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Generation means analysis of phytic acid and inorganic phosphorus contents in corn (*Zea mays* L)

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Abstract

This study reported the effects of gene action in controlling the traits with respect to the contents of phytic acid (PA) and inorganic phosphorus (InP) in corn seeds by using an analysis of six generation means (P_1, P_2, F_1, F_2, BC_1, and BC_2) in six crosses of elite inbred lines. The crosses of Ki16 x Ki10, Ki52 x Ki51, and 30A10-S_{10}-14-1-2 x Ki23 for the PA content and 30A10-S_{10}-11-1-10 x Ki20 for the InP content were adequately described by the additive-dominance model which it showed the importance of the additive and dominance gene effects on both the PA and InP traits. The non-allelic gene action (epistasis) study in the PA trait in the three crosses of 30A10-S_{10}-11-1-10 x Ki20, Ki51 x Ki20, and C5219041-S_6-95 x Ki23 revealed that there was a statistically significant difference only in the cross 30A10-S_{10}-11-1-10 x Ki20 which had an additive x additive gene action. For the study on the non-allelic gene action of the InP trait in the five crosses of Ki16 x Ki10, Ki51 x Ki20, Ki52 x Ki51, 30A10-S_{10}-14-1-2 x Ki23, and C5219041-S_6-95 x Ki23, although the different gene actions were observed, the gene effects of dominance and dominance x dominance were significantly inherited for the InP content in many crosses. From the yield study in the six generations in the six crosses, both heterosis and the additive gene effect were prominent action in the yield performance. Moreover, correlation between yield and the PA content in the crosses was positive.

Introduction

Phytic acid (PA) (myo-inositol-1,2,3,4,5,6-hexakisphosphate) is the main storage form of phosphorus (P) in seeds and grains, with around 1% or more of the dry weight and 50-80% of the total P (Ockenden et al, 2004). This chemical agent is an essential precursor in several pathways in plant cells including IAA (Indole-3-acetic acid) metabolism and cell wall polysaccharide synthesis (Raboy, 2003). In plants it is also involved in different important stress responses such as salt tolerance and water deficit (Loewus and Murthy, 2000).

In corn, more than 80% of organic phytate is contained in the germ and about 20% is found in the aleurone tissue of corn (O'Dell et al, 1972). In animal and human being, this substance may have a positive nutritional role as an anti-oxidant and anti-cancer agent (Lott et al, 2000). Nevertheless, the main negative effect of this substance is that phytate is considered as an anti-nutritional substance in both animals and human (Raboy, 2002; Shi et al, 2003).

The high content of PA in feed has become to be a challenging problem in animal production around the world (Maga, 1982; Lott et al, 2000; Tongoona, 2005). This organic compound is indigestible by monogastric animal, such as pig and poultry, which are two of the commercial animals produced extensively in Thailand.

It can also cause environmental hazard if the unabsorbed phytate passes through the animal gastrointestinal tract and is discharged to the environment causing eutrophication (Lott et al, 2000; Shi et al, 2003; Ockenden et al, 2004).

The unusable organic phosphorus is thus a threat to the environment if the waste from producing these animals has not been properly managed (Sharpley et al, 1994). The excessive phytate in the raw material has been normally reduced by adding the phytase enzyme during the process of producing the animal feedstuff, leading to an increased production cost (Cromwell et al, 1995; Liu et al, 1997; Liu et al, 1998).

Reducing PA content in maize may be achievable with the conventional breeding. Genetic control of the PA content in maize should thus be studied so that the conventional breeding program aiming to reducing PA content is implementable. Not only should the genetic of PA content be determined, but also the genetic of inorganic phosphorus (InP) and total phosphorus (P) be investigated as well.

Genetic control with respect to the PA and relative traits, such as inorganic phosphorus (InP), in corn have been investigated (Ertl et al, 1998; Raboy et al, 2000; Raboy et al, 2001). These studies indicated that

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there was a negative correlation between PA content and InP of mutant maize (Raboy et al, 2000; Raboy et al, 2001) and normal lines (Na Chiangmai et al, 2011b). In contrast, Lorenz et al (2008) reported positive non-significant between PA and InP in Western normal lines germplasm. The difference between the relationship among PA, InP and yield has been reported in normal lines. The correlation between PA, InP and yield also was reported in maize by Lorenze et al (2007) in which both PA and InP were negative correlated with yield in Western normal lines germplasm. However, yield was reported to be positive correlated with PA and had negative correlation with InP in tropical normal lines germplasm (Na Chiangmai et al, 2011b). Lorenze et al (2008) also reported that broad-sense heritability value in InP trait was higher than that in PA character. This may indicate that other factors, apart from genetic, have influenced the level of PA more than InP content.

Although broad-sense heritability may be appropriate to determine the size of selection intensity or selection differential in the population, this value may not be suitable to use in selecting specific method for breeding purpose. The understanding of the gene action controlling the PA content in maize would lead to the selection of an appropriate breeding program for improving maize with required traits. The information on the gene action both on additive and dominant for the PA content and other related chemical compounds would lay a proper foundation for a rational set up of breeding program to produce corn varieties with low PA content.

The objective of this study was to determine the gene action (additive, dominance, and epistatic effects) controlling the PA and InP contents on tropical maize germplasm. The result will be used to select the method in the breeding program to obtain corn with low PA content trait. Thus, six crosses of tropical maize lines were studied by using a generation mean analysis (GMA).

Materials and Methods

Plant materials and experimental design

Inbred lines of corn provided by the corn germplasm bank at the National Corn and Sorghum Research Center (NCSRC), Thailand were studied. In this study the contents of PA and InP were determined with the method as described by Haug and Lantzsch (1983).

The contents of PA and InP were evaluated twice; the first and second preliminary evaluations were carried out with corn seeds in 2007. Parent was selected from either low (ie, Ki10, Ki20, Ki23, and Ki52) or medium-high (ie, Ki16, Ki51, 30A10-S_{10}-11-1-10, 30A10-S_{10}-14-1-2, and C5219041-S_6-95) of the PA contents for crossing for the GMA study. The PA contents were arbitrarily set at < 900 mg 100 g^{-1} seed for low PA and ≥ 900 mg 100 g^{-1} seed for medium-high PA.

The GMA study was conducted in a randomized complete block design with four replications at Suwan Farm at Pak Chong district, Nakhon Ratchasima province, Thailand.

