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Heterosis and heritability analyses for plant yield and some quality traits in F_1 and F_2 generations of maize

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ABSTRACT
This study was conducted to analyze the genetic effects for grain yield and some important kernel quality traits in maize. Eight parental lines and their six hybrids were used as plant material. Field experiments to evaluate plant material were carried out in two locations (Çanakkale and Bursa) in 2013. The observed traits were single plant yield, protein content and oil content. Additive, dominance and additive × additive models were utilized to analyze the data. Variance component estimations showed that single plant yield was under the control of dominance type gene action; while protein and oil content were controlled by additive type gene action. High values (> 60 %) of broad (H^2) and narrow sense (h^2) heritabilities were observed for protein and oil content. The mean of F_1 generation for single plant yield and oil content were higher than the mean of F_2 generation for these traits. Most of hybrids had positive mid parent heterosis (Hmp) and better parent heterosis (Hbp) for single plant yield, while they had negative heterosis values for protein content. Except for one cross (A680×IHO), all of crosses had positive Hmp values for oil content.

Keywords:
Protein
Oil
Genetic analysis
Zea mays

Mısırın F_1 ve F_2 nesillerinde bitki verimi ve bazı kalite özellikleri için heritabilite ve heterosis analizleri

ÖZET
Bu çalışma mısırda bazı önemli tane kalite özellikleri ile tane veriminin genetik analizlerini yapmak amacıyla yürütülmüştür. Çalışmada sekiz ebeveyn hat ve bunlara ait 6 adet hibrit, materyal olarak kullanılmıştır. Tarla denemeleri 2013 yılında iki ayrı lokasyonda (Çanakkale ve Bursa) yürütülmüştür. Gözlemlenen özellikler tek bitki verimi, protein oranı ve yağ oranıdır. Verilerin analizinde eklemeli, dominans ve eklemeli × eklemeli modeller kullanılmıştır. Varyans bileşen analizleri, tek bitki veriminin dominans gen etkilerinin, protein ve yağ oranlarının ise eklemeli genlerin kontrolü altında olduğunu göstermiştir. Protein ve yağ oranı için geniş (H^2) ve dar anlamda (h^2) kalıtım dereceleri yüksek (>% 60) bulunmuştur. Tek bitki verimi ve yağ oranı için F_1 neslinin ortalaması F_2 neslinden daha yüksek bulunmuştur. Hibritlerin büyük kısmı tek bitki verimi için anaç ortalamalarına (Hmp) ve üstün anaca (Hbp) göre pozitif heterosis gösterir iken, protein oranı için negatif heterosise sahip olmuşlardır. Bir melez (A680×IHO) dışında, bütün melezlerin Hmp değerleri pozitif bulunmuştur.

Anahtar Sözcükler:
Protein
Yağ
Genetik analiz
Mısır

1. Introduction

The main breeding objective in maize is increasing the grain yield to serve food requirements of human and animals. Additionally, enhancing some quality traits such as protein and oil has become important breeding objectives in maize research. Maize breeders have spent out a great effort to achieve these objectives. Obtaining successful results in breeding experiments is related to understanding the genetic structure and effective type of gene action in breeding materials.

Different types of genetic analyses are performed to understand the type of gene actions on the studied traits. Among these, heterosis analysis is applied to determine the degree of hybrid vigor for the investigated trait. Heterosis was first described by Shull as overexpression of F_1 individuals over their midparent values (Shull, 1908). Other terms about hybrid vigor are heterobeltiosis and useful heterosis, which describe the overexpression of F_1 individuals over better parent and a commercial variety, respectively (Ryder et al., 2014). In the effort to explain heterosis, two prominent theories are dominance and over dominance theories, both of which depend on single locus theory (Crow, 1952).

