

Genetic Analysis of Grain Yield and Starch Content in Nine Maize Populations

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Abstract: The objective of this study was to estimate main genetic effects including digenic non-allelic epistasis for yield and starch content in grain by generation mean analysis performed in 9 maize populations (biparental crosses) and their subsequent 6 generations (2 parental, F1 and F2, and 2 backcrosses). The estimated additive-dominance model of inheritance was, due to epistasis, only partially successful in explaining inheritance model for investigated traits and crosses. The additive-dominance model was adequate at 6 crosses for grain yield and 3 crosses for starch content. A digenic epistatic model was sufficient to explain the inheritance model at 6 crosses for grain starch content. The obtained estimations of genetic effects showed varying importance of genetic effects among the investigated crosses and traits. Due to heterosis, the dominance effects appeared to be prevailing in most crosses for yield. These results indicate that adequacy of certain models of inheritance as well as importance of genetic effects for certain traits was dependant upon the particular cross, stressing the importance of the selection of parental genotypes for the success of breeding programmes.

Key Words: Maize, quantitative traits, generation mean analysis, genetic effects

Introduction

Maize is one of the major cereal crops providing raw material for the food industry and animal feed (Ünay et al., 2004). Grain yield is agronomically the most important trait in maize, while starch content in grain is becoming very attractive because of value-added food/feed production, as well as of burgeoning biofuel production. Both of these traits are quantitative and complex in nature. It means their expression is caused not only by genetic effects, but also by environmental effects and genotypexenvironment interaction. Melchinger et al. (1986) described how knowledge about the nature of gene action allows maize breeders for optimising their breeding programmes better.

Both grain yield and starch concentration are well documented in maize (Hallauer and Miranda, 1988, for a review). However, most of the reports were limited only to some well known maize populations or crosses

providing just a piece of information regarding the gene action of the most important traits. Illinois long-term selection strains served for more than a century as a case study for quantitative and molecular genetics (Dudley, 2007; Wassom et al., 2008), but there are no reports published recently comprising more populations or crosses of maize for quantitative genetic studies.

Assessment of genetic effects involved in the expression of quantitative traits in maize can be accomplished by generation means analysis (Frank and Hallauer, 1997). Generation mean analysis is a simple but useful technique for estimating genetic effects for a polygenic trait. Its greatest merit lies in the ability to estimate epistatic genetic effects such as additive \times additive, dominance \times dominance, and additive \times dominance effects (Singh and Singh, 1992). Frank and Hallauer (1997) found the generation means analysis as a useful tool because genetic information is

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usually lacking for quantitative traits, especially in simultaneous investigations of more maize crosses. Since this analysis takes into account trait means and not variances, its both sensitivity and accuracy might be of significant influence to maize breeding programmes (Hallauer and Miranda, 1988). The objective of this investigation was to estimate the main genetic effects including digenic non-allelic interactions (epistasis), as well as to test the adequacy of the inheritance model for yield and starch content in grain for 9 biparental crosses of maize inbred lines.

Materials and Methods

A 2-year investigation was carried out at Osijek and Karanac in eastern Croatia (45-46°N, 18-19°E with an approximate elevation of 100 m AMSL) during the 1999 and 2000 growing season. The investigated genotypes originated from a set consisted of 28 single crosses developed by 8 × 8 partial diallel mating design (Zdunić, 2001). The 8 genotypes chosen for this investigation represent a sample of high yielding single crosses obtained by crossing elite inbreds of the most used genetic background at the Agricultural Institute Osijek past and present, including genotypes of the most widespread heterotic pattern in maize breeding, such as BSSS×Lancaster Sure Crop (Troyer, 1999). They cover a range of genetic diversity representatives of the US Corn-Belt dent germplasm adapted to Eastern European conditions. The inbreds were Os36-16 (SSS-B14), Os3-48 (Iodent), B84 (SSS-B73), Va99 (OH43), Os163-9 (from a single cross), Os645Kr (SSS-B37), Os6-2 (Lancaster Sure Crop), and Os86-39 (Wf9). In parentheses is the categorisation of the inbred lines in respective maize families-subfamilies. Mikel and Dudley (2006) gave detailed pedigree information for a greater understanding of relations among maize families-subfamilies. With the exception of 2 public inbred lines, B84 and Va99, all other lines in this study were developed at the Agricultural Institute Osijek.

