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The Genetic Structure of a Maize Population: The Role of Dominance

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Abstract
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RESEARCH

The Genetic Structure of a Maize Population: The Role of Dominance

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ABSTRACT

The combined effects of dominance and inbreeding on covariances between relatives are still poorly understood in maize (*Zea mays* L.) populations. Our objectives were to address the following questions: (i) What is the importance of dominance in a maize synthetic? (ii) How does inbreeding affect the genetic variance among individuals in a maize synthetic. (iii) How do the covariance parameters compare between populations? (iv) How does breeding design impact estimators? We estimated covariance components for inbred relatives in the maize synthetic BSCB1(*R*)C13. Previous estimates of covariance parameters have been used to explain the ineffectiveness of inbred progeny selection in the stiff-stalk population BS13. We found that the dominance variance was larger than the additive variance for grain yield, whereas the additive variance was larger than the dominance variance for all other traits. Negative estimates of the covariance between additive and homozygous dominance deviations were found for all traits with the exception of traits associated with reproductive maturity, suggesting a negative relationship between inbred and outbred performance. The correlation between genotypic values and breeding values was lower for grain yield than for any other trait. Our results were similar to previous results found in the stiff-stalk maize population BS13, suggesting similarity in structure among populations.

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Abbreviations: BSCB1, Iowa Corn Borer Synthetic No. 1; DAP, days after planting; REML, restricted maximum likelihood.

The debate about the predominant type of dominance in maize, dominance or overdominance, has been prevalent in the maize community for a number of years (Crow, 2000). What has never been a major source of debate, however, is that dominance exists and is important in maize. Hallauer and Miranda Filho (1988) reported that over an average of 99 studies, the dominance variance for grain yield was 286.8 g plant^{-1}, whereas the estimate for the additive variance was 469.1 g plant^{-1}. They also reported an average dominance to additive ratio of 0.94 for grain yield and 0.53 for plant height. Thus dominance variance constitutes a large portion of the total genetic variance, at least for grain yield. Grain yield is unique in maize in that it routinely shows a higher proportion of dominance variance than other traits.

The presence of dominance, specifically directional dominance, coupled with inbreeding can have a large impact on both individual and population performance via inbreeding depression. Hallauer and Miranda Filho (1988, p. 314–315) outline inbreeding depression estimates in maize for eight studies (Levings et al., 1967; Sing et al., 1967; Genter, 1971; Harris et al., 1972; Hallauer and Sears, 1973; Cornelius and Dudley, 1974; Rice and Dudley, 1974; Good and Hallauer, 1977), which vary in their method of inbreeding and germplasm evaluated. The results were consistent across all studies in that inbreeding depression was observed for

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all grain and plant traits with the lone exception of days to anthesis. Numerous other studies which measure inbreeding depression at the population level have been performed in maize, but to the authors' knowledge no studies have estimated the variability in inbreeding depression among individuals within the same maize population.

Several studies exist which have investigated the quantitative genetic properties of inbreeding with dominance while using Harris' (1964) model. Coors (1988) evaluated the response to half-sib and S_1 recurrent selection in a narrow-based maize synthetic. He found a significant reduction in inbreeding depression after four cycles of selection following a combined half-sib and S_1 selection procedure. Coors (1988) also found a large negative covariance between additive effects and homozygous dominance deviations (D_1). This was the first published estimate of D_1 in any species. Coors hypothesized that the lack of effectiveness of inbred progeny selection was due to D_1 affecting the variance among inbred progenies. Shaw et al. (1998) investigated the genetic components of flowering time and morphology in a *Nemophila menziessi* population that was undergoing inbreeding. Their breeding design consisted of three generations that contained a wide array of inbreeding coefficients and genetic relationships. They found that $D_2^\star$ (the variance of homozygous dominance deviations) contributed significantly to petal length, petal width, and flowering date (all reproductive traits). However, they found no influence of the inbreeding components for plant size measurements. Although they found significant inbreeding depression for the size traits, the variance of homozygous dominance deviations was not significant for these traits.

Edwards and Lamkey (2002) analyzed the maize population BS13 with the genetic model of Harris (1964). Their breeding design took into account suggestions made previously (Cockerham, 1983; Cornelius and Van Sanford, 1988) and included inbred progenies from early in the inbreeding process in addition to outbred progenies of the inbred material. Probabilities of identity by descent were calculated by Cockerham's suggestions (1971, 1983). Significant inbreeding depression was found for all of the traits investigated. They found, in general, a significant contribution of all the inbred variance components to genetic variance. In their analysis, they found that the variance of inbred dominance deviations was 2.65 times greater than the variance of noninbred dominance deviations. They also found a negative correlation between inbred dominance deviations and breeding values in the BS13 population.