In the field experiment, two seeds of the tested inbred lines and crosses were planted in a row 5 m long with two rows for each inbred line and cross in each replication. There was a distance of 25 cm between hills and 75 cm between rows. Plants were thinned to one plant per hill after planting 14 days. Fertilizer was broadcasted before planting at the rates of 25 kg ha^{-1} of Nitrogen (N) and 31.25 kg ha^{-1} of P_2O_5 with an additional of 86.25 kg $ha^{-1}$of N which was side dressed at the six to eight leaf stages.

Cross and generations

The corn inbred lines using for crossing were selected from the lines containing either low or medium-high PA contents. Our previous study revealed that the PA and InP contents of the inbred lines from the germplasm bank were negative correlated (Na Chiangmai et al, 2011b). As a consequence, only the PA trait was chosen for crossing, but the InP trait can also be inherently investigated simultaneously.

The crossing of these inbred lines for the GMA study was 30A10-S_{10}-11-1-10 x Ki20, Ki16 x Ki10, Ki51 x Ki20, Ki52 x Ki51, 30A10-S_{10}-14-1-2 x Ki23, and C5219041-S_6-95 x Ki23. Each cross consisted of six generations included the P_1 and P_2 parental inbred lines, the F_1 and F_2 of the first and the second filial generations, and the BC_1 (female F_1 backcrossed to P_1) and BC_2 (female F_1 backcrossed to P_2). The parental inbred lines of the six crosses were selected and the six populations of each cross were established during 2007 - 2009, and the PA and InP contents of the six generations which planted simultaneously in the 2010 dry season were subsequently evaluated.

Data analysis

The allelic gene action (additive and dominance) and non-allelic gene action (additive x additive, additive x dominance, and dominance x dominance) were evaluated based upon the scaling test proposed by Mather and Jinks (1982). The estimate values of *A*, *B*, and *C* included as:

$$A = 2\overline{BC}_1 - \overline{P}_1 - \overline{F}_1$$

$$B = 2\overline{BC}_2 - \overline{P}_2 - \overline{F}_1$$

$$C = 4F_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2$$

with $\overline{P}_1$, $\overline{P}_2$, $\overline{BC}_1$, $\overline{BC}_2$, $\overline{F}_1$, and $\overline{F}_2$ representing observed generation means of P_1, P_2, BC_1, BC_2, F_1, and F_2 respectively.

The variances of the observed generation means were used to estimate the variance of the *A*, *B*, and *C* values as:

$$V_A = 4V_{\overline{BC}_1} + V_{\overline{P}_1} + V_{\overline{F}_1}$$

$$V_B = 4V_{\overline{BC}_2} + V_{\overline{P}_2} + V_{\overline{F}_1}$$

$$V_C = 16V_{\overline{F}_2} + 4V_{\overline{F}_1} + V_{\overline{P}_1} + V_{\overline{P}_2}$$

with $V_{\overline{BC}_1}$, such as the variance of the mean measure-

ment of the BC_1 generation. The *A*, *B*, and *C* and standard error were tested with the t-test. The *A*, *B*, and *C* scaling tests were carried out to study the non-allelic interactions of the PA trait.

If non-significant values of the *A*, *B*, and *C* are detected by the scaling test, the additive-dominance model is perfectly adequate for the analysis of the variation in these single sets of data (Mather and Jinks, 1982). If significant values of the *A*, *B*, and *C* are detected, the additive-dominance model is not valid to explain the gene action governing the PA trait. Hence, the joint scaling test proposed by Cavalli (1952) would be employed to estimate the parameter, i.e. m, [d], [h] from the generation means. Chi-square (χ^2) is used to test the goodness of fit in the additive-dominance model in each parameter using the formula described by Mather and Jinks (1982) as follows:

$$\sum_{i=1,\ldots,6} [(\text{observed value - expected value})^2 \times \text{corresponding weight}]$$

where i is generation.

The matrix algebra method modified from the analysis method of the scaling test (Mather and Jinks, 1982) by Kunkaew et al (2008) was used to explain the additive-dominance model as follows:

$$M = [B_1' \times B]^{-1} \times [B_1' \times C]$$
$$V = D \times V_1$$
$$SE = \sqrt{V}$$

where *M* is the matrix of parameters; *B* is the matrix of coefficient of parameters; B_1 is the matrix of weight; B_1' is the matrix transpose of B_1; *C* is the matrix of six generation means; *V* is the matrix of parameter variances; V_1 is the matrix of six generation means; *D* is the matrix of the squared of each values in matrix $[B_1' \times B]^{-1} \times B_1'$, and *SE* is the standard error of parameters.

If the additive-dominance model by the scaling test is not valid to explain the gene action governing the PA trait as shown by the significance of the scale *A* or *B* or *C*, the non-allelic interaction model would be employed to explain the epistasis for gene action of the trait.

The matrix algebra modified from the analysis method of the joint scaling test (Gamble, 1962) by Kunkeaw et al (2008) was used to analyze the generation means as follows:

$$M = B^{-1} \times C$$
$$V = E \times V_1$$
$$SE = \sqrt{V}$$

where *M* represents the matrix of parameters, *B* the matrix of coefficient of parameters, B^{-1} the matrix inverse of *B*, *C* the matrix of six generation means, *V* the matrix of parameter variances, V_1 the matrix of variances of six generation means, *E* the matrix of the squared of each values in matrix $[B^{-1}]$, and *SE* the standard error of parameters.

Results

Comparison of the inbred lines for the PA and InP contents and correlations of the traits in the six generations in the six crosses

The value of the PA content in the inbred lines selected to be parents for crossing in the GMA study showed that inbred lines were categorized basing upon the difference in the value of PA content between the selected parents (Supplementary Table 1). There were five crosses in which the value of the difference in the PA contents was greater than 60 mg/100 g seed in the preliminary test. On the contrary, the difference in the PA values between Ki16 and Ki10 was at 17.3 mg 100 g^{-1} seed. There were also five crosses in which the difference in the PA values was positive, except that the cross Ki52 x Ki51 was negative.

The value of the InP content in the inbred lines selected to be parents for crossing in the GMA study showed that there were three crosses in which the value of the difference in the InP contents was greater than 18 mg 100 g^{-1} seed (Supplementary Table 1). There were also three crosses in which the difference

Table 1 - Means of the PA content in six generations and the scaling tests in six crosses of corn.