Six basic generations of each genotype (P_1 , P_2 , F_1 , F_2 , BC_1 , and BC_2) were set up as a simple lattice design (Cochran and Cox, 1957) and evaluated on an individual plant basis including the sample size of 80 plants for uniform generations and 240 plants for segregating generations. For uniform generations, the plot size was 14 m² (4 rows, 5 m long, 70 cm between-row spacing, and 25 cm within-row spacing). For segregating

generations, the plot size was 42 m² (12 rows, 5 m long, 70 cm between-row spacing and 25 cm within-row spacing). At each plot, 2 border rows were added. Data for analysis were not collected from the 2 border rows of each plot because of possible competition effects among plots. Generation means analysis was performed for the crosses using the genetic model described by Mather and Jinks (1982) and notation by Hayman (1958). The genetic effects for yield and starch content in grain were estimated for selected genotypes. The adequacy of the additive/dominance model was tested according to goodness-of-fit test using chi-square statistic. If the p value for the calculated chi-square is < 0.05, the additive/dominance model is declared adequate (Fisher and Yates, 1963). All statistical procedures in this study were performed by PLABSTAT (Utz, 1995). Grain starch content was analysed by Ewers polarimetric method (International Organization for Standardization, 1997).

Results

The overall mean values, their standard errors and variances for the analysed traits of the 9 crosses combined across 2 locations and 2 growing seasons are presented in Table 1. The parental inbreds of each cross differed in both traits, although the differences were not consistent in starch content. The mean grain yield of the F_1 generation was greater than the better parent inbred for most of crosses, but the means of grain starch content of the F_1 generation were not greater than the corresponding means in 4 and 3 crosses. The observed variances were lower for grain yield compared to starch content for most of the generations, whereas the greatest variance was determined for starch content in most instances.

The estimates of the main and first order interaction genetic effects for the traits investigated, as well as confirmation of the chi-square tests, are presented in Tables 2 and 3. For grain yield, an additive-dominance model was adequate for 6 crosses, while a digenic epistatic model was adequate for 3 crosses (non-significant chi-square test). It means that in those 3 cases, because of the presence of epistasis, the additive-dominance model failed (Table 2). For all the investigated crosses, the preponderance of effects for this particular trait appears to be dominance. It means that the predominant type of gene action in all crosses was dominance. Thus, for starch content, an additive-

Table 1. Means and variances for 6 generations of 9 maize biparental crosses for grain yield and grain starch content.

