Research Article

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Generation mean analysis for grain yield and its components in popcorn

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Abstract: Knowledge about genetic composition of a character helps plant breeders to plan their breeding programs. Grain yield and related traits are very important in maize breeding programs. In our experiment four each of parents, F_1 s, F_2 s, BC_1 s and BC_2 s were evaluated at Cereal Crops Research Institute (CCRI), Pirsabak, Nowshera and Agriculture University Peshawar. The experimental material at both locations were replicated thrice in randomized complete block design. In all crosses dominance gene action was found to be important in the inheritance of ear diameter, ear length, percent shelling and grain yield. Additive genetic effects were found negative and non-significant in all four crosses for percent shelling. Duplicate type of non-allelic interactions was observed for shelling percentage in all crosses. Duplicate type of epistasis was observed in cross, PS-1 $\times$ BD-1 and PS-2 $\times$ BD-1 for ear length. For grain yield both complementary and duplicate type of epistasis were observed. Additive genetic effects were found significant with positive and negative magnitude in two crosses each. It is concluded that crosses, where dominant gene action was found predominant, should be effectively utilized in hybrid maize programs for improved grain yield and related traits.

Keywords: Additive $\times$ additive, dominant, ear length, epistasis, grain yield, Popcorn

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Abbreviations

BD-POP, Bangladesh popcorn, **CCRI**, Cereal Crops Research Institute, Pirsabak, Nowshera, Khyber Pakhtunkhwa-Pakistan; **d**, additive effect; **h**, dominance effect; **i**, additive $\times$ additive effect; **j**, additive $\times$ dominance effect; **l**, dominance $\times$ dominance effect; **m**, mean effect of F_2 ; **PS-POP**, Pirsabak popcorn; **UOA**, University of Agriculture, Peshawar

1 Introduction

Maize (*Zea mays* L.) is the world leading cereal crop and locally known as ‘makai’ or ‘Jowar’. It is indigenous to America and was domesticated about 8,000 years ago. Maize does not survive in its wild form probably because of its highly cross pollinated nature (Ram and Singh 2003: 105-109). Due to great diversity of morphological, physiological and biochemical traits of maize, together with a very broad adaptability and genetic variability provide the development of types with various purposes in the process of selection. Different maize types with specific traits are also grown like, high-lysine maize, high-oil maize, white-seeded maize, sweet maize and popping maize. Corn variation may be artificially defined according to kernel type as follows: dent, flint, flour, sweet, pop and pod corn. Excluding for pod corn, these divisions are based on the quality, quantity and pattern of endosperm composition in the kernel and are not indicative for natural relationships. Endosperm composition may be changed by a single gene difference, as in the case of floury (fl) versus flint (FI), sugary (su) versus starchy (Su), waxy (wx) versus non-waxy (Wx), and other single recessive gene modifiers that have been used in breeding special-purpose types of corn (Khan et al. 2018). The presence of great genetic diversity in the form of abundant favourable alleles in germplasm banks for biotic and abiotic resistance, productivity and high nutritional quality makes corn the most important cereal to combat food security problem (Prasanna 2012). Like other corn

types, popcorn with its nutritional benefits is one of the most important snack food worldwide. The distinguished characteristic of popcorn (*Zea mays everta* Sturt.) is that it expands from the kernel and puffs up when heated. Corn is able to pop because, its kernels have hard moisture-sealed hull and a dense starchy interior at temperature of about 177°C (Hoseney et al. 1983; Byrd and Perona 2005; Jele 2014). It is used primarily for human consumption as freshly popped corn or as the basis of popcorn confections. The optimum grain moisture content at popping varies over genotypes, however it usually ranges from 12% to 15% (Hoseney et al. 1983). Generation mean analysis is one of the genetic models which were developed for the estimation of different genetic effects in breeding populations (Kearsey and Pooni 2004). Generation mean analysis, a biometrical method developed by Mather and Jinks (1982: 396), is a useful technique for determining gene effects for polygenic traits. Its greatest merit lies in the ability to estimate epistatic gene effects such as additive $\times$ additive, dominance $\times$ dominance and additive $\times$ dominance effects (Singh and Singh 1992). Beside gene effects, breeders would also like to know; how much of the variation in a crop is genetic and to what extent this variation is heritable, because efficiency of selection mainly depends on additive genetic variance, influence of the environment and interaction between genotype and environment. Despite increasing consumption of popcorn the most important constrain is lack of narrow genetic base present in germplasm and popcorn varieties/hybrids production (Pajic et al. 2008; Sanches 2011). This research was initiated with the investigation of local and exotic germplasm for development of new popcorn hybrids. The objectives of the study were to determine variability among hybrids for grain yield and related traits and gene action involved in conditioning of these traits in popcorn hybrids.

