

## ESTIMATES OF GENETIC VARIANCE COMPONENT OF AN EQUILIBRIUM POPULATION OF CORN

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### ABSTRACT

There are abundant maize populations in Hardy-Weinberg equilibrium, which can be used as source of gene to develop either a hybrid variety or an open pollinated variety. Genetic parameters of a population, such as additive genetic variance and variance due to dominance which can be estimated using North Carolina Design I, were used to decide a breeding method to be applied. The objectives of this research were to estimate the genetic variance component of important quantitative traits in an equilibrium corn population and to decide the best method to develop the population. The research was conducted at Agricultural Station of Agriculture Faculty, Gadjah Mada University, in 2012 which was carried out in two steps: to develop half-sib and full-sib families and to evaluate both families in randomized complete block design with three replications. The data was subjected to analysis of variance, and was followed by estimation of genetic variances. The additive variance of ear length and ear diameter of the corn population was greater than dominance variance. In contrary to kernel weight/ear, the dominance variance was greater than additive variance. So based on kernel weight/ear, the Hardy-Weinberg equilibrium corn population can be developed through inbreeding to form a hybrid variety.

Keywords: breeding, corn, genetic variance

### INTRODUCTION

Maize (*Zea mays* L.) is one of the three most important cereal crops in the world together with wheat and rice. Data from the United Nations (UN) and Food and Agriculture

Organization (FAO) showed that in 2006 world maize cultivation reached 144 million hectares, wheat was 216 million, and rice was 154 million hectares (FAOSTAT, 2008). In terms of production, however, maize surpasses wheat and rice. World maize production for 2006 was 695 million metric ton, while that of wheat was 606 and rice was 635 million ton. Although 70% of the world maize area was in developing countries, only 49% of the world's maize was produced there (FAOSTAT, 2008).

Maize is naturally a cross-pollinated plant, and if they are maintained as such, they will eventually in equilibrium. In 1908 Hardy and Weinberg independently demonstrated that in a large random mating population both gene frequencies and genotypic frequencies remain constant from generation to generation in the absence of mutation, migration, and selection. Such a population is said to be in Hardy-Weinberg equilibrium and remains so unless any disturbing force changes its gene or genotypic frequency (Hallauer *et al.*, 2010). Therefore, there are abundant maize populations in Hardy-Weinberg equilibrium, which can be used as source of corn improvement.

Many traits that are economically important in crops are quantitative rather than qualitative in nature (Bernardo, 2002). The genetical analysis of quantitative traits can not follow the standard procedures used to analyze major gen traits, because it is not possible to follow the segregation of the separate, underlying polygenes. Instead, it is necessary then, to look at the degree of similarity or difference among related individuals and families using various statistical components such as means and variances. Different population will have different means and different variances because they

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contain the genotypes maybe similar but their frequencies are different (Kearsey and Pooni, 1996). An information on the magnitude of various components of genetic variation is important in determining the best selection and breeding procedure for a particular set of material under given circumstances (Subandi and Compton, 1974). The large range of variation and the high values of heritability for some traits suggested good potential for improvement through an intrapopulation selection program. However, the large dominance effects and the small additive effects for grain yield indicated that an interpopulation selection program would be effective (Malvar *et al.*, 1996). The improvement of maize yields for ear weight depends on the knowledge of the type of gene action involved in its inheritance and also the genetic control of related traits such as the capacity for production. Also the choice of breeding methods for genetic improvement of a crop depends upon the nature and magnitude of present genetic variability (Singh and Chaudhary, 1985; Hallauer and Miranda, 1988; Pal and Prodham, 1994).

The total phenotypic variation is conditioned by the joint action of genetic and environmental forces. The total variance of a given character is its phenotypic variance ( $\sigma_p^2$ ) and environmental variance ( $\sigma_E^2$ ) where the part of the phenotypic variance is attributed to environmental conditions. The total genetic variance, ( $\sigma_G^2$ ) also known as variance of genotypic value, is the part of phenotypic value which can be attributed to genotypic differences among the phenotypes. Total genetic variance is further partitioned into additive genetic variance ( $\sigma_A^2$ ), dominance genetic variance ( $\sigma_D^2$ ) and epistatic genetic variance ( $\sigma_I^2$ ) (Dudley and Moll, 1969; Falconer and Mackay, 1996; Hallauer *et al.*, 2010). Different mating designs are used in the estimation of genetic variability and other components of variance such as North Carolina Design I (Hallauer and Miranda, 1988; Hallauer *et al.*, 2010).