Generation ¹	Grain yield (t ha ⁻¹)		Grain starch content (%)		Generation ¹	Grain yield (t ha ⁻¹)		Grain starch content (%)	
	Mean ± SE ²	Variance	Mean ± SE ²	Variance		Mean ± SE ²	Variance	Mean ± SE ²	Variance
Cross Os36-16 × Os6-2					Cross B84 × Os163-9				
P ₁	6.23 ± 0.26	0.27	70.1 ± 1.03	4.28	P ₁	6.83 ± 0.55	1.21	73.43 ± 1.12	4.99
P ₂	4.99 ± 0.37	0.54	73.16 ± 1.16	5.37	P ₂	4.34 ± 1.25	6.24	69.96 ± 1.11	4.94
F ₁	13.24 ± 0.26	0.27	72.82 ± 1.06	4.51	F ₁	17.56 ± 0.8	2.59	74.59 ± 1.64	10.7
F ₂	9.44 ± 0.07	0.02	72.45 ± 1.51	9.13	F ₂	10.37 ± 0.27	0.29	74.21 ± 1.23	6.04
BC ₁	12.49 ± 0.25	0.24	70.81 ± 1.10	4.83	BC ₁	14.22 ± 0.69	1.88	73.32 ± 1.2	5.77
BC ₂	13.41 ± 0.47	0.89	74.6 ± 1.47	8.69	BC ₂	16.01 ± 0.37	0.55	74.18 ± 1.12	5.02
Cross Os36-16 × Va99					Cross B84 × Os163-9				
P ₁	6.23 ± 0.26	0.27	70.10 ± 1.03	4.28	P ₁	6.91 ± 0.15	0.1	68.18 ± 1.02	4.2
P ₂	5.7 ± 0.81	2.64	70.31 ± 1.35	7.33	P ₂	4.99 ± 0.37	0.54	73.16 ± 1.16	5.37
F ₁	14.04 ± 0.74	2.2	72.95 ± 1.10	4.88	F ₁	12.98 ± 0.95	3.62	71.93 ± 1.28	6.53
F ₂	9.77 ± 0.17	0.12	71.39 ± 1.31	6.84	F ₂	9.02 ± 0.2	0.17	69.83 ± 1.05	4.4
BC ₁	12.55 ± 0.32	0.42	70.98 ± 1.05	4.38	BC ₁	12.96 ± 0.45	0.82	68.01 ± 1.66	11.1
BC ₂	15.04 ± 0.33	0.44	71.70 ± 1.19	5.62	BC ₂	16.53 ± 0.43	0.73	72.3 ± 1.07	4.54
Cross Os36-16 × Os3-48					Cross Os86-39 × Os163-9				
P ₁	6.23 ± 0.26	0.27	70.1 ± 1.03	4.28	P ₁	6.91 ± 0.15	0.1	68.18 ± 1.02	4.20
P ₂	5.75 ± 0.46	0.86	71.39 ± 1.11	4.89	P ₂	4.34 ± 1.25	6.24	69.96 ± 1.11	4.94
F ₁	13.08 ± 0.71	2.01	71.67 ± 1.36	7.39	F ₁	13.86 ± 0.98	3.83	70.38 ± 1.27	6.40
F ₂	8.43 ± 0.24	0.23	69.38 ± 1.33	7.05	F ₂	10.56 ± 0.21	0.17	69.14 ± 1.06	4.49
BC ₁	12.58 ± 0.21	0.18	70.23 ± 1.22	6.00	BC ₁	18.06 ± 0.88	3.07	71.97 ± 1.50	9.01
BC ₂	12.82 ± 0.58	1.34	71.21 ± 1.05	4.42	BC ₂	15.94 ± 0.3	0.36	70.28 ± 1.09	4.71
Cross Os645Kr × Os3-48					Cross Os6-2 × Os3-48				
P ₁	5.59 ± 0.99	3.91	71.43 ± 1.21	5.84	P ₁	4.99 ± 0.37	0.54	73.16 ± 1.16	5.37
P ₂	5.75 ± 0.46	0.86	71.39 ± 1.11	4.89	P ₂	5.75 ± 0.46	0.86	71.39 ± 1.11	4.89
F ₁	13.96 ± 0.93	3.43	70.22 ± 2.4	23.12	F ₁	15.01 ± 0.11	0.05	73.95 ± 1.18	5.54
F ₂	9.39 ± 0.26	0.28	73.57 ± 1.08	4.67	F ₂	8.93 ± 0.14	0.07	72.44 ± 1.39	7.76
BC ₁	13.44 ± 0.52	1.07	73.33 ± 1.08	4.66	BC ₁	13.97 ± 0.38	0.57	74.19 ± 1.12	5.02
BC ₂	13.42 ± 0.28	0.32	72.1 ± 1.14	5.23	BC ₂	14.08 ± 0.54	1.17	70.77 ± 1.12	5.03
Cross B84 × Os6-2					¹ P ₁ , P ₂ = parental inbred lines;				
P ₁	6.83 ± 0.55	1.21	73.43 ± 1.12	4.99	F ₁ , F ₂ = first and second filial generations;				
P ₂	4.99 ± 0.37	0.54	73.16 ± 1.16	5.37	BC ₁ , BC ₂ = first and second backcrosses.				
F ₁	18.55 ± 1.17	5.44	73.46 ± 1.1	4.86	² SE = standard error.				
F ₂	11.21 ± 0.4	0.63	74.1 ± 1.09	4.73					
BC ₁	17.19 ± 0.4	0.66	72.43 ± 1.07	4.6					
BC ₂	15.27 ± 0.43	0.78	73.84 ± 1.08	4.69					

Table 2. Results of generation mean analysis for grain yield.