Some researchers reported that epistatic interactions also played an important role on the occurrence of heterosis (Schnell and Cockerham, 1992). Conventional method of heterosis estimation gives limited information to breeders as it is not able to determine the type of gene action (Smith, 1986). Estimations based on dominance and over dominance theories also lack the ability to determine epistatic effects. Xu and Zhu (1999) developed a mixed linear model, namely as additive, dominance and additive × additive model (ADAA), to predict epistatic effects more efficiently. This model can be used to estimate genetic variance component, heterosis, genetic effects and their interactions with environment. The most important advantage of this model is that it is applicable to both balanced and unbalanced data (Xu and Zhu, 1999). ADAA model was used to estimate genetic effects and genotype-by environment interaction for some other plant species. Shahid et al. (2012), used this model for genetic analysis and heterosis evaluation for grain yield and some quantitative traits in autotetraploid rice. Xing et al. (2014) applied ADAA model for parental selection in hybrid breeding based on maternal and paternal inheritance of traits in rapeseed. Ma et al., (2012) conducted a multiple environment study to understand genetic behavior of some quality traits in tobacco using ADAA model. To our best knowledge, this model has not been utilized to study genetic mechanism of single plant yield and kernel quality traits in maize.

The objectives of this study were; (i) to determine genotype × environment interaction for yield and some quality traits in maize using an ADAA model, (ii) to determine the heterosis levels and find out the appropriate hybrids with high level of heterosis and mean values.

2. Material and Methods

2. 1. Material

We used six parental lines in this study as plant material (Table 1). Six F_1 crosses (IHO×B73, IHO×HYA, IHO×Mo17, A680×IHO, IHP×IHO, Mo17×IHO) were generated in 2011 and their F_2 generations were generated in 2012.

Table1. The plant materials used in this study.

Parent	Specialty	Kernel type	Source
IHO	High oil line	Flint	USA
A680	Normal line	Dent	Turkey
IHP	High protein line	Flint/Dent	USA
Mo17	Elite inbred	Dent	Turkey
B73	Elite inbred	Dent	Turkey
HYA	High oil and protein	Flint/Dent	Turkey

All parents and crosses were tested at two locations (Çanakkale and Bursa) in Northwest of Turkey in 2013. Daily mean temperature and monthly rainfall values are summarized in Figure 1. Generally, Çanakkale location was hotter than Bursa location. Also more precipitation was observed in Bursa location between May and July (Figure 1). Soil characteristics of both experimental areas were similar; loamy, low on organic matter content, slightly alkaline.

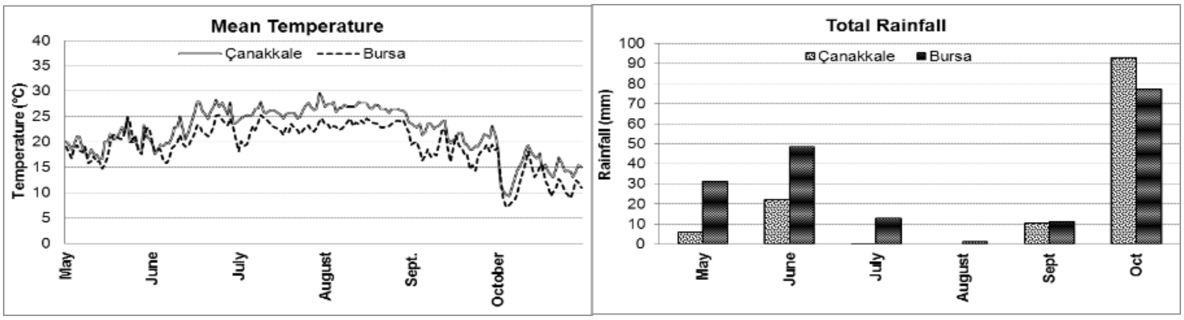

Figure1. Daily temperature and monthly total rainfall values during experimental session (2013) in Çanakkale and Bursa locations.

2. 2. Method

Evaluation experiments used a randomized complete block design with three replicates. Each genotype was planted in 2-row plots, 2 m in length and 0.70 m row apart. Planting was made at 17 May 2013 in Çanakkale location and 24 May 2013 in Bursa location. Drip irrigation was applied as needed. Plots were fertilized with 180 kg/ha pure nitrogen. Controlled pollination was applied to prevent pollen contamination among the genotypes. Five to six randomly selected plants were pollinated by hand for each genotypes. Harvest was made by hand and five to six self-pollinated ears were sampled. In each location, 10 plants were selected at random from P_1, P_2 and F_1 generations while 30 plants were taken from F_2 generations. Same numbers of open pollinated ears were also taken from each generation to determine single plant yield. Thus, a total of 720 ears (360 from each location) were analyzed in this study.

