive genetic variance was reported to express greater influence on the inheritance of flour gel consistency in rice (Kaw & Cruz, 1991). Additive genetic variance was observed to influence the inheritance of gel texture in a stiff maize flour porridge ('tuwo'), whereas time for gelatinization of 'tuwo' was found to be controlled by non-additive genetic variance (Alika, 1994).

This study was undertaken to determine the type and amount of gene action that influence the starch yield and pasting properties of maize.

MATERIALS AND METHODS

Six maize cultivars were selected as parents for this study. The cultivars were: (1) ACR 8363; (2) TZB-SR-SE; (3) TZUT-SR-W C_5; (4) EV 8728.SR-BC_6; (5) BC 63 C_2; and (6) TZSR-W. Parent (4) has a yellow endosperm kernel; however, the rest of the parents are white. Parent (5) is a local composite with a high starch yield (Alika, 1993). Parents (2) and (6) are recommended varieties for grain production. The parents were crossed in all possible diallel fashions including reciprocals in the field between March and June 1994. At the same time the parental cultivars were individually multiplied by hand pollination using bulk pollen. At maturity, seeds were obtained from parents, F1s and their reciprocals.

Starch was extracted from the seeds obtained from the parents, F1s and the reciprocals using the wet-milling method (Akingbala *et al.*, 1981), with some modifications. Briefly, a 50-g sample was soaked in 200 ml of tap water in a plastic bowl for 72 h at 28°C, then ground in a Philips blender at the fastest setting for 2 min. The slurry was passed through a BS 410 sieve with an aperture of 150 μm and washed in 300 ml of tap water. The resulting filtered liquids were transferred into a 1-litre plastic container and left to stand for 2 h at 5°C in a refrigerator. The wash water was finally decanted and the white mass of solid starch was dried in a Gallenkamp Moisture Extraction Oven at 50°C for 12 h. The dried starch was weighed and the values expressed as percentage of the grain weight. Three separate samples were processed for each entry.

Determination of pasting properties

Three starch pasting properties, i.e. gel consistency, gelatinization time and temperature, were tested. Gel consistency in the form of 'gel spread' was measured by modifying the procedure suggested by Murty *et al.* (1982) for sorghum flour. Dry starch was milled using a kitchen grinder at the fastest setting for 2 min. The ground sample was passed through 1.0-mm sieve. Two grammes of milled starch were mixed with 25 ml of tap water in a 75 ml beaker and heated over a Gallenkamp Magnetic Stirrer hotplate with continuous stirring until gelatinization occurred. The gelled starch was poured on to a clean 15×15 cm ceramic plate smeared with drops of vegetable oil and allowed to cool for 2 h. The diameter of the gel was measured, which represented the extent of gel spread.

Gelatinization temperature was measured by inserting a thermometer into the boiling starch slurry in the beaker until gelatinization began.

Gelatinization time was recorded as the time taken from the onset of heating the starch slurry until gelatinization occurred.

Analysis of variance for the combining ability of each of the traits was based on mean values using the procedure described by Griffing (1956) for method 1 and model 1. The analysis was performed using an Agrobase 4 computer software package.

RESULTS

Mean starch contents among parents, F1s and reciprocals are presented in Table 1. The mean starch content for parents was 40.8%, whereas the average for all hybrids including reciprocals was 36.9%, suggesting a lack of dominance in the inheritance of starch. Diversity between hybrids (32.6–49.8%) was less than that between parents (26.2–61.9%) for starch content. Parents BC 63 C_2 and TZB-SR-SE expressed the highest starch values with corresponding highest values for array means. A close correspondence ($r = 0.93^{**}$) between the parental means and the array means suggests a high prepotency of the parents in transmitting the starch trait to its progenies. For the F1 crosses, BC 63 C_2×TZB-SR-SE produced the highest starch value of 59.3%.

Means for gelatinization time and gel spread for the parents and the F1s are presented in Table 2. There was a larger spread (19.5 mm) among the hybrids than the parents (13.0 mm) for gel spread. For gel time, the hybrids expressed a smaller range (10.3 min) than the parents (20.7 min). There was minimal correspondence ($r = 0.34$) between the array means and the parent

Table 1. Mean per cent starch in the parents (bold), direct crosses (above diagonal) and in reciprocal crosses (below diagonal) in a six-parent diallel cross in maize

