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INHERITANCE OF INORGANIC AND PHYTIC PHOSPHORUS IN MAIZE (*Zea mays* L.) KERNEL

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A set of fifteen elite inbred lines of maize (used as mothers) and three tester inbred lines (used as fathers) were investigated using line x tester statistical model, including both hybrids and inbreds. Four traits were measured: grain yield, 1000 kernel weight, phytic phosphorus (P_{phy}) and inorganic phosphorus (P_i) in the kernel. P_{phy} content among hybrids ranged from 2.342 to 4.812 g kg^{-1} and P_i content from 0.562 to 2.340 g kg^{-1}, while among inbreds (lines and testers) they ranged from 2.503 to 4.180 g kg^{-1} and from 0.587 to 1.629 g kg^{-1}, respectively. Correlations between the four traits allow breeding for high P_i and low P_{phy}, as well as for both high P_i and phytate, without compromising grain yield. Correlation for hybrids between P_{phy} and P_i was 0.185 ($p<0.05$) and for inbreds 0.142 (non-significant). General combining ability / special combining ability (GCA/SCA) values for all the traits were below 1 (very low) indicated non-additive inheritance. In the investigated set of genotypes, multiple selection indices should be used for simultaneous improvement of grain yield and phosphorus profile of maize grain.

Key words: line x tester analysis, phytate, inorganic phosphorus, phytic phosphorus

INTRODUCTION

Although maize endosperm and aleurone contain a portion of mineral maters, embryo is the richest kernel part with these compounds. It contains 78% of the total minerals of the kernel, probably required for the early growth and development of the embryo. The most pronounced compound is phosphorus (P). About 72% of P is bound in the form of phytate (a mixed cation

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salt of *myo*-inositol hexakis phosphate acid) that can contribute from one to several percentage of dry kernel weight. Ninety percent of phytate is located in the embryo (MIKUŠ, 1995).

The largest fraction of all P taken up by crops from soil is ultimately translocated to the kernel and incorporated into phytic acid (InsP_6). Phosphorus bound in phytate is non-available to the monogastric animals and humans. Once consumed, phytic acid chelate certain minerals, such as K^+, Mg^+, Ca^+, Zn^+, Ba^{2+}, and Fe^{3+} (LOTT *et al*., 2000), that can lead to mineral deficiency in humans and monogastric animals (BROWN and SOLOMONS, 1991; RABOY, 2002). The bioavailability of P from maize-based staple food and feed is only 15%, and it results in demands for P supplementation (CROMWELL and COFFEY, 1991) that further elevates the costs of animal feed. Moreover, the excretion of phytate can contribute to environmental pollution and a great public health problem (namely iron and zinc deficiency) in the developing world, where maize is the staple food. On the other hand, dietary InsP_6 can have positive health effects acting as an anti-cancer and anti-oxidant agent (GRAF *et al*., 1987). Phytic acid and its derivatives are also implicated in RNA export, DNA repair, signalling, endocytosis and cell vesicular trafficking (BOHN *et al*., 2008).

There are three possible approaches to improve mineral nutrition value of crops. They include elevating the concentration of minerals in cereal endosperm, elevating the levels of substances that enhance the mineral use and decreasing the content of anti-nutrients, like InsP_6.

In maize, as in many other crops, *low phytic acid* (*lpa*) mutants were found (RABOY *et al*., 2001). These mutants have up to 66% decrease in phytate P and a molar equivalent increase in P_i (5- to 10-fold). P availability is much improved in *lpa* maize compared to wild-type maize, as shown by animal feeding trials. Moreover, nutritional studies with humans showed increased iron and zinc retention from test meals with *lpa1-1* maize, compared to the wild-type (ADAMS *et al*., 2000; MENDOZA *et al*., 1998). However, *lpa* mutants show significant reductions in grain yield (ERTL *et al*., 1998). PILU *et al*. (2005) concluded that breeding *lpa* maize cultivars equal in grain yield to their wild-type counterparts is not possible.

Many studies have been performed on P_i and phytate in different maize genotypes and the results were evaluated for breeding purposes. LORENZ *et al*. (2007) indicated that selection for both reduced phytate and increased P_i is more than possible and suggested that the best method of breeding is multiple trait selection based on selection indexes. Selection differentials of multiple trait indices for simultaneous improvement of P profile, grain yield and grain moisture were proposed in LORENZ *et al*. (2008), but with such approach many cycles of recurrent selection would be needed. They found low phenotypic and genotypic correlations between P_i and phytate, indicating that they are largely genetically independent, and can be improved by recurrent selection simultaneously.

The objective of the investigation presented in this paper was to get insight into the genetics and establish the mode of inheritance of P_i and P_{phy} in the kernel of elite maize inbred lines. For this purpose line x tester analysis (SING and CHOUDHARY, 1976), the less used model in maize, was applied on a set of 15 elite inbred lines and their crosses with 3 inbred testers.

MATERIALS AND METHODS

A set of fifteen elite inbred lines (used as mothers) were tested with three elite Lancaster inbreds (used as fathers). Mother's lines represented three different genetic backgrounds, with good combining ability with Lancaster. They were designated as: 1) A1-A5, 2) B1-B5, and 3) C1-C5. Fathers were designated as Z1-Z3. Crosses were performed in 2009 and trials in 2010,

according to the randomized complete block (RCB) design with two replications, including parents and crosses, at three locations.

First two loactions are situated within the research fields of Maize Research Institute in Zemun Polje and Skolsko dobro at 44º51'58"N, 20º20'25"E (Location I) and 44º50'52"N, 20º17'15"E (Location II), respectively. Third location is situated near the city of Srbobran, 100 km north of Maize Research Institute at 45º33'07"N, 19º43'54"E (Location III). Irrigation (30 mm) was done at all locations around 7-10 days prior to flowering.