For purposes of estimating components of genetic and environmental variance, the progenies developed from the mating design need to be evaluated over environments in an appropriate experimental design. From the

analysis of variance of experimental designs, expectations are expressed in terms of the appropriate components of variance; from the components of variance, translations are made to the appropriate relationships (covariances) of relatives based on the mating design used; finally, translations are made from the relationships of relatives to the theoretically determined functions of genetic components of variance for the covariances of relatives. Different mating designs are used in the estimation of genetic variability and other components of variance such as North Carolina Design I. Design I involves biparental crosses among random plants within a population.  $M$  male plants are each crossed to  $n$  females to produce  $mn$  progenies. The genetic structure of the progenies includes full-sibs that have both parents in common and half-sibs that have a male parent in common. Therefore, expected mean squares can be expressed in covariance of relatives (Hallauer *et al.*, 2010; Hallauer and Miranda, 1988).

The objectives of this research were to estimate the genetic variance component of important quantitative traits in an equilibrium corn population and to decide the best method to develop the population.

## MATERIALS AND METHODS

The research was conducted at Experiment Station of Agriculture Faculty of Gadjah Mada University, Yogyakarta, Indonesia, in 2012. The research was carried out in two steps: to develop half-sib and full-sib families and to evaluate both families. Equilibrium corn population used in this study was a mixture of nine corn varieties (composites) that had undergone open-pollinated nine times. The population was grown in an area of 50 m x 22 m, as row plots, with row length of 5 m, and row to row and plant to plant distance of 0.75 m and 0.25 m, respectively. Two seeds per hill were planted; these were thinned to one plant per hill two weeks after germination. Fertilizers in the form of urea, TSP, and KCl were applied at the rate of 100, 200, and 100 kg ha<sup>-1</sup>, respectively seven days after sown. Two hundred kg ha<sup>-1</sup> urea was applied again 30 days after sown. Standard cultural practices followed from sowing until harvesting.

Table 1. Expectation of mean square for analysis of variance of NC<sub>1</sub> experiment

Source of variation	df <sup>†</sup>	MS	E(MS)
Replication	$r - 1$	MS <sub>1</sub>	
Male	$m - 1$	MS <sub>2</sub>	$\sigma_{EFS}^2 + r\sigma_{F(M)}^2 + rf\sigma_M^2$
Female (Male)	$m(f - 1)$	MS <sub>3</sub>	$\sigma_{EFS}^2 + r\sigma_{F(M)}^2$
Error	$(r-1)(mf-1)$	MS <sub>4</sub>	$\sigma_{EFS}^2$
Total	$rmf-1$		

Remarks: <sup>†</sup> $m$ ,  $f$ , and  $r$  are numbers of males, females, and replications respectively  $\sigma_{EFS}^2 = \sigma_{ew}^2 + \sigma_{WithinFS\ family}^2$ ,  $\sigma_{ew}^2$  is environmental variance within plot

At the time of pollination, 250 plants as males were randomly chosen. Each male was crossed to as many as three female plants. At maturity, ears were individually collected, threshed, and numbered. Ears without apparent abnormalities and enough seed for a replicated experiment were selected.

Progeny test of 80 pairs of half-sib families was conducted. The trial was laid out in completely randomized block design with three replications as blocks. The population was grown as single row plots, with row length of 5 m, and row to row and plant to plant distance of 0.75 and 0.25 m, respectively. The cultural practice from sowing to harvesting at this season was carried out similar to that of the first step. Data collected on each plot included ear length (cm), ear diameter (cm), and kernel weight/ear (g).

Genetic components of variance estimated for the family performed a genetic interpretation. In the absence of epistasis, the family shows the following expectation (Table 1).

By using the appropriate mean square obtained from the analysis of variance, estimates of the variance among males,  $\hat{\sigma}_M^2$ , and variance among females mated to the same male,  $\hat{\sigma}_{F/M}^2$ , could be obtained. The estimated genetic components due to variations among family means of full-sib and half-sib families were used to estimate population variances as follows (Hallauer *et al.*, 2010; Hallauer and Miranda, 1988; and Singh and Chaudhary, 1985):

$$\hat{\sigma}_M^2 = CovHS = \frac{1}{4}\hat{\sigma}_A^2 = \frac{MS_2 - MS_3}{rf}$$

$$\text{Thus } \hat{\sigma}_A^2 = \frac{4(MS_2 - MS_3)}{rf} = 4\hat{\sigma}_M^2$$

$$\hat{\sigma}_{F/M}^2 = CovFS - CovHS = \frac{1}{4}(\hat{\sigma}_A^2 + \hat{\sigma}_D^2) = \frac{MS_3 - MS_4}{r}$$

$$\text{Thus } \hat{\sigma}_D^2 = \frac{4(MS_3 - MS_4)}{r} - \hat{\sigma}_A^2$$

$$\text{and } \hat{\sigma}_G^2 = \hat{\sigma}_A^2 + \hat{\sigma}_D^2 = 4\hat{\sigma}_{F/M}^2$$