2 Material and methods

Experiment was carried out at Cereal Crops Research Institute Pirsabak, Nowshera and Agriculture University

Peshawar, Pakistan. The genetic material used in this experiment comprised a set of four inbred lines of popcorn. Two of the four inbred line were from Bangladeshi origin and the other two were developed in Cereal Crops Research Institute, Pirsabak (Table 1). Six generations including two Parents, F_1 , F_2 , BC_1 and BC_2 were developed in two growing seasons for each cross by using manual pollination procedure of crossing and selfing as described by Russell and Hallauer (1980: 299-312). During the first growing season, four parents were crossed with each other to produce F_1 hybrids (Table 2). Part of seed from each inbred line and their resultant F_1 hybrid were grown in the field for the production of F_2 , BC_1 and BC_2 generations. F_2 generation of each cross was produced by selfing each F_1 , while BC_1 and BC_2 generations were developed by crossing F_1 with their male and female parents, respectively (Table 3 and 4).

Table 2: F_1 hybrids after crossing inbred lines

S.No	Female		Male
Cross-I	P-1	$\times$	P-3
Cross-II	P-1	$\times$	P-4
Cross-III	P-2	$\times$	P-3
Cross-IV	P-2	$\times$	P-4

The material encompassing 20 entries containing four each of parents, F_1 , F_2 , BC_1 and BC_2 were evaluated in triplicate using randomized complete block (RCB) design at Cereal Crops Research Institute Pirsabak, Nowshera and University of Agriculture Peshawar Pakistan. The plot size varied for different generations; where the non-segregating P_1 , P_2 and F_1 generations were planted in one row, while F_2 , BC_1 and BC_2 generations were sown in four rows each. Row length, row to row and plant to plant distances were kept at 5, 0.75 and 0.25m, respectively. Data were recorded in each plot for each replication on twenty plants in P_1 , P_2 and F_1 , while 60 plants were used for data recording in F_2 , BC_1 and BC_2 . Ear weigh at harvest, ear diameter, ear length, percent shelling and grain yield were also observed during the study.

Table 1: Pedigree of the parental inbred lines

S.No	Name	Code	Pedigree	Maturity
1	P-1	PS-1	PS-POP-1-1-4	Early
2	P-2	PS-2	PS-29-2-1	Early
3	P-3	BD-1	BD-POP-1-2-3-3	Moderate
4	P-4	BD-2	BD-POP-2-1-2	Moderate

Table 3: BC1 Generations

S.No	Female			Male	
1	(P-1	×	P-3)	×	P-1
2	(P-1	×	P-4)	×	P-1
3	(P-2	×	P-3)	×	P-2
4	(P-2	×	P-4)	×	P-2

Table 4: BC2 Generations

S.No	Female			Male	
1	(P-1	×	P-3)	×	P-3
2	(P-1	×	P-4)	×	P-4
3	(P-2	×	P-3)	×	P-3
4	(P-2	×	P-4)	×	P-4

2.1 Shelling Percentage

Grains from 10 randomly selected ears of each treatment were shelled after drying and then shelling percentage was calculated according to John (1991).

$$\text{Shelling (\%)} = \frac{\text{Weight of grains}}{(\text{Weight of grains} + \text{Weight of cobs})} \times 100$$

2.2 Grain Yield (kg ha⁻¹)

The grain yield of each plot was calculated in tones after harvesting and then adjusted the fresh ear weight to 150 g kg⁻¹ grain moisture (Carangal et al. 1971) using the following formula:

$$\text{Grain Yield Kg ha}^{-1} = \frac{(100 - \text{MC}) \times \text{FEW} \times \text{Shelling Co-efficient} \times 10,000}{(100 - 15) \times \text{Plot Area}}$$

Where,

MC = moisture content (%) in grains at harvest

FEW = Fresh ear weight (kg) at harvest

Shelling Co-efficient = Shelling percentage/100

2.3 Statistical Analysis

Combined analysis of variance (Gomez and Gomez 1983) procedure for randomized complete block (RCB) design for two locations were used to estimate components of variance using computer program SAS and to detect if significant variations existed among generations for the

standard plant parameters. Generation mean analysis was applied on parameters showing significant variations ($P \leq 0.05$) among generations.