The soil at Location I and Location II is slightly calcareous chernozem with 47 % clay and silt and 53 % sand, while at Location III soil is calcareous chernozem with 52 % clay and silt and 47 % sand. The 0 – 30-cm layer contained 0.21 % total N, 1.9 % organic C, and 14 and 31 mg per 100 g soil of available P and extractable K, respectively, 9.7 % total $CaCO_3$ and pH 7.8 for Location I and 0.25 % total N, 1.7 % organic C, and 18 and 40 mg per 100 g soil of available P and extractable K, respectively, 9.5 % total $CaCO_3$ and pH 7.5 for Location II. Also, at Location III, 0 – 30-cm layer contained 0.212 % total N, 1.65 % organic C, and 26 and 18 mg per 100 g soil of available P and extractable K, respectively, 11.3 % total $CaCO_3$ and pH 7.5. Fertilisation was carried out with 150 kg ha^{-1} Monoammonium phosphate (MAP) at all Locations, as well as 300 kg ha^{-1} of UREA at Locations I and II and 250 kg ha^{-1} at Location III, accordingly to previous soil analysis.

Grain yield (tha^{-1}, adjusted to 14% moisture), 1000 kernel weight (test weight, in g adjusted to 14% moisture), contents of P_{phy} (g kg^{-1}) and P_i (g kg^{-1}) in the grain were measured. Since significant difference for P_{phy} and P_i in different replications in the field usually does not exists (V. Dragicevic, personal communication), seeds from two replications per each location were pooled to form a single sample for chemical analysis.

Estimation of P_{phy} and P_i in maize kernel was done by the method of DRAGICEVIC *et al*. (2011).

Statistical analysis was done according to SINGH and CHOUDHARY (1976) for line x tester model. This analysis provides estimation of general and specific combining abilities of parents included, and different types of gene effects. Firstly, the analysis of variance (ANOVA) of the RCB design is performed in order to test the significance of differences among genotypes. If these differences are found, line x tester analysis is done. In the type of analysis performed in this paper, where parents were included, total genotypic variance was partitioned to variance of parents, parents vs. crosses, crosses, lines, testers and lines x testers. Means of squares (MS) of lines and testers were tested against MS of lines x testers. The former and also MS of parents, parents vs. crosses and crosses were tested against MS of error.

General combining ability (GCA) effects were calculated as:

a) for lines:

$$g_i = \frac{x_{i..}}{tr} - \frac{x_{...}}{ltr}$$

where g_i is GCA of the line i; $x_{i..}$ is total of values for that line; $x_{...}$ is the grand total; l is the number of lines; t is the number of testers; r is the number of replications. For the check, it should be:

$$\sum g_i = 0$$

b) for testers:

$$g_j = \frac{x_{.j.}}{lr} - \frac{x_{...}}{ltr}$$

where $x_{.j.}$ is total of values for tester *j*. For the check it should also be:

$$\sum g_j = 0$$

Estimation of specific combining ability (SCA) effects was performed as:

$$s_{ij} = \frac{x_{ij.}}{r} - \frac{x_{i..}}{tr} - \frac{x_{.j.}}{lr} - \frac{x_{...}}{ltr}$$

where $x_{ij.}$ is total of the values for the combination of *i* line and *j* tester. For the check it should be:

$$\sum_i s_{ij} = \sum_j s_{ij} = \sum_i \sum_j s_{ij} = 0$$

Genetic components were calculated as:

$$CovHS(line) = \frac{MS_l - MS_{lxt}}{rxt}$$

$$CovHS(tester) = \frac{MS_t - MS_{lxt}}{rxl}$$

$$CovHS(average) = \frac{1}{r(2lt - l - t)}\left[\frac{(l-1)(MS_l) + (t-1)(MS_t)}{1 + t - 2}\right] - MS_{lxt}$$

$$CovFS = \frac{(MS_l - MS_e) + (MS_t - MS_e) + (MS_{lxt} - MS_e)}{3xr} + \frac{6rCovHS - r(1+t)CovHS}{3r}$$

$$\sigma^2_{gca} = CovHS = \left[\frac{1+F}{4}\right]^2 \sigma^2_a$$

$$\sigma^2_{sca} = \frac{MS_{lxt} - MS_e}{r} \text{ i.e. } \sigma^2_{sca} = \left[\frac{1+F}{2}\right]^2 \sigma^2_d$$

F = 1 (coefficient of inbriding, equals 1 for inbred lines). Formulas are used according to SINGH and CHOUDHARY (1976).

Pearson's correlations were calculated for the four measured traits, as well as between values for the traits at three different locations of investigation.

RESULTS

ANOVA of line x tester model did not reveal any significant differences between replications for any trait at any of the three locations (data not shown). On the other hand, highly significant differences were found for treatments and crosses in all cases. The significances of

differences between measured traits for the three locations are shown in Table 1. There is a highly significant difference ($P \leq 0.001$) between all three locations for P_{phy} and P_i. However, differences between locations I and II, i.e. locations I and III were not significant for grain yield and 1000 kernel weight, respectively. Significant and highly significant differences were found between almost all lines and testers for P_{phy} except for B2 and B4 at location II, Z2 and Z3 at location III as well as for C3 at location II for P_i (Table 2).

Table 1. Significance of differences between average values of four traits in three locations of investigation

Phytin	Loc.II	Loc.III	Pi	Loc.II	Loc.III	Grain yield	Loc.II	Loc.III	Test weight	Loc.II	Loc.III
Loc.I	***	***	Loc.I	***	***	Loc.I	ns	***	Loc.I	***	ns
Loc.II		***	Loc.II		***	Loc.II		***	Loc.II		***

*** - statistically significant at 0.001 level; ns – statistically non-significant

Table 2a. GCA values for lines and testers, for four investigated traits in three locations