Value	30A10-S_{10}-11-1-10 x Ki20 (MH x L)§	Ki16 x Ki10 (MH x L)	Ki51 x Ki20 (MH x L)	Ki52 x Ki51 (L x MH)	30A10-S_{10}-14-1-2 x Ki23 (MH x L)	C5219041-S_6-95 x Ki23 (MH x L)
$\bar{P}_1$	793.7 ± 4.6	804.6 ± 1.6	913.0 ± 7.5	792.8 ± 23.9	834.7 ± 11.2	914.6 ± 3.3
$\bar{P}_2$	751.8 ± 14.5	771.6 ± 6.2	861.1 ± 11.8	826.8 ± 21.4	830.6 ± 18.4	878.2 ± 5.0
$\bar{F}_1$	810.6 ± 9.4	797.2 ± 2.1	912.6 ± 8.6	812.0 ± 16.2	851.4 ± 22.0	900.3 ± 3.5
$\bar{F}_2$	817.7 ± 3.1	808.8 ± 27.1	918.7 ± 5.4	834.6 ± 18.4	850.5 ± 20.4	902.3 ± 9.1
$\bar{BC}_1$	823.4 ± 5.0	782.0 ± 12.7	932.7 ± 8.9	828.4 ± 15.2	877.7 ± 19.4	918.3 ± 2.4
$\bar{BC}_2$	784.3 ± 8.7	782.5 ± 9.2	895.2 ± 3.3	813.2 ± 9.7	827.7 ± 14.6	904.1 ± 7.1
A	42.4 ± 14.5 **	-37.8 ± 25.5 ns	39.7 ± 21.1 ns	51.9 ± 41.9 ns	69.3 ± 45.9 ns	21.7 ± 6.7 **
B	6.2 ± 24.5 ns	-3.8 ± 19.7 ns	16.7 ± 16.0 ns	-12.4 ± 33.1 ns	-26.5 ± 40.9 ns	29.8 ± 15.5 ns
C	104.0 ± 27.2 **	64.4 ± 108.9 ns	75.5 ± 31.1 *	94.8 ± 86.7 ns	34.0 ± 95.3 ns	16.0 ± 37.4 ns

§MH - Medium-High PA content; L - Low PA content

*,** significant at the 0.05 and 0.01 probability levels, respectively; ns, not significant

Table 2 - Means of the InP content in six generations and the scaling tests in six crosses of corn.

Value	30A10-S_{10}-11-1-10 x Ki20 (MH x L)§	Ki16 x Ki10 (MH x L)	Ki51 x Ki20 (MH x L)	Ki52 x Ki51 (L x MH)	30A10-S_{10}-14-1-2 x Ki23 (MH x L)	C5219041-S_6-95 x Ki23 (MH x L)
$\bar{P}_1$	41.6 ± 2.0	78.0 ± 6.2	32.2 ± 2.5	25.5 ± 2.3	61.1 ± 3.1	35.4 ± 2.8
$\bar{P}_2$	37.1 ± 0.5	68.0 ± 4.9	40.0 ± 4.0	37.8 ± 1.9	39.3 ± 1.6	39.0 ± 7.1
$\bar{F}_1$	29.7 ± 1.4	28.7 ± 1.8	31.7 ± 1.1	25.1 ± 0.8	35.7 ± 1.7	37.5 ± 1.7
$\bar{F}_2$	33.1 ± 4.6	34.3 ± 3.0	72.1 ± 3.8	35.6 ± 3.2	41.6 ± 3.0	26.8 ± 2.1
$\bar{BC}_1$	34.0 ± 0.8	29.8 ± 2.4	30.4 ± 0.5	26.3 ± 2.6	34.4 ± 2.5	28.2 ± 2.2
$\bar{BC}_2$	30.0 ± 1.8	41.8 ± 3.4	34.5 ± 2.8	30.1 ± 0.7	34.7 ± 2.0	26.3 ± 1.7
A	4-3.3 ± 2.9 ns	-47.0 ± 8.1 **	-3.0 ± 2.9 ns	2.1 ± 5.7 ns	-28.0 ± 6.1 **	-16.5 ± 5.4 **
B	-6.8 ± 3.9 ns	-13.0 ± 8.6 ns	-2.7 ± 7.0 ns	-2.7 ± 2.5 ns	-5.5 ± 4.7 ns	-23.8 ± 8.0 **
C	-5.6 ± 18.8 ns	-66.1 ± 14.7 **	152.9 ± 16.2 **	29.0 ± 13.1 *	-5.3 ± 12.9 ns	-42.0 ±11.9 **

§MH - Medium-High PA content; L - Low PA content
*,** significant at the 0.05 and 0.01 probability levels, respectively; ns, not significant

in the InP value was less than 18 mg 100 g^{-1} seed. There were also five possible crosses in which the difference in the InP contents was negative, except that the cross Ki51 x Ki20 was positive.

The ANOVAs in the six crosses (i.e., 30A10-S_{10}-11-1-10 x Ki20, Ki16 x Ki10, Ki51 x Ki20, Ki52 x Ki51, 30A10-S_{10}-14-1-2 x Ki23, and C5219041-S_6-95 x Ki23) showed that there were statistically significant differences in the PA contents in the crosses 30A10-S_{10}-11-1-10 x Ki20 and Ki51 x Ki20 (Supplementary Table 2). There were also highly significant differences in the InP contents in the three crosses, namely Ki16 x Ki10, Ki51 x Ki20, and 30A10-S_{10}-14-1-2 x Ki23 (Supplementary Table 2).

Although there was only one cross (C5219041-S_6-95 x Ki23) which was statistically correlated with respect to the PA and InP contents, there were negative correlations in all the crosses (Supplementary Table 2).

Generation mean analysis by the scaling and joint scaling tests

Both non-significant and significant differences were found for the scalings *A*, *B*, and *C* and their variance for the PA (Table 1) and InP contents (Table 2).

For the PA content, there were three crosses which the values of the scalings *A*, *B*, and *C* were not significantly different (Table 1). Three crosses showed significant deviations from zero for those scales for the PA content, i.e., 30A10-S_{10}-11-1-10 x Ki20, Ki51 x Ki20, and C5219041-S_6-95 x Ki23. For the InP content, five crosses had significantly differences for the scaling values except for the cross 30A10-S_{10}-11-1-10 x Ki20 (Table 2).