All ears were shelled then kernels obtained from open pollinated ears were weighed and recorded. After shelling process, self-pollinated samples were ground in laboratory mill (Fritsch pulverisette 14, Germany) with 0.5 mm sieve. Determination of protein and oil content of samples was performed using NIR spectroscopy (Spectrastar 2400D, Unity Scientific, USA). Ground samples were put into NIR sample cup and scanned in 1200-2400 nm with one nm interval. Scans were applied to a local calibration model to estimate protein, oil and contents of the samples.

To estimate variance components, heritability and heterosis values, we used an additive, dominance and additive × additive model (Zhu and Weir, 1996). Heterosis over parent mean was estimated by the following formula; $Hmp(Fn)=(1/2)^{n-1}\Delta_D+2AA$. Heterosis over better parent was estimated as $Hbp(Fn)=(1/2)^{n-1}-1/2\omega_G$. In these formulas, AA, Δ_D and ω_G indicated the additive + additve effects, dominance heterosis and genotypic differences between the parents, respectively (Xu and Zhu, 1999). Adjusted unbiased prediction method (AUP) for predicting genetic effects and jackknife sampling procedure was applied to for testing the significance of estimated values (Xu and Zhu, 1999). General heritability in broad sense (H^2G), narrow sense (h^2G), interaction heritability values in narrow (h^2GE) and broad sense (H^2GE) values were estimated based on the variance component estimations. A t test was applied to evaluate the significance of estimated parameters. Statistical analysis was performed by the QGAStation 1.0 (Chen and Zhu, 2003).

3. Results and Discussion

The means and the ranges by the locations are shown in Table 2. Mean of single plant yield (125.3 g) and oil content (7.93%) were higher in Çanakkale, while protein content was higher in Bursa location (12.79%). A considerable variation was observed for all traits in all generations (Table 2). The variation in protein and oil contents can be attributed to the fact that there were special maize genotypes in pare ntal sets, such as IHO and IHP.

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Table 2. Mean and range values for observed traits in generation by locations.

		Single Plant Yield		Oil Content		Protein Content	
	n	Mean	Range	Mean	Range	Mean	Range
Bursa	360	114.2	57.5-205.0	7.41	3.58-11.38	12.79	9.38-21.78
P	60	96.3	61.2-131.5	6.43	3.58-10.93	13.31	10.06-21.78
F_1	60	142.8	57.5-205.0	8.42	6.92-11.38	12.36	9.38-17.33
F_2	240	109.4	62.3-160.6	7.70	6.24-11.33	12.54	10.18-16.33
Çanakkale	360	125.3	34.5-227.9	7.93	3.45-13.27	11.74	8.54-20.38
P	60	84.9	34.5-177.6	6.93	3.45-13.27	12.37	8.55-20.38
F_1	60	156.9	74.7-227.9	8.66	7.06-11.70	11.13	8.54-17.03
F_2	240	147.7	93.9-199.1	8.55	6.68-12.53	11.51	9.10-15.41

The results of variance component estimations are summarized in Table 3. The ratio of additive and dominance variances to phenotypic variance (VA/VP and VD/VP) was significant for all observed traits. Dominance variance had the highest proportion in phenotypic variance for single plant yield. The proportion of additive + additive variance in phenotypic variance was only significant for protein and oil contents. Proportional value of interaction effects of dominance and additive + additive with environment were significant ($p<0.01$) for single plant yield; while, the ratio of interaction of additive effects with environment were significant ($p<0.01$) for protein and oil content. General heritability in narrow sense (h^2G) and broad sense (H^2G) were significant ($p<0.01$) for the three observed traits. However, heritability values for protein and oil content had higher values than single plant yield. The interaction heritability values in broad and narrow sense were higher in single plant yield compared to kernel biochemical traits (Table 3). When considering relatively higher values of narrow sense heritability values for protein and oil contents one can argue that the gene action for these traits is mostly additive, while single plant yield seem to be controlled by dominance gene action (Table 3).

Table 3. Proportion of variance component estimations and heritability values for observed traits.