	Phytin			P_i		
Lines	Loc.I	Loc.II	Loc.III	Loc.I	Loc.II	Loc.III
A1	-0.25**	-0.29**	0.14**	-0.07**	-0.02**	-0.09**
A2	-0.08**	-0.35**	-0.05*	-0.09**	0.01**	-0.04**
A3	-0.37**	-0.16**	-0.28**	-0.15**	-0.05**	-0.12**
A4	-0.25**	-0.44**	-0.18**	0.01*	-0.04**	-0.03**
A5	-0.08**	-0.40**	-0.18**	-0.05**	-0.01**	-0.05**
B1	-0.17**	-0.09**	-0.26**	-0.25**	-0.02**	-0.23**
B2	-0.55**	-0.02ns	-0.12**	-0.18**	-0.02**	-0.17**
B3	-0.19**	-0.15**	-0.17**	-0.09**	-0.09**	-0.15**
B4	-0.41**	0.02ns	0.04*	-0.23**	0.02**	-0.15**
B5	-0.40**	0.37**	-0.12**	-0.15**	0.02**	-0.12**
C1	0.17**	0.46**	0.13**	0.23**	0.06**	0.22**
C2	0.39**	0.05*	0.35**	-0.04**	-0.09**	0.10**
C3	0.61**	0.30**	0.30**	0.35**	0.00 ns	0.22**
C4	0.87**	0.36**	0.20**	0.35**	0.09**	0.26**
C5	0.73**	0.37**	0.21**	0.35**	0.14**	0.34**
Z1	-0.16**	-0.06**	-0.02*	-0.03**	-0.04**	-0.06**
Z2	0.11**	0.03**	0.00ns	0.06**	0.06**	0.07**
Z3	0.04**	0.04**	0.01ns	-0.03**	-0.02**	-0.01**
LSD lin 0.05	0.032	0.039	0.036	0.010	0.008	0.0088
LSD lin 0.01	0.042	0.051	0.047	0.013	0.010	0.0052
LSD test 0.05	0.014	0.017	0.016	0.005	0.003	0.0039
LSD test 0.01	0.019	0.023	0.021	0.006	0.004	0.0052

*,** - statistically significant at 0.05 and 0.01 level, ns – statistically non-significant

Table 2b. GCA values for lines and testers, for four investigated traits in three locations

	Grain yield			1000 kernel weight		
Lines	Loc.I	Loc.II	Loc.III	Loc.I	Loc.II	Loc.III
A1	1.16**	0.63ns	0.79*	33.30*	34.35*	31.20**
A2	1.41**	0.53ns	-1.47**	30.98*	30.17*	18.82ns
A3	1.30**	0.88*	0.82*	18.57ns	18.68ns	19.96ns
A4	1.38**	0.88*	1.63**	23.56ns	23.15ns	23.42*
A5	0.41ns	0.38ns	0.57ns	22.64ns	21.24ns	14.28ns
B1	0.54ns	-0.37ns	-0.07ns	5.60ns	5.84ns	10.96ns
B2	-0.61ns	0.40ns	-1.27**	23.87ns	22.88ns	35.23**
B3	-0.35ns	-0.21ns	-0.89*	-5.04ns	-4.13ns	-1.49ns
B4	-0.38ns	0.04ns	0.00ns	9.86ns	9.24ns	13.31ns
B5	-0.36ns	-0.47ns	-0.82*	5.05ns	4.32ns	11.99ns
C1	-1.01*	-3.10**	-0.93*	-46.31**	-44.42**	-51.41**
C2	-0.31ns	0.38ns	0.57ns	-29.06ns	-29.21*	-34.07**
C3	-0.45ns	1.01*	1.09**	1.65ns	0.54ns	0.47ns
C4	-1.60**	-0.48ns	-0.06ns	-48.43**	-46.39**	-49.40**
C5	-1.13**	-0.51ns	0.04ns	-46.24**	-46.25**	-43.26**
Z1	-0.86**	-0.09ns	-0.59**	10.14	9.91	9.10
Z2	1.25**	0.59**	0.36*	-9.34	-8.15	-5.86
Z3	-0.39*	-0.49*	0.22ns	-0.80	-1.76	-3.24
LSD lin 0.05	0.767	0.857	0.741	30.466	27.004	23.307
LSD lin 0.01	1.019	1.139	0.985	40.495	35.892	30.978
LSD test 0.05	0.343	0.383	0.331	13.625	12.076	10.423
LSD test 0.01	0.456	0.510	0.441	18.110	16.052	13.854

*,** - statistically significant at 0.05 and 0.01 level, ns – statistically non-significant

Table 3a. Components of genetic variance for measured traits

Trait	Grain phytin			Grain Pi		
Loc.	I	II	III	I	II	III
Va(F=1)*	0.0092	0.0038	0.0019	0.0020	0.0010	0.0019
GCA variance	0.0046	0.0019	0.0010	0.0010	0.0005	0.0009
Vd(F=1)**	0.2291	0.1170	0.0425	0.0517	0.0503	0.0268
SCA variance	0.2291	0.1170	0.0425	0.0517	0.0503	0.0268
GCA/SCA	0.0201	0.0162	0.0226	0.0193	0.0099	0.0346

*Va – additive variance, **Vd – non-additive variance

Table 3b. Components of genetic variance for measured traits

Trait	Grain yield			1000 grain weight		
Loc.	I	II	III	I	II	III
Va(F=1)*	0.1139	0.0543	0.0559	21.7620	17.7504	3.8134
GCA variance	0.0569	0.0272	0.0280	10.8810	8.8752	1.9067
Vd(F=1)**	0.2462	0.7164	0.2941	893.1438	1074.9825	1876.5294
SCA variance	0.2462	0.7164	0.2941	893.1438	1074.9825	1876.5294
GCA/SCA	0.2310	0.0380	0.0950	0.0122	0.0083	0.0010

*Va – additive variance, **Vd – non-additive variance

The values for P_{phy} among hybrids ranged from 2.34 g kg^{-1} (C2xZ1 at I location) to 4.81 g kg^{-1} (C1xZ2 at II location). Average values varied from 3.18 (I location) to 3.62 (II location), with overall mean of 3.40 g kg^{-1} for hybrids (Table 10). Minimum value for inbreds (lines and testers) were 2.50 g kg^{-1} (C1 at I location), and maximum 4.18 g kg^{-1} (C5 at I location). Average values ranged from 3.22 g kg^{-1} (I location) to 3.59 g kg^{-1} (II location), with the overall mean value for inbreds of 3.428 g kg^{-1} (Table 9).

As far as P_i is concerned, minimum value for hybrids was 0.56 g kg^{-1} (B1xZ2 at III location) and maximum 2.34 (C5xZ1 at I location). Average values varied from 0.91 g kg^{-1} (III location) to 1.40 g kg^{-1} (I location), with the total average of 1.1 g kg^{-1} (Table 11). Inbreds exhibited P_i values from 0.58 (B1 at III location) to 1.62 g kg^{-1} (Z1 at I location), with average values from 0.94 (III location) to 1.29 g kg^{-1} (I location), and the mean value over locations of 1.09 g kg^{-1} (Table 9).