There were non-significant differences in four crosses by Chi-square test in the PA content in the crosses of Ki16 x Ki10, Ki51 x Ki20, Ki52 x Ki51, and 30A10-S_{10}-14-1-2 x Ki23 (Table 3). Two crosses, namely 30A10-S_{10}-11-1-10 x Ki20 and C5219041-S_6-95 x Ki23 were significantly different by the Chi-square test in the PA content. However, there was a significant difference of the value of *m* in every cross and there was a significant difference in the value of [*d*] in four crosses, i.e., 30A10-S_{10}-11-1-10 x Ki20, Ki16 x Ki10, Ki51 x Ki20, and C5219041-S_6-95 x Ki23. The [*h*] values of the PA content were significantly differences in three crosses, i.e., 30A10-S_{10}-11-1-10 x Ki20, Ki16 x Ki10, and Ki51 x Ki20 (Table 3).

There were non-significant differences using the

Table 3 - The results of the joint scaling test for mean of the PA content in grain of corn.

Value	30A10-S_{10}-11-1-10 x Ki20 (MH x L)§	Ki16 x Ki10 (MH x L)	Ki51 x Ki20 (MH x L)	Ki52 x Ki51 (L x MH)	30A10-S_{10}-14-1-2 x Ki23 (MH x L)	C5219041-S_6-95 x Ki23 (MH x L)
m	782.2 ± 5.7 **	787.9 ± 3.3 **	893.6 ± 5.4 **	817.1 ± 13.1 **	830.8 ± 9.9 **	900.0 ± 2.8 **
[*d*]	17.2 ± 5.5 **	16.5 ± 3.3 **	27.2 ± 4.9 **	-2.3 ± 11.8 ns	9.1 ± 9.6 ns	19.4 ± 2.7 **
[*h*]	57.1 ± 10.6 **	9.1 ± 4.0 *	32.1 ± 10.8 **	0.7 ± 22.8 ns	28.0 ± 21.6 ns	6.9 ± 4.5 ns
χ^2	21.49 **	2.59 ns	7.56 ns	2.90 ns	3.52 ns	12.82 **

The values received from the joint scaling test by Mather and Jinks (1982)
§MH - Medium-High PA content; L - Low PA content
*,** significant at the 0.05 and 0.01 probability levels, respectively; ns, not significant

Table 4 - The results of the joint scaling test for mean of the InP content in grain of corn.

Value	30A10-S_{10}-11-1-10 x Ki20 (MH x L)§	Ki16 x Ki10 (MH x L)	Ki51 x Ki20 (MH x L)	Ki52 x Ki51 (L x MH)	30A10-S_{10}-14-1-2 x Ki23 (MH x L)	C5219041-S_6-95 x Ki23 (MH x L)
m	38.7 ± 0.8 **	55.2 ± 2.7 **	38.0 ± 1.8 **	31.5 ± 1.2 **	46.5 ± 1.5 **	25.4 ± 2.0 **
[*d*]	1.7 ± 0.7 *	-6.7 ± 2.8 *	-7.8 ± 1.7 **	-4.9 ± 1.2 **	7.5 ± 1.5 **	5.0 ± 2.0 *
[*h*]	-10.5 ± 1.7 ** **	-29.8 ± 3.7 ** **	-6.3 ± 2.3 ** **	-6.5 ± 1.6 ** **	-13.2 ± 2.4 ** **	9.1 ± 3.1 **
χ^2	3.66 ns	40.31 **	100.16 **	6.92 ns	22.13 **	19.58 **

The values received from the joint scaling test by Mather and Jinks (1982)
§MH - Medium-High PA content; L - Low PA content
*,** significant at the 0.05 and 0.01 probability levels, respectively; ns, not significant

Chi-square test for the InP content in two crosses of 30A10-S_{10}-11-1-10 x Ki20 and Ki52 x Ki51 (Table 4). In contrast, there were significantly differences in four crosses, i.e., Ki16 x Ki10, Ki51 x Ki20, 30A10-S_{10}-14-1-2 x Ki23, and C5219041-S_6-95 x Ki23. The *m* value in every cross was significantly different. The [*d*] and [*h*] values in all crosses for the InP content were also significantly different (Table 4).

Generation mean analysis for epistasis effect

There were statistically significant differences in the PA content tested by both the scaling and Chi-square tests in the crosses of 30A10-S_{10}-11-1-10 x Ki20, Ki51 x Ki20, and C5219041-S_6-95 x Ki23 (Tables 1 and 3).

The parameter test using the matrix algebra found that there were statistically significant differences by the non-allelic model in the PA content in both the *m*, [*d*], and [*i*] values (Table 5).

The analysis of the non-allelic interaction model in the PA trait (Table 5) also revealed the influence of the allelic gene action and there was a significant difference from the analysis using the joint scaling test (Table 3).

Using the joint scaling test to analyze for the PA content in the crosses 30A10-S_{10}-11-1-10 x Ki20 and Ki51 x Ki20, the [*d*] and [*h*] values showed statistically significant differences from zero (Table 3). However, only the [*d*] value was significantly different in both crosses when it was analyzed by non-allelic interaction model (Table 5). While the [*d*] value was found to be significantly different in the cross C5219041-S_6-95 x Ki23 from the analysis using the joint scaling test (Table 3), there was no statistically significant difference of the [*d*] value tested with the non-allelic interaction model (Table 5).

The study of the non-allelic gene action for the PA content, particularly in the cross 30A10-S_{10}-11-1-10 x Ki20, revealed that there was a statistically significant difference in the [*i*] value. However, there was no a statistically significant difference which indicated the influence of the non-allelic gene action in the other two crosses (Ki51 x K20 and C5219041-S_6-95 x Ki23) (Table 5).

There were statistically significant differences in the value of the InP content tested by the scaling or Chi-square tests in the following crosses i.e., Ki16 x Ki10, Ki51 x Ki20, Ki52 x Ki51, 30A10-S_{10}-14-1-2 x Ki23, and C5219041-S_6-95 x Ki23 (Tables 2 and 4). From the parameter test by the non-allelic interaction model in these crosses, the value of *m* was significantly different in all crosses. However, there were some statistically significant differences in other parameters ([*d*], [*h*], [*i*], [*j*], and [*l*]) (Table 6).