The standard errors of genotypic variance components were estimated following the methods given by Hallauer and Miranda (1988):

$$SE = \left[ 2C^2 \left\{ \sum_i M.S._i^2 / (df_i + 2) \right\} \right]^{1/2}$$

where  $C$  = coefficient of the component in the expected mean squares,  $M.S._i$  = mean square for the  $i$ th trait, and  $df_i$  = degrees of freedom for the  $i$ th trait.

Data of quantitative traits were analyzed using the PROC MIXED procedure of SAS (SAS, 2003). Assumptions are necessary for the adequate interpretation of the genetic composition of covariance of relatives across mating designs. The population sampled should have the following:

- 1) Normal Mendelian diploid inheritance
- 2) No maternal effects
- 3) Linkage equilibrium
- 4) Non-inbred relatives
- 5) Random selection of parent and relatives

- 6) No correlation of environmental effects with relatives
- 7) No epistasis
- 8) Arbitrary allelic frequencies (Hallauer *et al.*, 2010).

**RESULTS AND DISCUSSIONS**

Analysis of variance of the progenies derived from mating designs are used to evaluate additive and dominance genetic effects, average level of dominance, and epistasis. Public breeding programs allow growing progenies for not only estimating genetic variances but also for selection without relying on just the coefficient of coancestry. Estimating genetic variances is useful for designing breeding programs, predicting response to selection, constructing selection indices, predicting hybrid performance, and allocating breeding resources more efficiently (Bernardo, 2002).

The analysis of variance (Table 2) indicated significant differences among males for ear length and ear diameter, significant differences among females within males for ear diameter but not significant differences among females within males for ear diameter, and not significant differences for kernel weight/ear for all relatives families.

The estimates of environmental variance within plot ( $\hat{\sigma}_{ew}^2$ ) can be calculated from  $\hat{\sigma}_{E(FS)}^2 = \hat{\sigma}_{Within FS}^2 + \hat{\sigma}_{ew}^2$  and finally,  $\hat{\sigma}_{ew}^2 = \hat{\sigma}_{E(FS)}^2 - (\frac{1}{2}\hat{\sigma}_A^2 + \frac{3}{4}\hat{\sigma}_D^2)$ . Genotypic variance, additive variance, dominance variance, environmental variance, environmental variance within plot of ear length, ear diameter, kernel weight/ear and their standard errors (SE) respectively are presented in Table 3.

For the ear length, ear diameter, and kernel weight/ear, estimates of genotypic, dominance, and additive variance were lower than two folds of their respective standard errors. The standard error of  $\hat{\sigma}_A^2$  and  $\hat{\sigma}_D^2$  also are included in Table 3. Relative to  $\hat{\sigma}_A^2$  and  $\hat{\sigma}_D^2$ , similar to research conducted by Hallauer *et al.* (2010), standard errors for yield were much larger for  $\hat{\sigma}_D^2$  (Table 3). The result showed that the population was genetically narrow. On the contrary, it was implied in Hallauer *et al.* (2010) that broad-based populations could be the result of crosses among a set of homozygous inbred lines (synthetic varieties), an open-pollinated variety, or a mixture of varieties and races.

Table 2. Analysis of variance of ear length, ear diameter, and kernel weight/ear

Source of variation	Degree of freedom	Mean Square		
		Ear length	Ear diameter	Kernel weight/ear
Replications	2	117.987**	2.165**	9053.756**
Males	79	4.127**	0.090**	244.889 <sup>ns</sup>
Females (Males)	160	2.118 <sup>ns</sup>	0.065**	224.472 <sup>ns</sup>
Error	469 <sup>#</sup>	1.754	0.045	207.105
Total	710 <sup>#</sup>			

Remarks: <sup>#</sup> = 9 units no data, \*\* = significantly different at 0.01 probability level, and <sup>ns</sup> = not significantly different