Parameters	Single Plant Yield	Protein Content	Oil content
VA/VP	0.051**	0.519**	0.681**
VD/VP	0.386**	0.161**	0.066**
VAA/VP	0.000	0.107**	0.051**
VAE/VP	0.000	0.057**	0.049**
VDE/VP	0.109**	0.016	0.063**
VAAE/VP	0.197**	0.000	0.000
VR/VP	0.256**	0.141**	0.090**
h^2G	0.051**	0.626**	0.732**
H^2G	0.437**	0.786**	0.797**
h^2GE	0.197**	0.057**	0.049**
H^2GE	0.306**	0.073**	0.112**

** Significantly different from zero at $p<0.01$. VA: Additive variance, VP: Phenotypic variance, VD: Dominance variance, VAA: Additive × additive variance, VAE: Interaction variance of additive, VDE: Interaction variance of dominance, VAAE: Additive × additive with environment, VR: Residual variance. h^2G, H^2G, h^2GE, H^2GE indicate general heritability and interaction heritability values in narrow (h^2) and broad sense (H^2), respectively.

Melchinger et al. (1986) reported that dominance effects were greater than additive effects for grain yield in maize. It was previously shown that oil content was under the control of additive gene actions (Dudley, 1977; Hussain et al., 2015). Our results were in consistence with previous studies. Interaction of additive, dominant and additive + additive variance had generally low portion of phenotypic variance. Heritability values suggest that protein and oil contents were highly heritable traits (heritability values over 60%), with relatively low effect of environmental changes on them.

General heterosis and predicted genotypic values are summarized in Table 3. Five crosses had higher genotypic values for single plant yield in F_1 generation compared to F_2 generation, except only one (IHP×IHO) cross. This suggests the occurrence of transgressive segregation, which is due to dominance + dominance and additive × additive interaction. Mean value for protein content in F_1 generation was lower (11.87%) than that in F_2 (12.24%); while, mean oil content was higher in F_1 (Table 3). It was found that mean grain yield was higher in F_1 generation than F_2 (Joshi et al., 2004); contrarily, protein content was higher in F_2 than F_1 generation in wheat (Yao et al., 2014). Our results were consistent with the results of previous studies which compared the genotypic performances in F_1 and F_2 generations.

Later generations also show some degree of heterosis (Flachenecker et al., 2006). In general, Hmp values in F_1 generation were higher than those in F_2 generation for single plant yield. For protein content, negative and low heterosis values were observed for all of the crosses. Although most crosses had positive values for Hmp for oil content, they were low and non-significant (Table 4). Highly significant Hbp in F_1 and F_2 generation were observed for protein and oil content, most of which were negative values. Falconer and Mackay (1996) argued that heterosis had inverse relationship with inbreeding depression. In maize, yield and related traits generally had high and positive heterosis; however, quality traits such as protein and oil content generally low and/or negative heterosis. On the other hand, single plant yield and related heterosis value were declined in later generations (Flachenecker et al., 2006). In our study, all of crosses had also higher heterosis values in F_1 generation, except IHP×IHO cross (Table 4).

Predicted interaction heterosis for each traits and heterotic performance of each specific cross are summarized Table 5. Positive Hmp and Hbp values were observed for single plant yield with the exception of F_2 generation in Bursa location (Table 4). Both types of heterosis showed positive significant values in Çanakkale location. Mean Hmp and Hbp values were negative in both locations for protein content. However, only Hbp for protein content was negative and significant in both locations. We observed positive and significant Hmp for oil content in Bursa location, while, it was negative and non-significant in Çanakkale location; Similarly, Hbp values for oil content were positive in Bursa location, while, they had negative values in Çanakkale location. Hbp values were significant for both locations except for F_2 generation in Bursa location (Table 5).

In practice, understanding the heterotic performance of each cross over the population mean is important. The heterotic performances of each experimental cross are given in Table 5. We found positive and significant Hmp in Çanakkale location for the hybrids IHO×B73, IHO×HYA and IHP×IHO. Hbp for single plant yield was nonsignificant for all crosses in Çanakkale location, however, there were significant but negative values in Bursa location for some crosses such as IHO×HYA and IHP×IHO.

Table 4. Genotypic values and heterosis of six maize crosses for observed traits in F_1 and F_2 generations.