The study of the allelic gene action in the InP content with the joint scaling test found that the [*d*] and [*h*] values were statistically significant different from zero in the five crosses (not considered in cross 30A10-S_{10}-11-1-1 x Ki20 because it was non-significant different for the scalings *A*, *B*, and *C* and their variance as shown in (Table 2 and 4). Nonetheless, the two values were significantly different only in the cross Ki16 x Ki10 when they were subject to analysis with the non-allelic interaction model (Table 6). While the other three crosses (i.e., Ki51 x Ki20, Ki52 x Ki51, and 30A10-S_{10}-14-1-2 x Ki23) had only the [*h*] value with statistically significant difference tested with the non-allelic interaction model (Table 6). Only the cross C5219041-S_6-95 x Ki23 was not significantly different in both the [*d*] and [*h*] values (Table 6).

For the study in the non-allelic gene action using the non-allelic interaction model (Table 6), it was found that the cross 30A10-S_{10}-14-1-2 x Ki23 had the values of [*i*], [*j*], and [*l*] with statistically significant dif-

Table 5 - The generation mean analysis by the non-allelic interaction model on the PA content in grain of corn.

Value	30A10-S_{10}-11-1-10 x Ki20 (MH x L)§	Ki51 x Ki20 (MH x L)	C5219041-S_6-95 x Ki23 (MH x L)
m	817.7 ± 3.1 **	918.7 ± 5.4 **	902.3 ± 9.1 **
[*d*]	39.1 ± 10.0 **	37.5 ± 9.5 **	14.1 ± 7.5 ns
[*h*]	-17.5 ± 26.5 ns	6.5 ± 30.9 ns	39.5 ± 39.5 ns
[*i*]	-55.34 ± 23.6 *	-19.1 ± 28.8 ns	35.6 ± 39.2 ns
[*j*]	18.1 ± 12.6 ns	11.5 ± 11.8 ns	-4.1 ± 8.1 ns
[*l*]	6.7 ± 48.5 ns	-37.4 ± 48.9 ns	-87.1 ± 47.9 ns

§MH - Medium-High PA content; L - Low PA content
*,** significant at the 0.05 and 0.01 probability levels, respectively; ns, not significant

Table 6 - The generation mean analysis by the non-allelic interaction model on the InP content in grain of corn.

Value	Ki16 x Ki10 (MH x L)§	Ki51 x Ki20 (MH x L)	Ki52 x Ki51 (MH x L)	30A10-S_{10}-14-1-2 x Ki23 (MH x L)	C5219041-S_6-95 x Ki23 (MH x L)
m	34.3 ± 3.0 **	72.1 ± 3.8 **	35.6 ± 3.2 **	41.6 ± 3.0 **	26.8 ± 2.1 **
[*d*]	-12.0 ± 4.2 **	-4.1 ± 2.9 ns	-3.8 ± 2.7 ns	-0.3 ± 3.2 ns	1.9 ± 2.8 ns
[*h*]	-38.2 ± 15.2 *	-163.1 ± 16.6 **	-36.2 ± 13.8 *	-42.7 ± 13.8 **	2.0 ± 10.9 ns
[*i*]	6.1 ± 14.6 ns	-158.6 ± 16.4 **	-29.6 ± 13.7 *	-28.2 ± 13.5 *	1.8 ± 10.1 ns
[*j*]	-17.0 ± 5.8 **	-0.2 ± 3.7 ns	2.4 ± 3.1 ns	-11.2 ± 3.6 **	3.7 ± 4.7 ns
[*l*]	53.9 ± 22.4 *	164.4 ± 19.8 **	30.2 ± 16.9 ns	61.7 ± 18.2 **	38.5 ± 16.2 *

§MH - Medium-High PA content; L - Low PA content

*,** significant at the 0.05 and 0.01 probability levels, respectively; ns, not significant

ference. The cross Ki16 x Ki10 had the significant values of [*j*] and [*l*]. The cross Ki51 x Ki20 had the significant values of [*i*] and [*l*]. The crosses Ki52 x Ki51 and C5219041-S_6-95 x Ki23 had the significant values of [*i*] and [*l*], respectively.

Discussion

Comparison of the inbred lines for the PA and InP contents and correlations of the traits in the six generations in the six crosses.

The difference of the PA content (as shown in Supplementary Table 1) between the two lines selected for crossing was greater than 60 mg 100 g^{-1} seed in each of the five crosses. This indicated that there was a genetic variation between the inbred lines, although the difference was quite low when it was compared with the result as reported by Lorenze et al (2007).

The difference of the PA content was not too high because there was a narrow variation of the PA content in the inbred lines collected at the National Corn and Sorghum Research Center, Thailand. This is because the selected inbred lines in the collection have been developed from the elite corn varieties or hybrids with good performance in which the high yield was the primary trait in the tropical environment. The selection may restrict the genetic background and exclude the germplasm sources of inbred lines having varied PA content, especially the low PA inbred lines. This observation is supported by the finding that the PA trait was positively correlated with grain yield (Na Chiangmai et al, 2011b). On the other hand, there was a comparatively greater difference in PA content between low and high groups as reported by Lorenze et al (2007) who used the maize lines from Iowa, North Carolina, and Nebraska from the temperate environment. The distinction between these two studies may be a result of dissimilarity in genetic background of maize as well as the techniques used to analyze PA content.

Apart from the reason stated above, the comparatively narrow difference of the PA contents occurred in the cross Ki16 x Ki10 because both inbred lines had been developed from the same cycle of the OPV Suwan 1(S)C4. The positive or negative of the difference in the PA contents may indicate that the P_1 was selected from the inbred lines which were grouped as having either medium-high or low PA, respectively (Supplementary Table 1).

As for the difference of the InP content, there were two groups of inbred lines which were classified based upon the InP value (Supplementary Table 1). The first group has the difference of the InP content greater than 18 mg 100 g^{-1} seed, while the second group has the distinction of the InP content lower than 18 mg 100 g^{-1} seed. The difference of the InP content in the inbred lines (compared with mid-parent in individual crosses) was greatest at 72.66% in the cross 30A10-S_{10}-14-1-2 x Ki23 and was lowest at 21.43% in the cross Ki16 x Ki10. This evidence indicates that the parent selected for crossing has more genetic variation in InP character than that of the PA trait. Lorenze et al (2007) also reported the relatively greater difference of InP values between low and high groups from 50 maize lines using Modified Wade assay. As there was a genetic coefficient of variation in this study, it was possible that InP had more genetic variation and should be responsive to selection (Lorenze et al, 2007).

