Genetic control of the number of leaves above the ear in maize

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ABSTRACT. In this study, we examined the genetic control of the number of leaves above the first ear in maize. The F_2 generations and the backcrosses were obtained from 2 contrasting lines for this trait. All generations were assessed in a completely randomized block design with 2 replications. The number of leaves above the ear was counted when the plants were in the tasseling stage at the level of plants per plot. Mean and variance components were estimated using the weighted least square method. We observed a predominance of non-additive effects in the genetic control of number of leaves above the ear. These results indicate that this trait shows high heritability.

Key words: Genetic components; Leaf area; *Zea mays* L.

INTRODUCTION

Leaf area is closely related to the photosynthetic capacity of maize plants. Thus, reductions in leaf area can substantially alter physiological activity, reducing plant metabolism and grain yield (Alvim et al., 2011). In addition, the photosynthetic potential of a crop can be inferred based on leaf area, which depends on leaf number and size as well as development stage of the plants.

Generally, leaf area increases up to a limit, and then decreases because of leaf senescence (Brito et al., 2011). Quickly reaching the maximum leaf area index and maintaining this state for a long period will result in greater yield (Manfron et al., 2003). Recent studies showed that removing leaves above the ear results in grain yield losses (Lima et al., 2010; Alvim et al., 2010; Khaliliaqdam et al., 2012), while removing half or all leaves below the ear has inexpressive consequences with respect to these losses. Alvim et al. (2010) found that leaves located above the ear provide most of the photoassimilates necessary for grain filling in the ear.

According to Camacho et al. (1995), approximately 50% of carbohydrates accumulating in maize kernels originate from the leaves located in the upper third of the stalk, approximately 30% from leaves located in the middle third, and the remaining from the leaves distributed along the base. According to Mock and Pearce (1975), plants with firm and vertically directed leaves above the ear are in accordance with the ideotype of this crop. Recent studies have also shown that these characteristics are important in breeding programs in which a main objective is increasing the number of plants per hectare with hybrids/cultivars of low plant height (Combs and Bernardo, 2013). Despite the importance of number of leaves above the ear, there have been few studies examining the genetic control of this trait. Understanding the genetic control of leaf number above the ear is important for beginning a breeding program selecting for this characteristic to develop an ideotype of plants that maximize yield.

In this study, we examined the variability for this trait. Contrasting genotypes for number of leaves above the first ear are frequently observed in experimental fields of maize lines, allowing studies to determine the genetic control of this trait.

In light of the above, this study was carried out to understand the genetic control of the number of leaves above the first ear in maize.

MATERIAL AND METHODS

The experiment was conducted in the experimental area of the Department of Biology of Universidade Federal de Lavras in the city of Lavras, located in the south of Minas Gerais, Brazil. The altitude of the location is 910 m, with geographic coordinates of 21°58' latitude south and 45°22' longitude west.

To study the genetic control of the number of leaves above the ear in maize, 2 lines differing in this trait were identified from the maize breeding program of Department of Biology of Universidade Federal de Lavras. The first line (Lb) has an average of 3 leaves above the ear and the second line (Lf) has an average of 7 leaves (Figure 1). From these 2 lines, the F_2 generations and the backcrosses with both lines (BC_1 and BC_2) were obtained.

Figure 1. Maize breeding program lines from UFLA. **A.** Maize line with only a few leaves above the ear. **B.** Maize line with a large number of leaves above the ear. Lavras, MG, Brazil.

The parent lines (Lf and Lb) and the segregating populations (F_2, BC_1, and BC_2) were assessed in a completely randomized block experimental design with 2 replications. The plots were sown in November 2012 and consisted of two 4-m rows for the lines (32 plants), eight 4-m rows in the F_2 generation (128 plants), and six 4-m rows in the BC_1 and BC_2 generations (96 plants). Studies estimating genetic control in maize traits have used a similar number of plants to represent the different populations (Toledo et al., 2011; Entringer et al., 2014). Between-plant spacing was 0.25 m, with 0.60 m between rows. All recommended crop management operations were performed to provide the best conditions for plant development.

When the plants were in the tasseling stage, the number of leaves above the ear was assessed at the level of plants per plot. After analyzing variance, the mean components were estimated using the weighted least squares method with the following model: $\hat{\beta} = (C' NS^{-1}C)^{-1} (C' NS^{-1}Y)$ in which $\hat{\beta}$ was the vector of the parameters ($\hat{m}$ was estimator of the mean; $\hat{a}$ was the estimator of the deviations of the homozygote in relation to the mean; and $\hat{d}$ was the estimator of the deviations of the heterozygote in relation to the mean); C was the design matrix, consisting of the overall mean, contribution of homozygous loci, and of heterozygous loci; N was the matrix of the number of plants assessed within each generation; S was the matrix of the variances associated with the generations; and Y was the vector of the mean values observed in the generations (Ramalho et al., 2012).

Components of variance were estimated using the iterative weighted least squares method using the following model: $\hat{\beta} = (C'Z^{-1}C)^{-1}(C'Z^{-1}Y)$, in which $\hat{\beta}$ was the vector of the parameters ($\hat{\sigma}_A^2$ = estimate of additive genetic variance; $\hat{\sigma}_D^2$ = estimate of dominance genetic variance; and $\hat{\sigma}_E^2$ = estimate of environmental variance); C was the matrix of the model, consisting

of additive, dominance, and environmental variance within each generation; Z was the weighting matrix of the observations, and Y was the vector of the variances observed within each population (Ramalho et al., 2012).