	Pre(F_1)	Pre(F_2)	Hmp(F_1)	Hmp(F_2)	Hbp(F_1)	Hbp(F_2)
Single Plant Yield (g)						
IHO×B73	182.3	141.1	0.689	0.265	0.628	0.284*
IHO×HYA	144.5	115.5	0.485	0.137	0.434**	0.192**
IHO×Mo17	171.8	133.5	0.639	0.276	0.616	0.297**
A680×IHO	179.7**	142	0.629	0.159	0.565	0.251*
IHP×IHO	70.86	90.49**	-0.328	0.129	-0.343**	-0.179**
Mo17×IHO	181.6**	142.4	0.656*	0.161*	0.582	0.254*
Mean	155.1**	127.5	0.461**	0.231**	0.414	0.183**
Protein Content (%)						
IHO×B73	11.17	11.41	-0.076	-0.056*	-0.251**	-0.231**
IHO×HYA	10.53	12.55	-0.303	-0.138	-0.303*	-0.138**
IHO×Mo17	10.61*	11.24*	-0.144	-0.093*	-0.296**	-0.245**
A680×IHO	10.52**	10.31**	-0.047	-0.064*	-0.214**	-0.231**
IHP×IHO	17.03**	17.17**	-0.091	-0.081	-0.500**	-0.489**
Mo17×IHO	11.35	10.78**	-0.016	-0.062	-0.146**	-0.193**
Mean	11.87	12.24	-0.112**	-0.082**	-0.285**	-0.255**
Oil Content (%)						
IHO×B73	9.994**	9.412**	0.121	0.045	-0.504*	-0.580**
IHO×HYA	12.652**	12.320**	0.064	0.021	-0.158	-0.201**
IHO×Mo17	8.885**	8.777**	0.016	0.002	-0.649**	-0.663**
A680×IHO	8.508	8.692*	-0.051	-0.027	-0.586**	-0.562**
IHP×IHO	10.432	9.314**	0.222	0.076	-0.335	-0.481**
Mo17×IHO	8.553*	8.190*	0.047	0.000	-0.580**	-0.627**
Mean	9.837**	9.451**	0.070*	0.019	-0.468**	-0.519**

*,** Significantly different from zero at $p<0.05$ and $p<0.01$, respectively. Pre (F_1) indicates the predicted genotypic values of F_1. Hmp: General heterosis over mid parent. Hbp: General heterosis over better parent based on population mean for each cross.

Only one cross (A680×IHO) showed positive and significant Hmp for protein content in Çanakkale location. In Bursa location, none of the genotypes had significant Hmp values for protein content. Three crosses (IHO×B73, IHP×IHO and Mo17×IHO) showed negative significant Hbp in Çanakkale location for both F_1 and F_2 generations, while two crosses (IHO×HYA and IHP×IHO) and three crosses (IHO×HYA, IHO×Mo17, A680×IHO and IHP×IHO) had negative heterosis in Bursa location for F_1 and F_2 generations, respectively. None of the crosses had significant heterosis for oil content of F_1 generation in both locations. However, A680×IHO cross showed positive and significant Hmp in F_2 generation of Çanakkale location. Four (IHO×B73, IHO×HYA, IHO×Mo17 and Mo17×IHO) and two crosses (IHO×HYA and IHP×IHO) had significant Hbp for oil content of F_1 generation for Çanakkale and Bursa locations, respectively. Interestingly, those crosses had negative values in Çanakkale, but positive values in Bursa. Similarly, negative and significant Hbp in all crosses was observed in Çanakkale location, except the cross of A680×IHO. Two crosses (IHO×HYA and IHP×IHO) had positive and significant Hbp for oil content of F_2 generation in Bursa location, however, A680×IHO cross had negative value for this trait. Our results revealed that heterosis performances of crosses varied by the environmental effects.

4. Conclusion

In conclusion, results of this study showed that single plant yield was under the control of dominance gene effects; while, protein and oil content were controlled by additive type gene action in these genotypes. In general, positive heterosis was observed for single plant yield, while negative heterosis was observed for protein content. Environment had an effect on Hmp and Hbp for oil content, and it was observed that genotypes had positive heterosis in Bursa, while they had negative hetorosis in Çanakkale. Based on general Hmp values (Table 4), crosses had positive heterosis for single plant yield and oil content, except IHP×IHO and A680×IHO, respectively. All crosses showed negative general Hbp values for protein and oil content. But some of crosses, such as A680×IHO, showed positively significant Hmp values in Çanakkale location. Thus, we concluded that heterosis for oil and protein content could be affected by environmental conditions.