Ethical approval: The conducted research is not related to either human or animal use.

3 Results

3.1 Ear weight

Six parameter model was found adequate for the inheritance interpretation of ear weight (Table 4). It also disclosed that both heritable and non-heritable gene action were responsible for the control of this trait. A dispersed type of non-allelic gene action was observed in cross PS-1 × BD-1, with non-significant effects of both additive and dominance gene actions. In cross PS-1 × BD-2, negative and positive significant nature of additive and dominance gene actions as well as duplicate type of non-allelic gene actions were found as controlling factors in the inheritance of ear weight. Similarly in cross PS-2 × BD-1 and PS-2 × BD-2, additive and dominance gene action with positive magnitudes and complementary non-allelic interactions were responsive agents for the inheritance of ear weight.

3.2 Ear length

Generation mean analysis of ear length revealed significant c^2 values in all four crosses which indicate that six parameter model was adequate to explain the inheritance of this trait (Table 4). In all crosses, dominant gene effects were positive and predominant. Additive gene action of significant nature with positive and negative signs was observed in PS-1 × BD-2 and PS-2 × BD-1. In cross PS-1 × BD-1, the effect of additive genes was negative with non-significant nature, while dominance and dominance × dominance effects were significant with positive and negative magnitude in nature, respectively. In cross PS-1 × BD-1 and PS-2 × BD-1 duplicate type of non-allelic interaction was found predominant in the inheritance study. Additive × additive gene action was positive and also significant in all the crosses except, PS-2 × BD-2. In cross PS-2 × BD-1 and PS-1 × BD-2 additive × dominance effect was found negatively significant. Similarly in cross PS-1 × BD-2 and PS-1 × BD-1, dominance × dominance was predominant with negative magnitude.

3.3 Ear diameter

The genetic analysis revealed that complex six parameter model was adequate to explain the inheritance pattern of ear diameter in all four crosses at both locations (Table 4). Additive genetic effects were found positive and significant in cross PS-1 $\times$ BD-2 and PS-2 $\times$ BD-1 at UOA, and cross PS-2 $\times$ BD-2 in CCRI. Dominant genetic effects were found positive and significant apart from PS-1 $\times$ BD-2 at UOA. Dominant effects were predominant in all the crosses. Among the non-allelic interactions, dominance $\times$ dominance interactions were non-significant in all crosses at both locations, while additive $\times$ additive interactions were positively significant in all crosses at CCRI, excluding PS-1 $\times$ BD-1. Genetic analysis for the inheritance of ear diameter revealed that additive $\times$ dominance effects were significant in all crosses except PS-1 $\times$ BD-2 and PS-2 $\times$ BD-2. A dispersed duplicate type of non-allelic interaction was observed in all four crosses at both locations.

3.4 Percent shelling

Generation mean analysis of ear length revealed significant c^2 values in all four crosses which indicate

that six parameter model was adequate to explain the inheritance of this trait (Table 4). In all crosses, dominant gene effects were positive and predominant. Additive gene action of significant nature with positive and negative signs was observed in PS-1 $\times$ BD-2 and PS-2 $\times$ BD-1. In cross PS-1 $\times$ BD-1, the effect of additive genes was negative with non-significant nature, while dominance and dominance $\times$ dominance effects were significant with positive and negative magnitude in nature, respectively. In cross PS-1 $\times$ BD-1 and PS-2 $\times$ BD-1 duplicate type of non-allelic interaction was found predominant in the inheritance study. Additive $\times$ additive gene action was positive and significant in all the crosses except, PS-2 $\times$ BD-2. In cross PS-2 $\times$ BD-1 and PS-1 $\times$ BD-2 additive $\times$ dominance effect was found negatively significant. Similarly in cross PS-1 $\times$ BD-2 and PS-1 $\times$ BD-1, dominance $\times$ dominance was predominant with negative magnitude.