As a result, the InP trait may be utilized as the trait for the gene action study, although this trait has not been used in selecting the parents for the GMA study. The fact that the difference of the InP contents in parental lines was negative in the five crosses and positive in one cross consolidates the negativity of the correlation between the contents of PA and InP in the corn seeds of the inbred lines (Supplementary Table 1). The same negative relationship (but non-significant) in the correlation study in the six populations (both in inbred lines and F_1 hybrids) was also reported by Na Chiangmai et al (2011b).

The statistically significant differences in two crosses (30A10-S_{10}-11-1-10 x Ki20 and Ki51 x Ki20) could be explained that the genetic variation of the six generations will explicitly affect the distinction of the PA phenotype; which in turns reveals that the PA trait is governed by gene. This effect would elucidate and determine the type of the gene action which governs the expression of the PA trait (Supplementary Table 2).

The genetic control in the two crosses is consolidated by the fact that the PA contents of the inbred lines selected for crossing maintains the difference

between the parents both prior to the grouping and during the GMA study (Supplementary Tables 1, 2).

There were also highly significant differences of the InP contents in three crosses, i.e. Ki16 x Ki10, Ki51 x Ki20, and 30A10-S_{10}-14-1-2 x Ki23 (Supplementary Table 2). This suggests that the differences of the InP contents in the three crosses occurred as a result of gene effect. The effect of gene in controlling the InP trait may contribute to the possibility of using the GMA study to determine a type of gene action, particularly in the cross Ki51 x Ki20 which were significantly different among six generations in both PA and InP contents (Supplementary Table 2). The values of both genetic variance and broad-sense heritability of InP trait were higher than those of PA trait in maize used for feeding the animal (Lorenze et al, 2008; Na Chiangmai et al, 2011a). The broad-sense heritability may thus be influenced by genotype diversity in the populations. Although broad-sense heritability may be an indicator which can be used to elucidate the influence of gene, this value does not identify the type of gene action.

The correlation study between the PA and InP contents in the six generations in each cross which revealed the negative values means that the PA and InP contents are reversed, as shown by the significant negative value (-0.46) in the cross C5219041-S_6-95 x Ki23 (Supplementary Table 2). Raboy et al (2000), Raboy et al (2001), and Na Chiangmai et al (2011b) also reported the negative relationship between the PA and the InP contents in corn. Thus, the relationship between PA and InP in normal lines and that in the mutant lines were similar. However, this result was different from that reported in normal lines by Lorenze et al (2007), who showed non-significant positive between PA and InP. The discrepancy between our study and that of Lorenze et al (2007) may thus be attributable to the difference of genetic background of the maize used in both experiments.

Generation mean analysis by the scaling and joint scaling tests

The values of *A*, *B*, *C* and their variance in the PA trait were not significantly different after subjecting to the scaling test in the three crosses (Ki16 x Ki10, Ki52 x Ki51, and 30A10-S_{10}-14-1-2 x Ki23) and these values in InP trait were not significantly different in one cross (30A10-S_{10}-11-1-10 x Ki20). This means that the traits were controlled by the allelic gene action (Tables 1 and 2). The averages of the PA contents in F_1, F_2, BC_1, and BC_2 were higher than those of the mid-parent in the other significant three crosses (Table 1) which indicate that the relatively higher PA content is a dominant trait.

Shanmuganathan et al (2006) also reported the presence of heterosis of the PA trait in the hybrids of the pearl millet (*Pennisetum glaucum* L). The average of the PA content in BC_2 is lower than those of the other generation means (Table 1) because of backcrossing the F_1 to the lower parent. This may indicate that the PA trait follows the allelic frequency.

The average of the InP contents in F_1, F_2, BC_1, and BC_2 which were lower than those of the mid-parent in the crosses (Table 2) confirms the negative relationship between the PA and InP contents. The value of the InP content of the F_1 hybrid which was less than that of both mid parent and the lower parent in five crosses (except the cross C5219041-S_6-95 x Ki23) (Table 2) may indicate that the low InP trait was governed by a dominant gene.

Conversely, there were significantly different in the values of *A*, *B*, *C* and their variance in the PA trait after subjecting to the scaling test in three crosses (30A10-S_{10}-11-1-10 x Ki20, Ki51 x Ki20, and C5219041-S_6-95 x Ki23) and the InP in five crosses (Ki16 x Ki10, Ki51 x Ki20, Ki52 x Ki51, 30A10-S_{10}-14-1-2 x Ki23, and C5219041-S_6-95 x Ki23) which means that the traits are also controlled by the non-allelic gene action (epistasis) (Tables 1 and 2).

The detection of the non-allelic gene action in governing the PA and InP trait reveal an inheritance of quantitative characters. The epistasis, hybrid vigor, and the relationship between the two phenomena were found to play a role in dictating heterosis in the cross-pollinated crops (Ketata et al, 1976). The epistatic effect is crucial and beneficial for the formation of the hybrids from the inbred lines (Darrah and Hallauer, 1972; Wolf and Hallauer, 1977; Azizi et al, 2006), although it may hinder the genetic improvement in corn (Melchinger et al, 1988; Lamkey et al, 1995). Hallauer (1990) also reported that using inbred lines with related inbreds as a parent would maintain the epistatic gene combination, especially a linked epistatic combination.

The Chi-square test in joint scaling test with no statistically significant difference in the trait indicated that the additive-dominant model is adequate to use for the explanation of that trait in the generation mean in specific cross (Mather and Jinks, 1982). Although there were four crosses which were not significantly different by the Chi-square test in the PA content (Table 3), one cross (Ki51 x Ki20) of these was significant in the value of *C* by the scaling test (Table 1).

The Chi-square test and the scaling test could be used to verify whether the additive-dominance model had controlled the inheritance on the specific traits (Cavalli, 1952; Griffiths and Scott, 2001; Schroeder and Stimart, 2001; Khodambashi et al, 2012). The significant value of either the Chi-square test in joint scaling test or the scaling test may indicate the complexity of gene action in controlling the generation means of the traits (Griffiths and Scott, 2001; Khodambashi et al, 2012). However, if the testing does not fit the additive-dominance model, the specific traits may have been explained with the non-allelic model (Mather and Jinks, 1982).

As for the PA trait, the cross Ki51 x Ki20 (in which the additive x dominance model was not significantly different when tested with the Chi-square) was signif-

icantly different when analyzed with the scaling test. This may indicate that the cross Ki51 x Ki20 should be subject to the study with the non-allelic interaction model as well.