Varieties	1	2	3	4	5	6	Hybrid-array means
(1) ACR 8363	**41.4**	29.0	29.5	32.3	37.0	26.1	32.60
(2) TZB-SR-SE	42.7	**49.1**	42.6	42.7	43.7	45.6	44.4
(3) TZUT SR-W C_5	34.4	38.6	**32.2**	35.4	36.2	32.1	34.8
(4) EV8728-SR-BC_6	32.6	33.8	30.1	**26.2**	35.4	28.4	31.1
(5) BC 63 C_2	42.0	59.3	46.3	44.4	**61.9**	45.1	49.8
(6) TZSR-W-1	32.8	32.9	32.4	30.3	34.7	**34.1**	32.9

Table 2. Mean gel spread (above diagonal) and geltinization time (below diagonal) in a six-parent diallel cross in maize

Varieties	1	2	3	4	5	6	Gel spread (mm)		Gel time (sec)	
							Per se parents	Array means	*Per se* parents	Array means
(1) ACR 8363	—	70.8	74.9	71.7	69.5	73.6	69.8	72.1	52.0	53.9
(2) TZB-SR-SE	52.3	—	65.8	75.8	59.0	66.5	74.0	67.6	54.0	50.8
(3) TZUTSR-W-C_5	53.0	48.3	—	71.7	71.0	72.5	76.6	71.2	67.0	52.7
(4) EV 8728-SR-BC_6	58.3	53.3	57.0	—	70.0	78.5	81.3	73.5	46.3	54.3
(5) BC $63C_2$	52.0	52.0	50.0	51.0	—	66.3	71.0	67.2	50.3	51.8
(6) TZSR-W-1	54.0	48.0	54.3	52.0	53.3	—	68.3	71.5	50.3	52.3

Table 3. Mean gelatinization temperature in a six-parent diallel cross in maize[a]

Varieties	1	2	3	4	5	6	Array means
(1) ACR 8363	**83.3**	84.0	84.3	84.0	83.7	83.0	83.8
(2) TZB-SR-SE		**83.3**	81.6	82.0	83.0	83.0	82.7
(3) TZUT SR-W-C_5			**85.0**	83.0	85.0	84.0	83.6
(4) EV8728-SR-BC_6				**83.7**	83.0	84.0	83.2
(5) BC 63 C_2					**84.7**	85.0	83.9
(6) TZSR-W-1						**84.3**	83.8

Bold figures represent parental values.

Table 4. Analysis of variance for combining ability for starch and starch pasting properties in maize

Source of variation	Degrees of freedom	Mean squares			
		Starch	Gel spread	Gel time	Gel temperature
Genotypes	35	207.65***	56.47***	44.44***	2.64**
gca	5	318.87***	52.01**	18.02	1.17
sca	15	18.44***	19.78***	20.66***	0.59
Reciprocal	16	36.78***	6.81	7.90	1.08**
Residual	70	1.16	3.78	5.75	0.37
gca:sca		17.3	2.6	0.87	1.3

**, ***Significant at 1 and 0.1% levels, respectively.

means for gel spread. Similarly, a reduced but negative correlation ($r = -0.22$) was obtained between array means and parental means for gel time, indicating a considerable lack of prepotency of the parents in transmitting both traits. This further suggests that the prediction of hybrid performance from parental values was likely to be ineffective. In the case of gel spread, parents (1) and (6) produced stiffer gels, whereas parent (4) expressed a more fluid gel. For gelatinization time, parent (4) appeared to gel quicker than the rest of the parents, with parent (3) expressing highly delayed gelatinization. This appears to be in agreement with the findings of Alika (1994) and Murty *et al.* (1982) who separately reported that cultivars which tend to produce fluid gels, as in the case of waxy cultivars, usually gel more rapidly than cultivars with stiffer gels.

Mean values for gelatinization temperature for starch gel are presented in Table 3. The spread (3.4°C) for the hybrids was larger than that for the parents (1.7°C) for gelatinization temperature. Higher gelatinization temperature was recorded in a cross of parents (3)×(5).

Analysis of variance revealed that there was substantial genetic variability among the genotypes for the four physico-chemical grain quality characteristics (Table 4). Variances due to general combining ability (gca), specific combining ability (sca) and reciprocal differences (RD) were highly significant for percent starch. Mean squares for gca and sca were highly significant for gel spread while RD was not. In the case of gelatinization time, variability due to sca was significant whereas the other sources of variance were non-significant. Mean square for RD was highly significant for gelatinization temperature while there was a lack of significance for the sources of variation attributed to gca and sca.