3.5 Grain yield

Significant differences were revealed among six generations (P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2) obtained for grain yield (Fig. 1). Both additive and non-additive gen actions were found responsive in the inheritance of grain yield in all crosses both

Figure 1: Mean grain yield (kg/ha) P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 in Cross-I (a), Cross-II (b), Cross-III (c) and Cross-IV (d)

Table 5: Estimates of genetic effects for some quantitative traits in 4 maize crosses evaluated at UOA and CCRI

Parameter	Cross	Location	m	D	h	i	j	l	c2	Type of non-allelic interaction
Grain yield	PS-1 × BD-1		3806.68**	-378.77**	651.31*	-1181.20**	31.81ns	1204.11**	20.15**	Complementary
	PS-1 × BD-2	UOA	4274.7**	-229.24**	791.94**	-1764.03**	43.00ns	28.57ns	223.51**	---
		CCRI	3865.17**	-153.24ns	831.94**	-588.03*	119.00ns	-231.97ns	39.02**	---
	PS-2 × BD-1	UOA	3775.15**	271.10**	2204.02**	661.48**	184.32**	-2308.27**	88.27**	Duplicate
Ear length		CCRI	4184.69**	271.10**	2004.02**	661.48*	184.32*	-1621.07**	43.66**	Duplicate
	PS-2 × BD-2	UOA	3979.92**	391.35**	1520.06**	-234.38ns	166.23**	-1465.17**	175.99**	Duplicate
		CCRI	4566.12**	391.35**	613.39*	-941.05**	166.23*	-71.29ns	129.56**	---
	PS-1 × BD-1	-----	12.34**	-0.33 ^{ns}	8.96**	4.05**	0.40 ^{ns}	-6.15*	7.84*	Duplicate
Ear diameter	PS-1 × BD-2	-----	12.86**	0.67*	8.71**	2.17*	0.46 ^{ns}	-4.92 ^{ns}	8.44*	---
	PS-2 × BD-1	-----	13.16**	-1.06**	6.73**	2.75*	-1.02**	-5.95*	14.34**	Duplicate
		-----	13.05**	0.17 ^{ns}	3.79**	-0.80 ^{ns}	-0.73*	-0.92 ^{ns}	7.96*	---
	PS-1 × BD-1	UOA	2.82**	-0.17ns	1.81**	1.10**	-0.07ns	-1.39ns	12.59**	---
Percent Shelling		CCRI	3.44**	-0.27**	0.52*	-0.32ns	-0.19ns	0.75ns	8.06*	---
	PS-1 × BD-2	UOA	2.84**	0.28**	-0.04ns	-0.79**	0.06sn	1.10ns	3.69**	---
		CCRI	3.06**	-0.09ns	1.73**	1.14**	-0.31**	-2.31ns	41.08**	---
	PS-2 × BD-1	UOA	2.74**	0.24**	0.68**	0.22ns	0.14ns	0.94ns	25.3**	---
Ear weight		CCRI	2.98**	-0.04ns	1.57**	1.34**	-0.10ns	-1.35ns	24.23**	---
	PS-2 × BD-2	UOA	2.56**	-0.16*	1.02**	0.35ns	-0.58**	0.54ns	52.74**	---
		CCRI	2.87**	0.46**	1.78**	1.32**	0.10ns	-1.62ns	21.51**	---
	PS-1 × BD-1	-----	77.56**	-1.74ns	20.65**	13.14*	1.85ns	-26.67**	11.97**	Duplicate
Percent Shelling		UOA	80.99**	-1.08ns	29.13**	13.05ns	4.39**	-32.39**	24.06**	Duplicate
	PS-2 × BD-1	CCRI	73.80**	-1.34ns	13.66*	13.59*	4.12*	-3.06ns	24.56**	---
		UOA	74.43**	-0.25ns	17.63*	---	---	---	5.92ns	---
	PS-1 × BD-1	-----	96.12**	-4.47ns	15.05ns	-26.13**	6.15*	3.30ns	58.0**	---
Percent Shelling		-----	96.05**	-4.13*	30.42**	-15.73*	0.48 ^{ns}	-31.30**	161.0**	Duplicate
	PS-2 × BD-1	-----	99.27**	5.88**	20.85*	-16.97*	4.20ns	14.83*	9.9*	Complementary
		-----	99.17**	4.60*	25.25**	-18.20*	-3.08ns	4.97 ^{ns}	23.9**	Complementary
	PS-2 × BD-2	-----								