From the joint scaling test for the PA content, there were the significances from zero of the [*d*] in four crosses (the crosses 30A10-S_{10}-11-1-10 x Ki20, Ki16 x Ki10, Ki51 x Ki20, and C5219041-S_6-95 x Ki23), and the [*h*] value in three crosses (the crosses 30A10-S_{10}-11-1-10 x Ki20, Ki16 x Ki10, and Ki51 x Ki20) (Table 3). This indicated that the trait was clearly controlled by the additive and dominance gene effects in these crosses.

The two crosses Ki52 x Ki51 and 30A10-S_{10}-14-1-2 x Ki23 could be explained by the allelic gene action as a result of the study on the scaling test and Chi-square test analysis for the PA content (Tables 1 and 3). However, both [*d*] and [*h*] values which were not significantly different in the crosses Ki52 x Ki51 and 30A10-S_{10}-14-1-2 x Ki23 were detected. The allelic gene action in these crosses was not prominent as a result of the narrow of the difference of the PA content in the parents in these crosses (Table 1).

It was found that the difference in the PA contents in the two crosses Ki52 x Ki51 and 30A10-S_{10}-14-1-2 x Ki23 was quite higher than that of the other crosses in the preliminary test (-67.2 and 75.1 mg 100 g^{-1}), respectively (Supplementary Table 1). The high variation of the PA contents of the parents in the crosses was observed between the preliminary test and in the GMA study (Table 1 and Supplementary Table 1) which was normal as a result of the quantitative nature of the PA trait in corn. Nonetheless, the six generations study in the PA trait exhibited no variation resulting to the non- significant difference in the two crosses tested with ANOVA (Supplementary Table 2).

Both the additive and dominance gene action may govern the PA trait in all crosses, but the role of the gene effect may be varied based upon the pairing of each cross. This finding is in agreement with the research done by Shanmuganathan et al (2006) which used a diallel cross for gene effect determination in pearl millet and detected both additive and non-additive gene effects based upon the evaluation of 11 parents and 55 hybrids.

The detection of the difference of the gene action governing the PA trait among the crosses indicated that the study of the specific cross by suitable pairing was required in order to invent the high-yielding corn hybrid with low PA. Alternatively, composites or synthetic varieties of corn with low PA could be formed using the low PA inbred lines and developed by recurrent selection for high yield and low PA. Thus, parents with low PA may also be utilized in a population improvement program using recurrent selection to breed for the low PA content with good agronomic performance as reported by Shanmuganathan et al (2006).

Both the scaling test and Chi-square test for the InP content that were significantly different in these values were found in five crosses (without the cross 30A10-S_{10}-11-1-10 x Ki20) (Tables 2 and 4). Thus, the non-allelic interaction model was tested in these cross.

With the significant differences in both the [*d*] and [*h*] values of all of the six crosses from the additive-dominance model, the InP trait was controlled both by the additive and the dominance gene action (Table 4). However the allelic gene action was adequately used to explain the gene action of the InP content only in the cross 30A10-S_{10}-11-1-10 x Ki20.

Generation mean analysis for epistasis effect

The statistically significant differences of both the values of parameters in the scaling test and Chi-square test point out that the additive-dominance model is not adequate to explain the gene action controlling the PA trait in the generation means in the crosses 30A10-S_{10}-11-1-10 x Ki20, Ki51 x Ki20, and C5219041-S6-95 x Ki23 (Tables 1 and 3). Thus, the non-allelic interaction model should be used to explain the epistasis (Mather and Jinks, 1982) in these crosses for the PA trait.

From the study of the allelic gene action of the PA trait, it was found that there were significant differences when this trait was subject to analysis with either the joint scaling test or the non-allelic interaction model (Tables 3 and 5). Nevertheless, the effect of the additive gene action [*d*], which was found in three crosses, was more prominent for the allelic gene action by the joint scaling test analysis for PA trait. In this analysis, there was also the effect of the dominance gene action [*h*] for PA content in two crosses (i.e., 30A10-S_{10}-11-1-10 x Ki20 and Ki51 x Ki20) (Table 3).

The study of the non-allelic gene action of the PA trait (Table 5) found that only the [*i*] value in the cross 30A10-S_{10}-11-1-10 x Ki20 was significantly different. The statistically significant difference in the value of [*i*] of the non-allelic interaction means that the epistasis gene action is influenced by an additive x additive effect.

There was no statistically significant difference in the two crosses (Ki51 x Ki20 and C5219041-S_6-95 x Ki23) which possessed the non-allelic gene action (Table 5). The low variation of the PA content between the parents in the crosses may restrict the effect of the non-allelic gene action.

For the analysis with the scaling and Chi-square tests of the InP content, only the cross 30A10-S_{10}-11-1-10 x Ki20 could be adequately explained with the additive-dominant gene action model (Tables 2 and 4).

The study of the allelic gene action of the InP trait in the five crosses (i.e., Ki16 x Ki10, Ki51 x Ki20, Ki52 x Ki51, 30A10-S_{10}-14-1-2 x Ki23, and C5219041-S_6-95 x Ki23) revealed the difference between the analysis done by the joint scaling test (Table 4) and the non-allelic interaction model (Table 6).

Nevertheless, the effects of the additive gene ac-

tion [*d*] and the dominance gene action *[h*] were also prominent for InP trait in five crosses when the joint scaling test was analyzed in these crosses (Table 4).

However, the study of the non-allelic interaction model in the InP trait found that the [*d*] value was significantly different only in the cross Ki16 x Ki10 (Table 6). In addition, the values of [*i*], [*j*], and [*l*] were significantly different from zero in the other five crosses. This indicated that there were additive x additive [*i*], additive x dominance [*j*], and dominance x dominance [*l*] gene actions. However, the significantly different of the [*l*] value in the four crosses (from the total of five crosses) may indicate the importance of dominance x dominance gene action in the InP trait in corn.

The detection, of the influence of both the allelic and non-allelic gene action in each cross of the InP trait, may indicate that complicated gene expression exists in InP trait and specific pairing between the suitable parents is required in the breeding program to obtain corn with increased InP.

The PA trait was less influenced by the non-allelic gene action than the InP trait as a result of the lesser degree of difference in the PA value between the parents (Table 1 and Supplementary Table 1). However, the negative correlations between the PA and InP contents (Supplementary Table 2) may indicate that breeding for the low PA corn was as complicated as breeding for the high InP corn.