Hybrid yield varied from 6.88 t ha^{-1} to 14.47 t ha^{-1} (hybrids C1xZ1 and A2xZ2 at II location, respectively). Average yield for hybrids over all locations was 11.41 t ha^{-1} (Table 12). Minimum yield for inbreds of 2.28 t ha^{-1} was obtained for Z2 line at III location. Maximum inbred yield (7.49 t ha^{-1}) was obtained at I location for line B1 and average inbred yield over locations was 4.97 t ha^{-1} (Table 9).

A thousand kernel weight for hybrids ranged from 246.7 g (C3xZ3 at III location) to 465.3 g (B2xZ3 at II location). Average value was 339.2 g (Table 13). Considering inbreds, 1000 kernel weight ranged from 205.9 g (Z1 at locations II and III) to 402.5 g (A3 at II location), with the overall mean of 325.0 g (Table 9).

Considering all the traits, negative values of GCA and SCA for P_{phy} and positive values for other traits are preferred for low phytate breeding. GCA values for lines and testers are presented in Table 2. The most promising line was A4, followed by A1, while the most promising tester was Z2. On the other hand, line C3, followed by C2, is the most appropriate for increasing the level of phytate, as the favorable anti-oxidant and anti-cancer agent (NORAZALINA *et al*., 2010; URBANO *et al*., 2000). Tester Z2 is again the best choice among the testers.

Table 4. SCA values for phytin, for combinations of lines and testers in three locations of investigation

Tester	Z1	Z1	Z1	Z2	Z2	Z2	Z3	Z3	Z3
Line/Loc.	I	II	III	I	II	III	I	II	III
A1	0.07*	-0.16**	-0.13**	-0.21**	0.04ns	0.21**	0.14**	0.11**	-0.08*
A2	-0.33**	0.31**	0.12**	0.12**	-0.32**	-0.11**	0.21**	0.01ns	-0.01ns
A3	-0.11*	0.47**	-0.04ns	0.00ns	-0.24**	0.11**	0.12**	-0.23**	-0.08*
A4	0.31**	-0.24**	0.21**	-0.45**	-0.14**	-0.14**	0.14**	0.38**	-0.07*
A5	0.02ns	0.59**	0.00ns	-0.20**	-0.48**	0.00ns	0.17**	-0.11**	0.00ns
B1	0.58**	-0.19**	0.13**	-0.17**	-0.08*	-0.23**	-0.41**	0.27**	0.10**
B2	0.45**	-0.24**	-0.07*	-0.27**	-0.21**	-0.26**	-0.18**	0.45**	0.33**
B3	0.45**	-0.06ns	-0.04ns	-0.13**	0.09**	-0.03ns	-0.31**	-0.03ns	0.07*
B4	0.31**	0.02ns	0.00ns	0.00ns	-0.19**	0.04ns	-0.30**	0.17**	-0.04ns
B5	0.18**	0.11**	-0.32**	0.11**	0.27**	-0.03ns	-0.30**	-0.38**	0.35**
C1	-0.70**	-0.62**	0.00ns	0.64**	0.70**	0.08*	0.06*	-0.08*	0.08*
C2	-1.08**	-0.08*	-0.26**	0.35**	0.04ns	0.04ns	0.73**	0.03ns	0.22**
C3	-0.81**	-0.06ns	0.11**	0.62**	0.34**	-0.02ns	0.19**	-0.28**	-0.09**
C4	0.54**	-0.02ns	0.22**	-0.18**	0.16**	0.26**	-0.36**	-0.14**	-0.48**
C5	0.13**	0.17**	0.08*	-0.23**	0.01ns	0.08*	0.10**	-0.18**	-0.16**
LSD 0.05	0.055	0.067	0.062	0.055	0.067	0.062	0.055	0.067	0.062
LSD 0.01	0.074	0.089	0.082	0.074	0.089	0.082	0.074	0.089	0.082

*,** - statistically significant at 0.05 and 0.01 level, ns – statistically

The relation of GCA/SCA for investigated traits, indicating their mode of inheritance, is given in Table 3. SCA variance is several times larger than GCA variance for all the four traits, indicating strong non-additive inheritance.

SCA values for the four traits are shown in Tables 4-7. Considering all data, the most favorable two combinations are B4xZ2 (negative highly significant SCA for P_{phy} at one and non-significant SCA at the other two locations; positive highly significant SCA for Pi at two and non-significant at one location; non-significant SCA for yield and significant SCA for test weight at one location), and C4xZ3 (highly significant negative SCA for P_{phy} at all three locations; positive highly significant SCA for P_i at all locations and non-significant SCA`s at all locations for grain yield and test weight).

Table 5. SCA values for P_i, for combinations of lines and testers in three locations of investigation

Tester	Z1	Z1	Z1	Z2	Z2	Z2	Z3	Z3	Z3
Line/Loc.	I	II	III	I	II	III	I	II	III
A1	-0.05**	-0.03**	0.02*	-0.19**	-0.03**	-0.09**	0.24**	0.06**	0.07**
A2	0.12**	0.25**	0.06**	-0.19**	-0.08**	-0.16**	0.08**	-0.17**	0.10**
A3	-0.04**	0.01ns	0.07**	0.15**	0.06**	-0.06**	-0.11**	-0.08**	-0.01ns
A4	0.18**	0.21**	0.03**	-0.18**	-0.38**	-0.06**	0.00ns	0.16**	0.03**
A5	0.09**	0.20**	0.12**	0.01ns	-0.03**	0.07**	-0.10**	-0.17**	-0.19**
B1	0.01ns	-0.17**	-0.04**	-0.15**	-0.16**	-0.19**	0.14**	0.33**	0.23**
B2	-0.06**	0.05**	-0.02*	-0.09**	-0.04**	-0.10**	0.15**	-0.01ns	0.13**
B3	-0.27**	-0.02**	-0.07**	0.08**	0.23**	-0.07**	0.19**	-0.21**	0.14**
B4	-0.06**	-0.07**	-0.12**	0.17**	0.00ns	0.05**	-0.11**	0.07**	0.08**
B5	-0.17**	-0.14**	-0.13**	0.29**	0.29**	0.19**	-0.12**	-0.15**	-0.06**
C1	-0.11**	-0.26**	0.01ns	0.15**	0.22**	0.21**	-0.04**	0.03**	-0.22**
C2	-0.08**	0.16**	0.02*	0.06**	0.00ns	0.02*	0.01ns	-0.16**	-0.03**
C3	-0.01ns	-0.11**	-0.18**	0.24**	0.30**	0.39**	-0.23**	-0.20**	-0.21**
C4	-0.19**	-0.22**	0.04**	0.08**	-0.15**	-0.09**	0.11**	0.37**	0.05**
C5	0.63**	0.14**	0.21**	-0.40**	-0.25**	-0.09**	-0.22**	0.12**	-0.11**
LSD 0.05	0.017	0.013	0.016	0.017	0.013	0.016	0.017	0.013	0.016
LSD 0.01	0.023	0.017	0.021	0.023	0.017	0.021	0.023	0.017	0.021