m = mean, d = additive, h = dominance, i = additive × additive, j = additive × dominance, l = dominance × dominance

at UOA and CCRI (Table 4). Likewise additive gene action of negative sign was observed in cross PS-1 $\times$ BD-1. Additive gene action was negative and non-significant in cross PS-1 $\times$ BD-2 at CCRI, however it was negative but significant at UOA. PS-2 $\times$ BD-1 and PS-2 $\times$ BD-2 exhibited positive effects of additive effects at UOA and CCRI. Both complementary and duplicate type of non-allelic gene action was observed to be involved in the grain yield inheritance. Significant values of additive and dominance gene actions as well as additive $\times$ additive and dominance $\times$ dominance type of epistasis in cross PS-1 $\times$ BD-1, PS-2 $\times$ BD-1 and PS-2 $\times$ BD-2 revealed that the trait was under a complex control. In cross PS-1 $\times$ BD-1, with negative and positive magnitudes of additive and dominance gene actions, complementary type of epistasis was also observed. Similarly in cross PS-2 $\times$ BD-1 and PS-2 $\times$ BD-2, where the same female (PS-2) parent was utilized; both additive and dominance of positive magnitudes and duplicate type of non-allelic gene actions were found responsible for controlling grain yield in both UOA and CCRI.

4 Discussion

4.1 Ear weight

Both additive and dominance effects were found prominent in the controlling inheritance of ear weight. Role of dominance was more comparing to additive gene actions in all the crosses. Similarly, in digenic effects additive $\times$ additive was more predominant. This shows that effective role of both additive (d) and additive $\times$ additive (i) can be successfully utilized for the improvement of ear weight through selection. Ojo et al. (2006) also reported similar results of additive effects for ear weight in their study of maize inbred lines. Likewise in crosses where dominance and dominance $\times$ dominance genetic effects are prevailing could be utilized in hybrid programs efficiently. Mendes-Moreira et al. (2015) also reported the prevalence of digenic effects in the inheritance of ear weight at harvest in the QTL analysis of PB260 $\times$ PB266 progeny. A dispersed type of non-allelic gene action was observed in cross PS-1 $\times$ BD-1 having non-significant effects of both additive and dominance gene actions. In cross PS-1 $\times$ BD-2, negative and positive significant nature of additive and dominance gene actions as well as duplicate type of non-allelic gene actions were found in the inheritance of ear weight. Similarly in cross PS-2 $\times$ BD-1 and PS-2 $\times$ BD-2, additive and dominance gene action with positive magnitudes, and complementary non-allelic interactions were preponderant for the inheritance of ear

weight. Similar findings regarding the presence of non-additive effects for ear weight in maize was also reported by Sujiprihati et al. (2003).

4.2 Ear length

Being an important yield component, ear length was revealed to be controlled by a combination of additive and non-additive gene actions. In all crosses, dominant gene effects were positive and predominant over other allelic and non-allelic interactions. Based on prominent dominant gene action, ear length could be considered as important attribute in the selection of inbred lines for the development of maize hybrids. Similar results of dominant genetic effects have been reported by Dorri et al. (2014) and Wannows et al. (2015). Like dominant genes, additive gene action also exerted a role in the inheritance of ear length in two of the four crosses; which is an indication of improvement for this trait. Our results of additive effects for ear length are in conformity with Chandal & Mankotia (2014) and Alamerew & Warsi (2015). Non-allelic interaction of dominance $\times$ dominance was higher in magnitude with negative nature compare to other epistatic interactions. Similarly additive $\times$ additive interactions were positively significant in three crosses, which resulted in a duplicate type of non-allelic interaction in two crosses. Similar results of greater genetic diversity in maize inbred lines for ear length have also been reviewed by Ali et al. (2007) and Singh and Roy (2007) and Wannows et al. (2015).