Yield study in the six generations in the six crosses of corn

The grain yield of the higher parents was found in P_1 in four crosses, such as 30A10-S_{10}-11-1-10 x Ki20, Ki51 x Ki20, Ki52 x Ki51, and 30A10-S_{10}-14-1-2 x Ki23 (Supplementary Table 3). For the PA content, the higher parent of P_1 was found in the five crosses; i.e., 30A10-S_{10}-11-1-10 x Ki20, Ki16 x Ki10, Ki51 x Ki20, 30A10-S_{10}-14-1-2 x Ki23, and C5219041-S_6-95 x Ki23 (Table 1).

The correlation between the PA content and both plant and ear aspects in the inbred lines were positive (Na Chiangmai et al, 2011b). This means that the high PA content in the inbred lines may contribute to the better characteristics in both plant and ear aspects and increased grain yield. In this study, the crosses between the higher parent (in three crosses between 30A10-S_{10}-11-1-10 x Ki20, Ki51 x Ki20, and 30A10-S_{10}-14-1-2 x Ki23) brought about the progenies with both increased yield and PA content traits (Table 1 and Supplementary Table 3).

The positive correlation between grain yield and the PA content was found between the three crosses of inbred lines (out of six crosses of the inbred lines), indicating that yield and PA content traits could not be improved simultaneously. Lorenze et al (2008), on the other hand, reported that PA, InP and yield in maize may be improved simultaneously as a result of non-correlation and selection differentials of traits.

The hybrid generations (i.e., F_1, F_2, BC_1, and BC_2) had higher values of grain yield than those of the parents in all crosses, indicating that the heterosis may play a role in controlling this characteristic (Supplementary Table 3). However, the correlations between the PA content and grain yield reported by Na Chiangmai et al (2011b) were positive in the F_1 hybrids populations, although there were no statistically significant difference. As a consequence, the new hybrid with the low PA content may have the reduced grain yield.

There were five crosses which showed the highest grain yield value in the BC_1 generation (i.e., 30A10-S_{10}-11-1-10 x Ki20, Ki51 x Ki20, Ki52 x Ki51, 30A10-S_{10}-14-1-2 x Ki23, and C5219041-S_6-95 x Ki23) (Supplementary Table 3). The BC_1 generation was the hybrid which had high gene frequency in the P_1 parent, as a result of the backcrossing of F_1 hybrid to the P_1 parent. This result indicated that the additive gene effect may also play a role in controlling for grain yield.

In this study, P_1 parent of the four crosses (i.e., 30A10-S_{10}-11-1-10 x Ki20, Ki51 x Ki20, Ki52 x Ki51, and 30A10-S_{10}-14-1-2 x Ki23) had higher yield than the P_2 parent (Supplementary Table 3). As the PA content was the main characteristic, which was used to select the inbred line as a parent in the cross to form hybrid, the value of the correlation between the PA content and grain yield was always positive in this trial (Na Chiangmai et al, 2011b), but the two traits were not significantly correlated.

In this study, the backcrossing between P_1 and F_1 (30A10-S_{10}-11-1-10 x Ki20, Ki51 x Ki20, Ki52 x Ki51, 30A10-S_{10}-14-1-2 x Ki23, and C5219041-S_6-95 x Ki23) yielded the five populations of BC_1 which had both high yield and the high PA content (Table 1 and Supplementary Table 3). In addition, BC_1 in four possible crosses (30A10-S_{10}-11-1-10 x Ki20, Ki51 x Ki20, 30A10-S_{10}-14-1-2 x Ki23, and C5219041-S_6-95 x Ki23) had the highest value of the PA content than other hybrid generations (F_1, F_2, and BC_2). This result confirmed that there was the positive correlation between grain yield and the PA content.

The hybrid populations had grain yield higher than those of the parental populations in all crosses (Supplementary Table 3), suggesting that this characteristic was governed by heterosis, with the over dominant gene action that expressed from the heterozygous genes. However, the BC_1 had higher grain yield than those of the F_1 hybrid and other hybrid populations (F_2 and BC_2 populations) in many crosses. It was also possible that the high grain yield was controlled by the high allelic frequency of the higher parent (P_1), where the additive gene action also controlled this trait.

The grain yield of the F_1 population was higher than that of the F_2 population (except in cross C5219041-S6-95 x Ki23), although the value of the PA content of the crosses in these two populations was quite closed (Table 1 and Supplementary Table 3). This indicated that the heterosis was more prominent in grain yield

than in the PA content trait. However, both grain yield and the PA content characteristics were governed by both the additive and dominant gene action.

Conclusions

The additive-dominance model was adequate to explain the inheritance of both the PA and InP contents by the scaling and Chi-square tests in different crosses. The crosses Ki16 x Ki10, Ki52 x Ki51, and 30A10-S_{10}-14-1-2 x Ki23 for the PA content and 30A10-S_{10}-11-1-10 x Ki20 for the InP content were adequately described by the additive-dominant model. In these crosses that explained by the additive-dominant model, the join scaling test showed the importance of both the additive and dominant gene effects for the PA and InP traits.

From the study of the epistasis in the PA trait in the crosses 30A10-S_{10}-11-1-10 x Ki20, Ki51 x Ki20, and C5219041-S_6-95 x Ki23, it was found that only the cross 30A10-S_{10}-11-1-10 x Ki20 showed the influence of the additive x additive gene action.

Moreover, from the study of the InP trait in the five crosses (Ki16 x Ki10, Ki51 x Ki20, Ki52 x Ki51, 30A10-S_{10}-14-1-2 x Ki23, and C5219041-S_6-95 x Ki23), using the non-allelic gene action model, it was found that the additive x additive, additive x dominance, and dominance x dominance gene actions governed this trait but the gene action differed in each cross.

Nevertheless, the non-allelic interaction model testing showed the importance of dominance x dominance gene effect on the InP content.

For the yield study in the six generations in the six crosses selected for the GMA study, both the heterosis and the additive gene effect were the prominent actions in controlling grain yield which revealed the high grain yield in the F_1 and BC_1, respectively.

Moreover, the comparison between the grain yield and the PA content in the means of the generations in crosses showed the positive correlation between these traits. This finding may make it difficult to improve for the lower PA content without affecting yield performance in corn hybrid.

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