The idea that inbreeding depression is a variable trait amenable to selection was proposed by Pray and Goodnight (1995). The large variability of inbred dominance deviations found by Edwards and Lamkey (2002) supports this idea. The correlation between genotypic values of inbred individuals and inbred dominance deviations is a measure of the correlation between the value of an inbred individual and inbreeding depression because the expectation of inbred dominance deviations, namely, least-squares homozygous dominance deviations δ_{ii}, are the quantitative genetic basis for inbreeding depression. The correlation between inbred dominance deviations and breeding values is an estimate of the correlation between inbred performance and outbred performance. For grain yield, Edwards and Lamkey (2002) found a correlation between inbred genotypic value and inbred dominance deviations of 0.63 and between inbred genotypic value and breeding value of 0.34, suggesting that selection among inbred individuals in BS13(S)C0 would have a greater impact on changing inbreeding depression than it would on changing outbred performance. Given the importance of the relationship between inbred and hybrid performance in maize breeding programs, a better understanding is needed of how inbreeding affects individual genetic values and covariances among relatives. The following major questions are asked by this study: (i) What is the importance of dominance in a maize synthetic? (ii) How does inbreeding affect the genetic variance among individuals in BSCB1(*R*)C13? (iii) How do the genetic covariance parameters in BSCB1(*R*)C13 compare to BS13(S)C0? (iv) How does the current breeding design compare to previous designs used to estimate the genetic covariance parameters?

MATERIALS AND METHODS

Germplasm

The maize population Iowa Corn Borer Synthetic No. 1 (BSCB1), a member of the non-stiff-stalk heterotic pattern, was the source of germplasm in this study. BSCB1 was developed in the 1940s at Iowa State University via an intermating of 12 inbred lines (Penny and Eberhart, 1971). See Hagdorn et al. (2003) for a description of the 12 parents. BSCB1(*R*) was developed via reciprocal recurrent selection (Comstock et al., 1949) with Iowa Stiff Stalk Synthetic. Details for the first five cycles of selection in BSCB1(*R*) can be found in Penny and Eberhart (1971). Holthaus and Lamkey (1995), Keeratinijakal and Lamkey (1993), and Schnicker and Lamkey (1993) gave details concerning the selection and breeding methods for Cycles 6 through 11. The same procedure used in Cycle 11 was followed for Cycles 12 and 13. For the current study, Cycle 13 of BSCB1(*R*) [BSCB1(*R*)C13] was the germplasm source.

Mating Design

Four hundred random S_0 plants of the BSCB1(*R*)C13 population were self-pollinated. Resulting S_1 progenies were planted ear-to-row, and the first three plants in each row were self-pollinated. One ear was randomly chosen, the resulting S_2 ear was planted the following year, and the first three plants were self-pollinated. This process was repeated until S_5 seed from the initial 400 S_0 plants was obtained. Thus, each S_0 line was represented in five generations of inbreeding where each generation was a direct descendant of the initial S_0 plant (Fig. 1). The only selection applied during the inbreeding process was that enough seed be present to plant a full nursery row the following year. Two hundred lines were randomly selected

from approximately 350 lines that had adequate selfed seed to plant additional nursery rows to increase seed for evaluation. In the summer of 2003, the S_1, S_3, and S_5 generations of the 200 randomly chosen lines were planted in nursery rows 3.8 m long at a density of 15 plants per row. Seed quantities were increased via sib-mating within each nursery row. Effort was made to use each plant once as either a male or a female, and reciprocal crosses were not made. A balanced bulk of approximately 10 ears from each nursery row was made and used as the source for yield trial plots. Due to poor stands, some rows were regrown and subsequently sib-mated in the 2003/2004 winter nursery to obtain adequate quantities of seed for yield trials.

In addition to nursery rows, each S_1 and S_5 line was planted in isolation with BSCB1(*R*)C13. The S_1 and S_5 lines were detasseled and used as females, being open-pollinated with BSCB1(*R*)C13 used as the male (Fig. 1). The isolation rows were 5.49 m long and were planted at a density of 20 plants per row. All plants in a row were harvested and shelled in bulk. Harvested seed was treated with Maxim XL (fludioxonil [4-(2,2-difluoro-1,3-benzodioxol-4-yl)-1*H*-pyrrole-3-carbonitrile]) and mefenoxam (D-alanine, *N*-(2,6-dimethylphenyl)-*N*-(methoxyacetyl)-methyl ester) (Syngenta Crop Protection, Inc., Greensboro, NC) at the labeled rate for use in replicated yield trials.