Table 3. Variance value:  $\hat{\sigma}_G^2$ ,  $\hat{\sigma}_A^2$ ,  $\hat{\sigma}_D^2$ ,  $\hat{\sigma}_E^2$ ,  $\hat{\sigma}_{ew}^2$  of ear length, ear diameter, kernel weight/ear and their standard errors (SE) respectively

Character	$\hat{\sigma}_G^2 \pm SE$	$\hat{\sigma}_A^2 \pm SE$	$\hat{\sigma}_D^2 \pm SE$	$\hat{\sigma}_E^2 \pm SE$	$\hat{\sigma}_{ew}^2 \pm SE$
Ear length	0.530 ± 0.349	0.908 ± 0.307	-0.387 ± 0.464	2.239 ± 0.014	2.069 ± 0.296
Ear diameter	0.017 ± 0.010	0.011 ± 0.007	0.006 ± 0.013	1.754 ± 0.003	1.745 ± 0.009
Ear weight	25.044 ± 37.811	8.962 ± 20.381	16.082 ± 42.954	207.105 ± 13.496	190.562 ± 31.817

The basic idea in the study of variation is its partitioning into components attributable to different causes. The relative magnitude of these components determines the genetic properties of the population (Falconer and Mackay, 1996). The hereditary variance in a random mating population could be partitioned into three parts: (i) an additive portion, (ii) a dominance portion, and (iii) epistatic effect. Bernardo (2002) and Hallauer *et al.* (2010) described the additive variance, denoted by  $\sigma_A^2$ , is the variance among breeding values in the population. The  $\sigma_A^2$  measures the variation due to the average effects of alleles (additive effects, same locus) and the variation in the effects that are transmitted from one generation to the next. The dominance variance, denoted by  $\sigma_D^2$ , is the variance among dominance deviation or variance due to interaction of average effects of alleles (dominance effects, same locus). The dominance variance is a function of allele frequencies and the level of dominance. The additive variance and dominance variance comprise the total genetic variance within a locus, i.e., intralocus variance.

Epistasis refers to the interaction between genes at different loci. Epistatic effects result from the nonadditivity of effects at each locus. So that, the epistatic variance, denoted by  $\sigma_I^2$ , is the variance among epistatic effect in the population (Bernardo, 2002). Epistatic variance consist of epistatic variances due to interaction of (i) additive, (ii) dominance, and (iii) additive and dominance effects of two or more loci (Hallaur *et al.*, 2010).

The result of the research (Table 3) showed that additive variance was apparently greater than dominance variance for ear length and ear diameter, but for kernel weight/ear, it was found the dominance component more important than the additive component. Many reports indicated that additive variance was the most important genetic component for yield (Lindsey *et al.*, 1962; Goodman, 1965; Moll and Smith, 1981; Hallauer and Miranda, 1988; Guei dan Wasson, 1992; Sutoro, 2005). However, Shahi dan Sing (1985) and Gouesnard and Gallais (1992) found the dominance component more important than the additive component. Wardyn *et al.* (2007) found that the additive variance was

larger than the dominance variance for grain yield, whereas the additive variance was larger than dominance variance for all other traits. Hallauer *et al.* (2010) summarizes the estimates of additive variance and dominance variance available for 19 different traits of maize. The greatest number of estimates was reported for yield, and averages for each parameter show that the ratio of dominance to additive variance was quite large for yield when compared to other traits. Therefore, dominance variance seems important in the expression of yield.

Variance components, by definition, must be positive. Despite this, it was found the dominance variance for ear length was negative (Table 3). In maize, negative estimates may be due to inadequate model (genetic designs to epistatic variance), inadequate sampling (small numbers), and inadequate experimental techniques (competition among progenies (Searle, 1971). Guesnard and Gallais (1992) emphasized the negative estimation of genetic variance components could arise in a nested mating design. This may be due to inaccurate estimates, experimental problems, sampling errors, or failure of the assumptions of genetic or statistical models. Lindsey *et al.* (1962) found that estimates of dominance variance were more often negative when male and female plants were sown at the same date. If the females crossed to the same male were correlated, the estimate of the male mean square increased, but the female-within-male mean square estimate decreased. Subsequently, the additive variances would be overestimated, and the nonadditive variance would be underestimated.

## CONCLUSIONS AND SUGGESTIONS

The additive variance of ear length and ear diameter of the corn population was greater than dominance variance. On the contrary, in kernel weight/ear, the dominance variance was greater than additive variance. So, based on kernel weight/ear, the Hardy-Weinberg equilibrium corn population can be developed through inbreeding to form a hybrid variety.

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