The ratio of gca:sca was considerably larger than unity for percent starch and moderately greater than unity for gel spread. The ratios of gca:sca for gel time and gel temperature, respectively, were not considered important since there was a lack of significance for variation due to gca. The very high value of gca:sca for starch and gel spread suggests that additive gene effects were substantially more important than other types of gene action in the variation expressed for starch content and gel spread. In the case of starch content, the magnitude of RD to sca was substantial, an indication that RD is an important component of variation which has to be considered in any improvement programme for starch.

Estimates of the general combining ability effect of the parents for starch content and gel spread are provided in Table 5. Highly significant gca effects were obtained for all the parents for starch, whereas three parents [(2), (4) and (5)] were observed to have significant gca effects for gel spread. Parents BC 63 C_2 and TZB-SR-SE were the best combiners for favourable genes for increased starch content and were similarly the best combiners for favourable genes for harder gels.

Table 5. Estimate of gca effects of parents for starch and gel spread

Parents	Variables	
	Starch	Gel spread
(1) ACR 8363	−2.49**	0.24
(2) TZB-SR-SE	4.84**	−2.08**
(3) TZUT-SR-W-BC_5	−2.43**	1.06
(4) EV8728-SR-BC_6	−4.44**	3.36**
(5) BC 63 C_2	8.07**	−2.16**
(6) TZSR-W-1	−3.54**	−0.43
SE ($\hat{g}i-\hat{g}i$)	0.417	0.793

**Significant at 1% level.

Table 6. Good specific combiners for percent starch, gel spread and gel time, and reciprocal combiners for percent starch and gel temperature

Characteristics	Cross	sca effects	Cross	Reciprocal effects
Per cent starch	(3)×(4)	2.01**	(5)×(2)	7.78**
	(1)×(4)	1.79*	(5)×(3)	6.05**
Gel spread	(2)×(5)	−6.47**		
	(1)×(4)	−3.45**		
Gel time	(2)×(3)	−5.59**		
	(3)×(5)	−2.15		
Gel temperature	—	—	(4)×(2)	−1.667**
			(4)×(3)	−1.17

*, **Significant at 5 and 1% levels, respectively.

Crosses with good specific and reciprocal combiners for the physico-chemical grain quality traits are presented in Table 6. Two crosses with parent (4) as the common parent expressed high values for sca effects for starch content, whereas parent (5) was involved in crosses with the highest values of reciprocal effects. Parent (4) additionally expressed considerable reciprocal effects for gelatinization temperature.

DISCUSSION

Significant genotypic variability for the four physico-chemical grain qualities indicated that there was considerable genetic diversity among the parents and the hybrids. Reliability for predicting hybrid performance was observed to be high for starch but low for gel consistency and gel time. The high correlation between hybrid performance and mid-parent values can generally be expected when the hybrid vigour expression is predominantly caused by additive and additive×additive gene effects (Virmani *et al.*, 1982). The preponderance of gca over sca for starch content and gel spread indicates that additive genetic variance is more important in the inheritance of both traits than the other genetic effects. The considerably large gca effect for starch content suggests that preliminary screening of the relative potential of the parents used in hybrid combinations could be accomplished effectively by crossing to few tester lines and comparing the performance of the hybrids in several environments. However, in view of the significant effect due to sca it could be suggested that improvement of starch may be possible by utilizing biparental mating, followed by recurrent selection.

The significant RD for starch content as has frequently been reported for other endosperm chemical characteristics, such as oil (Yang & Davis, 1977) and protein (Mak & Yap, 1977) indicates that the importance of maternal effects must be recognized in the choice of parents to be used as females. Maize endosperm which consists of about 90% starch is a triploid tissue with two genomes from the female parent and one genome from the male. The reciprocal effect may be related to a dosage effect of the genes controlling the trait, which means that the starch content in heterozygous endosperm may not depend on the endosperm's genotype but rather on that of the female parent.

Parents BC 63 C_2 and TZB-SR-SE expressed the largest values of gca effects for starch, thereby proving to be the best combiners for starch content. Both also exhibited high *per se* performance in relation to their gca effects. In a similar manner, both parents expressed the least values for gca effects for gel spread, thereby proving to be the best combiners for harder gel. Both cultivars could be used as parents in hybridization for improvement of starch and gel consistency. Genetic studies for gel quality of maize 'tuwo' indicated that additive gene effects were more important than non-additive genetic variance for gel texture, whereas, for gel consistency in rice flour porridge, non-additive gene action was observed to be more pronounced (Kaw & Cruz, 1991). Where gelatination temperature and time are considered important for purposes of genetic improvement, adequate breeding methods that accumulate non-additive gene effects, in the case of gelatinization time, and cytoplasmic effects, in the case of gelatinization temperature, should be adopted.

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