*,** - statistically significant at 0.05 and 0.01 level, ns – statistically non-significant

Table 6. SCA values for grain yield, for combinations of lines and testers in three locations of investigation

Tester	Z1	Z1	Z1	Z2	Z2	Z2	Z3	Z3	Z3
Line/Loc.	I	II	III	I	II	III	I	II	III
A1	0.51	0.19	-1.30*	0.70	0.51	0.57	-1.20	-0.70	0.73
A2	0.16	-0.29	-0.57	-0.26	1.50*	1.54*	0.11	-1.21	-0.98
A3	1.43*	0.34	-0.78	-1.42**	-1.08	0.65	0.00	0.74	0.13
A4	-0.71	0.90	0.55	0.46	-0.07	-0.19	0.25	-0.82	-0.37
A5	1.78**	-0.01	0.12	-1.32	-0.44	0.35	-0.47	0.44	-0.47
B1	0.91	0.20	0.53	-0.64	1.07	-0.04	-0.27	-1.26	-0.48
B2	0.07	-0.31	-0.09	-0.62	-0.56	0.29	0.56	0.88	-0.21
B3	-0.60	0.34	0.72	0.65	-0.37	-1.16	-0.05	0.03	0.44
B4	-0.55	0.51	-0.48	0.67	0.01	0.76	-0.12	-0.52	-0.29
B5	-0.54	1.21	-0.92	0.21	-0.53	0.11	0.33	-0.68	0.81
C1	-0.23	-1.78**	0.22	0.33	0.23	-0.91	-0.09	1.55*	0.69
C2	-0.25	-0.26	0.69	-0.01	0.99	0.17	0.36	-0.73	-0.86
C3	-1.02	-0.70	0.16	0.54	-0.83	-0.17	0.48	1.53*	0.01
C4	-0.19	1.03	1.05	0.16	0.28	-1.50*	0.03	-1.31	0.45
C5	-0.74	-1.36	0.09	0.65	-0.71	-0.48	0.09	2.08**	0.39
LSD 0.05	1.328	1.485	1.284	1.328	1.485	1.284	1.328	1.485	1.284
LSD 0.01	1.765	1.974	1.706	1.765	1.974	1.706	1.765	1.974	1.706

*,** - statistically significant at 0.05 and 0.01 level, unmarked values are non-significant

Table 7. SCA values for test weight, for combinations of lines and testers in three locations of investigation

Tester	Z1	Z1	Z1	Z2	Z2	Z2	Z3	Z3	Z3
Line/Loc.	I	II	III	I	II	III	I	II	III
A1	-25.18	-25.57	-26.02	44.43	44.83	68.47**	-19.25	-19.27	-42.45*
A2	-8.85	-9.31	-0.77	-1.72	-2.60	-16.17	10.57	11.91	16.94
A3	35.82	35.48	27.43	-27.92	-26.61	-20.48	-7.91	-8.87	-6.94
A4	5.23	5.17	9.29	-0.72	-0.61	-4.23	-4.52	-4.56	-5.06
A5	-9.35	-10.63	-4.10	-11.41	-10.99	-15.08	20.76	21.61	19.18
B1	-59.57*	-58.62*	-76.78**	31.97	33.51	45.20*	27.60	25.11	31.58
B2	-42.57	-44.93	-63.11**	-26.76	-23.14	-22.89	69.34*	68.08**	85.99**
B3	11.31	8.61	22.13	0.36	0.48	2.63	-11.68	-9.09	-24.76
B4	-47.43	-50.10*	-38.75	36.59	37.40	44.76*	10.84	12.70	-6.00
B5	-51.35	-51.30*	-63.37**	6.59	5.76	13.59	44.76	45.54	49.78*
C1	37.03	41.84	43.96*	-7.12	-10.47	-25.33	-29.91	-31.37	-18.63
C2	47.95	47.74*	53.36*	-29.57	-30.69	-35.93	-18.38	-17.02	-17.43
C3	61.44*	61.60*	88.85**	11.77	11.18	-13.24	-73.21**	-72.78**	-75.61**
C4	35.46	38.32	18.90	-16.02	-17.92	-5.10	-19.43	-20.40	-13.81
C5	10.05	11.72	8.98	-10.48	-10.13	-16.19	0.43	-1.59	7.21
LSD 0.05	52.769	46.772	40.368	52.769	46.772	40.368	52.769	46.772	40.368
LSD 0.01	70.139	62.167	53.656	70.139	62.167	53.656	70.139	62.167	53.656

*,** - statistically significant at 0.05 and 0.01 level, unmarked values are non-significant

Correlations between the measured traits indicate the responses of correlated traits to multiple trait selection. Correlations for the four traits are given in Table 8, separately for all the genotypes, hybrids and inbreds. There is a significant positive correlation between P_{phy} and P_i for all genotypes (0.174, $p \leq 0.05$) and hybrids (0.185, $p \leq 0.05$), while for lines this correlation is non-significant (0.142). P_{phy} and P_i are non-significantly correlated with yield, for all three groups of genotypes. P_{phy} is significantly negatively correlated with test weight for hybrids, but not for inbreds, while for P_i it is *vice versa*. Yield is significantly correlated with test weight for hybrids, but not for inbreds.