Table 5. Genotypic values and heterosis and their interaction with environment for observed traits in F_1 and F_2 generations.

	Pre(F_1)		Pre(F_2)		Hmp(F_1)		Hmp(F_2)		Hbp(F_1)		Hbp(F_2)	
	Çanakkale	Bursa	Çanakkale	Bursa	Çanakkale	Bursa	Çanakkale	Bursa	Çanakkale	Bursa	Çanakkale	Bursa
Single Plant Yield (g)												
IHO×B73	25.2	24.2	6.04	13.3	0.69**	0.05	0.53**	-0.04	0.57	0.04	0.41	-0.05
IHO×HYA	9.07	9.06	-9.76	6.75	0.58**	0.04	0.42**	0.03	0.48	-0.08**	0.32	-0.10**
IHO×Mo17	26.1	6.49	30.0	-25.3	0.64	-0.04	0.67*	-0.30	0.46	-0.10	0.50	-0.37
A680×IHO	4.92	44.9*	8.40	14.0	0.55*	0.25	0.58**	-0.01	0.52	0.24	0.55	-0.02
IHP×IHO	-30.4**	-4.95	-20.4**	-0.65	0.26	-0.17	0.34	-0.13	0.23	-0.18**	0.32	-0.14**
Mo17×IHO	12.8	25.1	17.6*	-8.27	0.49	0.14	0.53	-0.14	0.34	0.07	0.37	-0.21
Mean	7.96	17.5*	5.32	-0.03	0.53**	0.05	0.51**	-0.10*	0.43**	0.00	0.41**	-0.15**
Protein Content (%)												
IHO×B73	0.46	-0.85	0.19	-0.47	0.04	-0.06	0.022	-0.031	-0.009**	-0.074	-0.031**	-0.043
IHO×HYA	-0.52	-0.44	0.06	-0.14	-0.09	-0.05	-0.047	-0.024	-0.101	-0.056**	-0.053	-0.032**
IHO×Mo17	-0.39	-0.23	0.01	-0.36	-0.07	0.02	-0.033	0.011	-0.078	-0.023	-0.046	-0.034*
A680×IHO	-0.73	0.09*	-0.76	0.03	0.01*	0.01	0.003**	0.005	-0.040**	0.005	-0.043*	0.000**
IHP×IHO	0.50**	1.29	0.65*	1.20	-0.02	0.01	-0.012	0.007	-0.108*	-0.074**	-0.096**	-0.081**
Mo17×IHO	-0.15	-0.07	-0.20*	-0.27	0.01	0.03	0.004	0.016	0.007**	-0.008	0.003*	-0.024
Mean	-0.14	-0.03	-0.01	0.00	-0.02	-0.01	-0.011	-0.003	-0.055**	-0.039**	-0.044**	-0.036**
Oil Content (%)												
IHO×B73	0.48	1.09	0.56**	0.31	-0.02	0.20	-0.010	0.101	-0.23**	0.19	-0.22**	0.08
IHO×HYA	1.20	1.02	1.37**	0.45	-0.04	0.15	-0.022	0.074	-0.13*	0.12**	-0.11**	0.05**
IHO×Mo17	0.21	0.28	0.41*	-0.05	-0.05	0.09	-0.027	0.044	-0.26**	0.08	-0.24**	0.04
A680×IHO	0.27	-0.45*	0.26	-0.22	0.00*	-0.06	0.001**	-0.030	-0.18	-0.11	-0.18	-0.08*
IHP×IHO	1.34**	1.05	0.87**	0.18	0.12	0.23	0.062	0.114	-0.04	0.19**	-0.10*	0.07**
Mo17×IHO	-0.81	1.45	-0.10*	0.31	-0.18	0.30	-0.092	0.149	-0.32**	0.24	-0.23*	0.09
Mean	0.45	0.74*	0.56**	0.16	-0.03	0.15**	-0.015	0.076**	-0.19**	0.12*	-0.18**	0.04

*, ** Significantly different from zero at $p<0.05$ and $p<0.01$, respectively. Pre(F_1) and Pre(F_2) indicates the predicted genotypic values of F_1 and F_2 generations, respectively. Hmp: General heterosis over mid parent. Hbp: General heterosis over better parent based on population mean for each cross.

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