4.3 Ear diameter

Generation mean analysis of ear diameter revealed that both additive and non-additive gene actions were involved in the inheritance of this trait. This indicates that selection of inbred lines in early generations and their exploitation in hybrid breeding program will lead to the production of useful hybrids. Additive effects observed in all the crosses were positively significant except, PS-1 $\times$ BD-1. This specifies that selection based on ear diameter will be effective in early generations. Our results are also corroborated by Haddadi et al. (2012) and Nataraj et al. (2014). Muraya et al. (2006) also suggested the existence of both additive and non-additive gene action for ear diameter. Positively significant and predominant nature of dominant gene actions observed in all crosses can be effectively utilized in hybrid breeding programs. Zivanovic et al. (2010) also reported involvement of dominant genes in the inheritance of ear diameter. Epistatic

interactions including additive $\times$ additive and additive $\times$ dominant were found to have a significant role in the control of ear diameter, while dominance $\times$ dominance epistatic interactions were negative and non-significant in all crosses. A dispersed duplicate type of non-allelic interaction was observed in all four crosses. Similar findings of non-allelic interactions for ear diameter were also confirmed by Sujiprihati et al. (2003), Kumar et al. (2006), Ali et al. (2007) and Singh and Roy (2007).

4.4 Percent shelling

The most important contributor to the inheritance of shelling percentage was dominant gene action although some of the non-allelic interactions like additive $\times$ additive and dominance $\times$ dominance also played their role. This indicates that these inbred parents could be effectively exploited for superior hybrids. Similar results of non-additive effects for shelling percentage were reported by Sujiprihati et al. (2003), Sah et al. (2014) and Pérez-López et al. (2014). Niyonzima et al. (2015) reported that inheritance of percent shelling was under control of additive, dominance and epistatic gene actions. In all crosses, additive $\times$ additive and dominant $\times$ dominant non-allelic interactions were significantly positive and negative, respectively. Such occurrence of non-allelic interactions represented duplicate type of digenic interactions which is an indication of greater genetic diversity. The fixable heritable epistasis could be effectively used in the selection of superior inbred lines. Our results of duplicate epistasis for shelling percentage in maize are corroborated by previous researchers like Ravikant et al. (2006). Similar results of epistatic effects for percent shelling were also reported by Niyonzima et al. (2015) in their maize populations.

4.5 Grain Yield

The presence of both additive and non-additive gene effects revealed the complex genetic nature of grain yield. Along with additive and dominance gene actions, all types of epistasis were also observed, showing presence of greater genetic diversity among the parents involved in the crosses. Presence of such genetic diversity is of prime importance for traits like yield and it must be exploited by plant breeders to achieve their goals (Idahosa et al. 2010). According to Iqbal et al. (2009) selection of desirable parents and information about the nature and magnitude of gene action for a quantitative trait is of paramount

importance for a plant breeder. In all crosses due to higher magnitude, dominant genes were having predominant effects for grain yield, whereas, additive gene action and additive $\times$ additive type of epistasis, was also found having its proportion in the inheritance of this trait. Due to fixable nature of selection from additive effects, gain from selection could be possible for grain yield. Wannows et al. (2010) also observed similar results of additive effects for grain yield while studying genetic variability through path coefficient analysis in maize. Our results corroborates the findings of Ojo et al. (2006), Musila et al. (2010) and Ofori et al. (2015) also observed additive gene action for grain yield in maize and proposed that simple selection would be effective to make desirable improvement in the studied genotypes for grain yield. Similarly due to predominance of additive gene to non-additive gene, Mhike et al. (2011) hinted the possibility of exploring early testing of genotypes. Crosses dominant nature of inheritance, could be judiciously utilized for hybrid development in maize breeding programs. The predominant nature of non-additive gene effects in the inheritance of grain yield were also reported by previous reviewers like, Mhike et al. (2011), Abuali et al. (2012) and Dawod et al. (2012). Similarly Khalil et al. (2010) also observed that along with non-additive effects additive gene action was responsible in controlling the inheritance of grain yield.

5 Conclusion

The evaluation of available popcorn germplasm revealed significant genetic diversity for grain yield and related traits. Generation mean analysis disclosed that almost all the yield related traits were controlled by dominant gene action which can be effectively utilized for hybrid production. The F_1 hybrid obtained from cross between PS-29-2-1 and BD-POP-2-1-2 was found the top yielder.

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