Table 8. Correlations between investigated traits

All genotypes	Pi	Yield	Test w.
Phytin	0.174*	-0.068ns	-0.165*
Pi		0.040ns	-0.187**
Yield			0.200**
Hybrids	Pi	Yield	Test w.
Phytin	0.185*	-0.076ns	-0.214*
Pi		-0.054ns	-0.171ns
Yield			0.195*
Inbreds	Pi	Yield	Test w.
Phytin	0.142ns	-0.194ns	0.000ns
Pi		0.214ns	-0.284*
Yield			0.166ns

*,** - statistically significant at 0.05 and 0.01 level ns – statistically non-significant

Table 9. Values for lines and testers, for four investigated traits in three locations

	Phytin (g kg^{-1})			P_i (g kg^{-1})			Grain yield (t ha^{-1})			1000 kernel weight (g)		
Lines	Loc.I	Loc.II	Loc.III	Loc.I	Loc.II	Loc.III	Loc.I	Loc.II	Loc.III	Loc.I	Loc.II	Loc.III
A1	3.43	3.13	2.88	1.21	0.85	0.71	5.95	5.62	5.45	295.0	304.8	286.0
A2	2.95	3.82	3.44	1.13	1.10	0.74	5.17	5.94	4.90	297.1	352.2	298.5
A3	3.11	3.80	3.49	0.98	0.94	0.76	4.26	5.01	5.31	323.0	402.5	375.9
A4	2.63	2.93	3.01	1.13	0.87	0.72	6.33	6.77	5.87	298.0	299.7	295.6
A5	2.73	3.72	3.05	1.23	1.01	0.72	4.15	4.39	3.81	279.5	359.7	288.2
B1	3.65	3.24	3.17	1.17	0.86	0.58	7.49	6.18	3.83	330.6	387.3	380.1
B2	2.62	3.64	3.47	1.26	0.99	0.96	6.43	5.95	4.27	351.4	383.0	384.7
B3	2.67	3.83	3.31	1.50	1.12	0.95	6.06	6.61	2.78	335.9	320.1	298.8
B4	2.90	3.47	3.35	1.42	1.25	1.14	6.06	6.75	3.85	347.1	337.7	331.6
B5	2.83	4.13	3.56	1.02	0.87	0.98	5.08	3.84	3.66	374.6	392.5	365.9
C1	2.50	3.31	3.56	1.17	0.89	0.92	5.26	5.16	3.64	337.4	316.0	328.8
C2	3.24	3.58	3.60	1.24	0.82	0.98	5.95	5.34	2.82	353.3	354.5	358.9
C3	3.56	3.38	4.15	1.41	1.13	1.07	6.45	4.67	2.72	300.1	305.5	273.8
C4	4.10	3.80	3.61	1.28	1.23	1.13	6.67	4.81	4.08	367.0	378.8	360.8
C5	4.18	3.55	3.43	1.51	1.19	0.99	5.67	3.62	3.77	340.3	292.8	319.8
Z1	3.98	3.96	3.96	1.62	1.29	1.29	5.24	5.51	2.52	234.3	205.9	205.9
Z2	3.41	3.35	3.43	1.46	1.34	1.30	7.36	3.83	2.28	287.8	285.9	283.1
Z3	3.54	3.92	3.84	1.40	0.98	1.03	5.22	5.70	2.46	349.1	342.5	289.9
Mean per loc	3.22	3.59	3.46	1.29	1.04	0.94	5.82	5.32	3.78	322.3	334.5	318.1
Overall mean	3.42			1.09		4.97			325.0			
LSD lin 0.05	0.12	0.14	0.10	0.02	0.02	0.02	0.92	1.16	1.26	47.86	51.41	44.09
LSD test 0.05	0.10	0.40	0.19	0.04	0.04	0.04	2.29	4.93	1.37	93.75	91.18	84.63

Table 10. Values for phytin, for combinations of lines and testers in three locations of investigation (g kg^{-1})

Tester	Z1	Z2	Z3	Z1	Z2	Z3	Z1	Z2	Z3
Line/Loc.	I	I	I	II	II	II	III	III	III
A1	2.85	2.83	3.11	3.11	3.40	3.48	3.39	3.75	3.47
A2	2.61	3.34	3.36	3.52	2.98	3.32	3.45	3.25	3.35
A3	2.54	2.92	2.97	3.87	3.26	3.27	3.07	3.24	3.06
A4	3.08	2.59	3.12	2.87	3.07	3.59	3.41	3.08	3.17
A5	2.97	3.02	3.31	3.75	2.77	3.15	3.20	3.22	3.24
B1	3.44	2.96	2.64	3.28	3.47	3.83	3.26	2.92	3.26
B2	2.93	2.48	2.50	3.30	3.41	4.09	3.20	3.02	3.63
B3	3.28	2.97	2.72	3.34	3.59	3.48	3.18	3.21	3.32
B4	2.92	2.89	2.51	3.60	3.47	3.85	3.42	3.49	3.42
B5	2.81	3.01	2.53	4.04	4.29	3.65	2.94	3.25	3.65
C1	2.50	4.11	3.46	3.40	4.81	4.04	3.52	3.61	3.47
C2	2.34	4.04	4.35	3.53	3.75	3.74	3.47	3.79	3.98
C3	2.82	4.52	4.02	3.80	4.29	3.67	3.80	3.68	3.63
C4	4.43	3.99	3.73	3.89	4.16	3.88	3.80	3.86	3.14
C5	3.89	3.79	4.05	4.09	4.03	3.84	3.68	3.69	3.46
Mean per loc		3.18			3.62			3.40	
Overall mean					3.40				
LSD 0.05		0.09			0.09			0.08	

Table 11. Values for P_i, for combinations of lines and testers in three locations of investigation (g kg^{-1})