Genotype	Genetic effects						Test of a/d model
	m	d	h	i	j	l	
Os36-16×Os6-2	4.37	0.7	8.15	0.32	-2.72	0.22	+
Os36-16×Va99	3.46	0.4	11.5	1.54	-3.29	-2.21	+
Os36-16×Os3-48	2.36	0.35	11.5	1.54	-3.29	-2.21	+
Os645Kr×Os3-48	0.43	0.06	17.59	4.32	0.96	-5.34	+
B84×Os6-2	5.42	0.73	7.22	-0.7	0.37	3.35	+
B84×Os163-9	-0.89	1.19	20.46	5.14	-4.68	-4.80	-
Os86-39×Os6-2	-1.94	0.75	23.8	6.68	-6.18	-9.96	-
Os86-39×Os163-9	-3.31	1.22	32.46	7.58	2.91	-17.13	-
Os6-2×Os3-48	-0.92	-0.35	21.26	5.26	1.48	-7.01	+

+ a/d model adequate at probability level $P < 0.05$;

- a/d model not adequate at probability level $P < 0.05$.

m = midparent value.

d = pooled additive effects.

h = pooled dominance effects.

i = pooled interactions between additive effects.

j = pooled interactions between additive and dominance effects.

l = pooled interactions between dominance effects.

dominance model adequately explained the variation between generations only in 3 out of 9 crosses, while a digenic epistatic model was applicable to 6 crosses (Table 3). Dominance type of gene action was important in 8 out of 9 crosses for starch content, suggesting a similar pattern of gene action for grain yield, while additive×additive epistatic effect was the strongest in only 1 case.

Discussion

The results presented demonstrate that an additive-dominance model could not fully explain the inheritance of the investigated traits for some crosses. Presence of non-allelic interactions (epistasis) suggests that a digenic epistatic model of inheritance could be adequate in such cases. These results also indicate an important role of digenic non-allelic interactions (epistasis), and therefore point out more complex mechanisms of genetic control for those traits.

The results obtained in this investigation are partially in accordance with Hallauer and Miranda (1988), who

emphasised that dominance effects for the traits showing strong expression of heterosis phenomenon are often more important than additive ones. High estimates of dominance effects compared to the additives are due to heterozygosity of those genes for which the parents are differing (Kearsey and Pooni, 1996). However, sometimes additive genetic effects are being underestimated because of the lack of knowledge about parental differences regarding the investigated traits (Wilson et al., 2000). The same authors emphasised that, for reliable estimates of genetic effects using generation mean analysis, genes of like effects must be completely associated in the parents. Therefore, selection of contrasting parents of the trait being measured is crucial for this type of investigation. Any dispersal of like genes among 2 parents may cause cancelling because of some effects, resulting in the underestimation of additive (d), additive×additive (i), and additive×dominance (j) effects. Since this study was performed without prior knowledge of differences among the inbreds for the traits investigated, some estimates of additivity could be underestimated. Dominance effects (h) are not influenced

Table 3. Results of generation mean analysis for grain starch content.

Genotype	Genetic effects						Test of a/d model
	m	d	h	i	j	l	
Os36-16×Os6-2	254.69	19.22	-17.96	-50.6	-46.54	36.63	-
Os36-16×Va99	194.86	9.72	91.73	-0.27	-48.01	-22.92	-
Os36-16×Os3-48	199.92	3.25	61.74	-11.8	-23.8	2.53	+
Os645Kr×Os3-48	128.81	6.28	270.52	68.85	46.49	-125.47	-
B84×Os6-2	211.69	11.47	113.48	0.15	19.81	-27.74	+
B84×Os163-9	184.7	4.13	227.46	19.8	-42.05	-88.73	-
Os86-39×Os6-2	138.01	30	215.68	55.31	-143.21	-109.37	-
Os86-39×Os163-9	20.47	22.66	563.92	165.5	-85.21	-306.51	-
Os6-2×Os3-48	162.14	15.97	177.94	45.2	-7.44	-79.96	+

+ a/d model adequate at probability level $P < 0.05$;

- a/d model not adequate at probability level $P < 0.05$.

by the distribution of the alleles in the parents, and estimates should be accurate (Mather and Jinks, 1982). From the breeders' point of view, having dominance as the major type of gene action for the most important traits suggests that selection for these traits would be quite difficult and a long-term process. The obtained results also indicate that there is no clear-cut relationship among estimated genetic effects. This relationship can be disturbed either by inappropriate (insufficient) sample size and/or structure or by higher order and complex gene interactions. The latter situation could make a breeding programme less optimistic and, therefore, a new

breeding strategy might be needed. Regarding epistatic effects, from a breeder's point of view, additive×additive effects are more favourable than other interaction effects due to a greater chance of breeding success (Novoselovic et al., 2004).

The results demonstrate that the adequacy of either additive-dominance or digenic epistatic model of inheritance was depending upon particular cross and trait, mainly because of presence of non-allelic interactions (epistasis). The preponderant type of gene action was dominance for yield and starch content for all crosses investigated.

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