Estimates of broad heritability patterns ($\hat{h}_\lambda^2$) were obtained using expressions described by Ramalho et al. (2012). All estimates were obtained using the R software (R Development Core Team, 2013).

RESULTS AND DISCUSSION

The lines Lf and Lb were contrasting for the leaf number trait; i.e., they differed in the number of leaves above the ear, with the lines Lf and Lb exhibiting phenotypic mean values of 6.90 and 3.45, respectively (Table 1). According to Cruz et al. (2012), contrast between the parent lines is essential for achieving greater precision in genetic analyses.

Table 1. Number of individuals assessed in each population, with the mean values of number of leaves above the ear and the respective variance, obtained in the 2012/2013 crop season in Lavras, MG, Brazil.

Population	No. of plants	Mean	Variance
Lf	64	6.90	0.4672
Lb	58	3.45	0.4573
F_2	246	6.57	0.6870
BC_1	180	7.10	0.5374
BC_2	187	5.71	0.4915

The mean value of the F_2 generation (6.57) was greater than the mean value of the parents (5.17), indicating that the genes involved have non-additive allelic interaction, i.e., the heterozygous loci, have a greater effect than homozygous loci. Backcrosses showed the expected behavior. When the line with the greatest number of leaves (Lf) was used as the recurrent parent, the mean value of BC_1 generally approached the maximum number of leaves above the ear. However, when the line with the lowest number of leaves (Lb) was used as the recurrent parent, the mean value of BC_2 was generally lower, but higher than the mean value of the parents. Estimates of variances were consistent with expected values, in which the F_2 generation showed the greatest variance (Table 1).

Estimates of the mean components are shown in Table 2. The coefficient of determination (R^2) was 0.99, indicating that the additive dominance model without epistasis fit the data for the trait under study. Component â, which estimates the deviation of the homozygotes compared to the mean, and component $\hat{d}$, which estimates the deviation of the heterozygotes compared to the mean, differed from 0. The estimate of component $\hat{d}$ was greater than that of component â, indicating again the predominance of the non-additive allelic interaction.

Table 2. Mean components, associated errors, and coefficient of determination of the model (R^2) of the number of leaves above the ear, obtained in the 2012/2013 crop season in Lavras, MG, Brazil.

Parameters	Estimate	Standard error
$\hat{m}$	4.6	±0.05
â	1.60	±0.04
$\hat{d}$	2.60	±0.13
R^2	0.99	

Estimates of the components of variance are shown in Table 3. The additive dominance model without epistasis fit the data well, as shown by the coefficient of determination of 0.99. Estimates of additive variance and of dominance variance differed from 0. These results agree with those of Lima et al. (2010), who found different behavior among genotypes tested for number of leaves above the ear.

Table 3. Components of variances, associated errors, and coefficient of determination of the model (R^2) of the number of leaves above the ear, obtained in the 2012/2013 crop season in Lavras, MG, Brazil.

Parameters	Estimate	Standard error
$\hat{\sigma}_E^2$	0.46	±0.05
$\hat{\sigma}_A^2$	-0.66	±0.23
$\hat{\sigma}_D^2$	0.89	±0.28
$\hat{h}_A^2$	0.66	
R^2	0.99	

These observations are interesting from the perspective of genetic breeding as an understanding of genetic control is fundamental for defining breeding strategies. In the present study, the additive variance was negative, which indicates that this value is equal to zero. Nevertheless these results indicate the importance of dominance in the expression of this trait. Hybrids are needed to assess traits with partial dominance, whereas traits with additive effects are desirable because of the ease of selection and the potential to transfer favorable alleles to genotypes of interest (Ramalho et al., 2012).

Bernardo (2010) found that the estimate of dominance variance should conceptually be of a lower magnitude because $\hat{\sigma}_D^2$ is estimated as the deviation from regression of the genotypic values and the number of alleles. As the estimator is of least squares, the $\hat{\sigma}_D^2$ should be minimal, i.e., although the estimate is underestimated, the $\hat{\sigma}_D^2$ is still near $\hat{\sigma}_A^2$. This result indicates the presence of a non-additive effect in genetic control of the trait. Studies estimating genetic control of other traits in maize, such as production components, revealed predominance of the dominance effect in expression of the trait (Srdić et al., 2007; Toledo et al., 2011).

To increase the efficiency in using this information for the genetic control of the number of leaves above the ear, it is necessary to verify the effect of the environment on this trait. Heritability is a genetic parameter that can be used to predict gains from selection. In this study, $\hat{h}_A^2$ was 65.92%, which is of high magnitude, indicating a little influence of the environment on expression of the trait, wich may facilitate gains from selection steps. Nevertheless, previous reports on the estimates of genetic components of this trait are limited. Therefore, additional studies are necessary to determine the best breeding strategy to achieve the ideotype of plants with the greatest number of leaves above the ear.

CONCLUSIONS

There is predominance of non-additive effects in the genetic control of the number of leaves above the ear. The number of leaves above the ear shows high heritability.

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