Tester	Z1	Z2	Z3	Z1	Z2	Z3	Z1	Z2	Z3
Line/Loc.	I	I	I	II	II	II	III	III	III
A1	1.25	1.20	1.53	0.97	1.07	1.08	0.78	0.81	0.88
A2	1.39	1.18	1.35	1.27	1.05	0.89	0.87	0.78	0.96
A3	1.17	1.46	1.11	0.98	1.13	0.92	0.79	0.79	0.77
A4	1.56	1.29	1.38	1.19	0.70	1.17	0.85	0.89	0.90
A5	1.40	1.41	1.21	1.20	1.08	0.86	0.91	1.00	0.65
B1	1.13	1.06	1.26	0.82	0.95	1.36	0.58	0.56	0.91
B2	1.13	1.19	1.34	1.04	1.06	1.01	0.66	0.71	0.86
B3	1.00	1.45	1.47	0.91	1.25	0.74	0.62	0.76	0.88
B4	1.07	1.41	1.02	0.96	1.14	1.13	0.58	0.88	0.83
B5	1.05	1.60	1.10	0.89	1.42	0.91	0.60	1.05	0.72
C1	1.48	1.83	1.55	0.82	1.40	1.13	1.08	1.41	0.91
C2	1.25	1.49	1.34	1.09	1.04	0.79	0.96	1.10	0.97
C3	1.70	2.05	1.49	0.91	1.42	0.85	0.89	1.59	0.91
C4	1.52	1.89	1.82	0.88	1.06	1.49	1.14	1.15	1.21
C5	2.34	1.41	1.49	1.29	1.01	1.30	1.39	1.23	1.13
Mean per loc		1.40			1.06			0.91	
Overall mean					1.1				
LSD 0.05		0.02			0.02			0.02	

Table 12. Values for grain yield, for combinations of lines and testers in three locations of investigation (t ha^{-1})

Tester	Z1	Z2	Z3	Z1	Z2	Z3	Z1	Z2	Z3
Line/Loc.	I	I	I	II	II	II	III	III	III
A1	12.11	14.41	10.87	12.58	13.58	11.29	9.96	12.78	12.80
A2	12.01	13.70	12.43	12.00	14.47	10.68	8.43	11.49	8.83
A3	13.17	12.43	12.21	12.98	12.24	12.98	10.51	12.89	12.23
A4	11.11	14.39	12.54	13.54	13.25	11.42	12.66	12.87	12.55
A5	12.64	11.65	10.86	12.14	12.39	12.18	11.16	12.34	11.39
B1	11.89	12.45	11.19	11.59	13.14	9.73	10.93	11.31	10.73
B2	9.90	11.32	10.86	11.85	12.28	12.64	9.12	10.45	9.81
B3	9.49	12.85	10.51	11.90	11.87	11.18	10.30	9.37	10.83
B4	9.52	12.85	10.42	12.31	12.49	10.88	10.00	12.18	11.00
B5	9.54	12.40	10.89	12.50	11.44	10.21	8.73	10.71	11.27
C1	9.20	11.87	9.81	6.88	9.57	9.81	9.77	9.59	11.04
C2	9.88	12.14	10.96	11.88	13.81	11.02	11.73	12.16	10.99
C3	8.98	12.64	10.94	12.08	12.62	13.90	11.72	12.34	12.38
C4	8.66	11.11	9.35	12.31	12.24	9.56	11.47	9.86	11.67
C5	8.57	12.08	9.87	9.89	11.22	12.93	10.61	10.98	11.72
Mean per loc		11.3			11.9			11.1	
Overall mean					11.41				
LSD 0.05		2.15			2.29			1.97	

Table 13. Values for 1000 kernel weight, for combinations of lines and testers in three locations of investigation (g)

Tester	Z1	Z2	Z3	Z1	Z2	Z3	Z1	Z2	Z3
Line/Loc.	I	I	I	II	II	II	III	III	III
A1	356.3	406.4	351.3	356.4	408.8	351.1	355.9	435.5	327.2
A2	370.3	357.9	378.8	368.5	357.2	378.1	368.8	338.4	374.2
A3	402.6	319.3	347.9	401.8	321.7	345.8	398.1	335.3	351.4
A4	376.9	351.5	356.3	376	352.1	354.6	383.5	355	356.8
A5	361.4	339.9	380.6	358.3	339.8	378.8	360.9	335	371.9
B1	294.2	366.2	370.4	294.9	368.9	366.9	284.9	391.9	381
B2	329.5	325.8	430.4	325.6	329.3	465.3	322.9	348.1	459.6
B3	354.4	324	320.5	352.1	325.9	322.8	371.4	336.9	312.2
B4	310.6	375.1	357.9	306.8	376.2	357.9	325.3	393.9	345.7
B5	301.9	340.3	387	300.7	339.7	385.8	299.4	361.4	400.2
C1	338.9	275.3	261	345.1	274.7	260.2	343.3	259.1	268.4
C2	367	270.1	289.8	366.2	269.7	289.8	370	265.8	286.9
C3	411.3	342.1	265.7	409.8	341.3	263.7	440.1	323	246.7
C4	335.2	264.2	269.4	339.6	265.3	269.2	320.3	281.3	275.2
C5	312	272	291.4	313.1	273.2	288.1	316.5	276.3	302.4
Mean per loc		338.0			338.6			341.3	
Overall mean					339.3				
LSD 0.05		8.18			43.87			18.91	

DISCUSSION

Breeding for quantitative traits in maize requires the knowledge about its mode of inheritance and the sources of favorable alleles. Improvement of phosphorus profile in maize kernel, without compromising grain yield, is a time-consuming and comprehensive task, which requires search for appropriate germplasm (WARDYN and RUSSELL, 2004; LORENZ *et al*., 2007, 2008; MLADENOVIC DRINIC *et al*., 2009). The results of the investigation presented here indicated the mode of inheritance and favorable sources of the target traits.

A consistence over locations for minimum and maximum values was observed for Pi, as maximum values were obtained at location I for both lines and hybrids, and minimum values at location III. However, there was a discrepancy of maximum values in phytate content for hybrids and inbreds, i.e. maximum value for hybrids was obtained at location II and for inbreds at location I. The maximum range of yield for hybrids was obtained at location II. All this indicates a large influence of locations on the measured traits. This specially relates to P_{phy} and P_i, what is in accordance with results of RABOY *et al*. (2001) and COELCHO *et al*. (2002). The line x tester approach (SING and CHOUDHARY, 1976) proved to be the most appropriate for this kind of research, where traits are largely influenced by environment, since it gives results for each location separately.

The obtained values for P_{phy} and P_i were somewhat higher when compared with the previous studies on wild type maize breeding materials (LORENZ *et al*., 2007; LORENZ *et al*., 2008; RABOY *et al*., 1989, 2001; SHI *et al*., 2003) and unselected landraces (MLADENOVIC DRINIC *et al*., 2009). In our investigation higher range among both hybrids and inbreds were obtained for P_i than for P_{phy}. This is in accordance with the results of LORENZ *et al*. (2007) for inbred lines and LORENZ *et al*. (2008) for S1 families from a broad base synthetic population. Similar results were

obtained with unselected material by MLADENOVIC DRINIC *et al*. (2009). Also, our investigation showed lower range for both traits among inbreds when compared to hybrids.

Considering GCA values alone, two sources for divergent selection of P_{phy} were identified. First, lines A1 and A4 belonging to source A (the same heterotic group) that could be crossed for pedigree breeding for lower P_{phy}, high P_i and increased grain yield. On the other hand, lines C2 and C3 from source C could be used for breeding for high levels of P_{phy}. Tester Z2 could be used in pedigree selection with both sources as an elite inbred tester.

However, this approach has some drawbacks. GCA variance is the indicator of additive gene effects, while SCA variance is the indicator of dominant gene effect. The mode of inheritance of a particular trait can be concluded based on the GCA/SCA relation. Since SCA variance was much greater than additive (GCA) variance, the value of lines for these traits needs to be checked in hybrids during breeding process. This means that GCA values of the lines and testers are not a good predictor for the values of their hybrids. That is why only hybrid performances of these inbreds can indicate their value for low/high phytate maize breeding. Non-significant correlations between inbreds GCA and their hybrids SCA`s (data not shown) also support these findings. Another proof for this are statistically highly significant correlations between values of hybrids *per se* and their SCA`s (0.602 for P_{phy}, 0.527 for P_i, 0.534 for grain yield and 0.719 for test weight, respectively).

The only exception in this investigation was inbred Z2, a favorable tester for grain quality traits, that was most yielding *per se* and also had a very good GCA for grain yield at all three locations. This tester should be considered for breeding programs on grain yield and quality improvement with more divergent material than the one used in this study.

Simultaneous breeding for grain yield and grain quality implies improvement of several traits at the same time, thus requiring the use of selection indices. This conclusion is based on the results of two hybrids with acceptable SCA for all the traits and the fact that these traits are inherited non-additively. LORENZ *et al*. (2007, 2008) and RABOY *et al*. (1989, 2001) concluded the same.

Correlations between investigated traits are important, since they imply response to selection of mutually dependent traits. The most important correlations in this study (all non-significant) were found between grain yield and P_i, i.e. P_{phy}. This is favorable for simultaneous improvement of grain yield, P_i and P_{phy} content. Selection for phytate can go in two directions, depending on the desired goal - low phytate for food and feed (BROWN and SOLOMONS, 1991; ERDMAN, 1981; SHARPLEY *et al*., 1994) or high phytate as anti-aging and anti-cancer agent in human food (COELCHO *et al*., 2002; DORIA *et al*., 2009; MLADENOVIC DRINIC *et al*., 2009).

Two expected but weak negative correlations were found between phytate and test weight, i.e. P_i and test weight. This clearly shows the seed deposition of organic and inorganic P. MAGA (1982) and O`DELL (1972) showed that about 90% of phytate is deposited in the germ that constitutes only a small portion of the whole kernel.

Another important correlation was found between P_i and P_{phy} and it was significantly positive for hybrids, i.e. non-significant positive for inbreds. This is in accordance with the investigations of LORENZ *et al*. (2007, 2008) while in the investigation of MLADENOVIC DRINIC *et al*. (2009) this correlation was negative. Correlations obtained in our study indicate that breeding for high P_i and low phytate at the same time, as well as for high P_i and high phytate is possible. Moreover, since strong negative correlations between P_i, i.e. P_{phy} and test weight were not detected, altering P profile in the analyzed material would not jeopardize test weight.

The research on 18 elite maize inbred lines clearly indicated strong non-additive inheritance of grain yield, test weight and content of P_{phy} and P_i in the kernel. These results imply that selection for simultaneous improvement of grain yield and phosphorus profile in the grain would be a complex task requiring use of selection indices. However, correlations between the traits indicate that this is an attainable goal.

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NASLEĐIVANJE PROFILA FOSFORA U ZRNU KUKURUZA (*Zea mays* L.)

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Izvod

Ispitivana je serija od 15 elitnih inbred linija kukuruza (korišćene kao majke) i tri inbred linije testera (korišćene kao očevi) upotrebom statističkog modela linija x tester, uključujući i hibride i inbred linije. Ispitivane su četiri osobine: prinos zrna, masa 1000 zrna, fitinski fosfor (P_{phy}) i neorganski fosfor (P_i) u zrnu. Sadržaj P_{phy} kod hibrida se kretao od 2,342 do 4,812 g kg^{-1}, a sadržaj P_i od 0,562 to 2,340 g kg^{-1} , dok je kod inbred linija (majki i očeva) sadržaj varirao od 2,503 do 4,180 g kg^{-1}, odnosno od 0,587 do 1,629 g kg^{-1}. Korelacije između četiri osobine su pokazale da je moguće oplemenjivanje na visok sadržaj P_i i nizak sadržaj P_{phy}, kao i visok sadržaj i P_i i fitata, bez ugrožavanja prinosa zrna. Korelacija između P_{phy} i P_i kod hibrida je bila 0,185 ($p<0,05$), a za inbred linije 0,142 (bez značaja). Odnos između opšte kombinacione sposobnosti (OKS) i posebne kombinacione sposobnosti (PKS) za sve osobine je bio ispod granične vrednosti 1 (veoma niže) što pokazuje da je u nasleđivanju ispitivanih osobina zastupljena neaditivna varijansa. Zaključak je da se kod ispitivanih genotipova trebaju koristiti višestruki selekcioni indeksi radi istovremenog poboljšanja prinosa zrna i fosfornog profila u zrnu kukuruza.

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