Experimental Design

The 200 lines in five generations of inbreeding were planted near Ames, Carroll, Crawfordsville, and Rippey, IA, in 2004 and near Ames and Carroll, IA, in 2005. Each location contained two replications of the experiment, laid out in a split-plot design with generation of inbreeding (S_1, S_3, S_5, S_1 topcrossed, S_5 topcrossed) as the whole plot factor and individual lines within generations as subplots. Whole plots were laid out in a randomized complete block design. Subplots were randomized in a 10 × 20 resolvable row–column block design within each generation of inbreeding (John and Williams, 1995). Row–column randomizations were generated by the computer software CycDesigN (Whitaker et al., 2002). Bulks were made of each generation and used as border rows that surrounded each whole plot. An individual yield trial plot consisted of two rows, both 5.49 m in length with 0.76 m between rows. Seeds were machine planted at a density of 76 540 plants ha^{-1} and thinned to 62 190 plants ha^{-1}. Again, cultural practices were consistent with commercial maize production in central Iowa.

Data were collected on an individual plot basis for days from planting to midsilk, days from planting to midpollen shed, root lodging (%), stalk lodging (%), harvestable grain weight (g adjusted to 15.5% grain moisture), and grain moisture (%). Days to midsilk were determined when half of the plants in a plot had visible silks, and days to midpollen were determined when half of the plants in a plot had begun shedding pollen. Plant height (cm) and ear height (cm) were obtained by measuring 10 plants per plot on the out-crossed generations and six plants per plot for the S_1, S_3, and S_5 generations. Plant height was the distance between the soil surface and the uppermost leaf collar. Ear height was measured as the distance between the soil surface and the uppermost ear node. The mean value for plant height and ear height was calculated on a per plot basis and used in the analysis. Fewer plants were measured in the inbred generations due to the reduced variability within plots for inbred

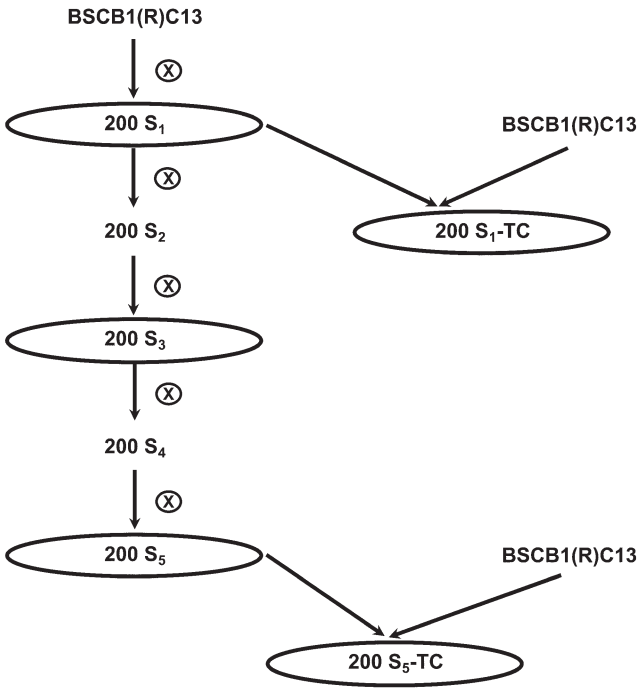

Figure 1. A diagram representing the mating design used for estimation of the genetic covariance parameters. Ovals encompass the generations used in the analysis.

generations. Grain yield was on a harvestable weight basis as all plots were machine harvested.

Genetic Model

The same genetic model used by Edwards and Lamkey (2002) was used for this study. The model is based on an extension of Fisher's (1918) genetic model by Harris (1964) to include inbred relatives. Harris developed a completely general parameterization of the genetic covariance between two individuals with arbitrary levels of inbreeding. The general parameterization requires the following assumptions: (i) there is no linkage among the loci that influence the traits being evaluated, (ii) the original population is random mating, (iii) there has been no selection practiced during the development of the two individuals, and (iv) the individuals have autosomal diploid loci.

Harris (1964) defines the genetic value of an individual as

$$g_{ij} = \mu + \alpha_i + \alpha_j + \delta_{ij}$$

where g_{ij} is the expected phenotypic value of an individual with genotype A_iA_j, μ the population mean, α_i the additive effect of allele A_i, and δ_{ij} the dominance deviation of genotype A_iA_j.

Under this model, the covariance between two individuals (X and Y) can be represented by

$$\mathrm{Cov}(X,Y) = 2\theta_{XY}\sigma_A^2 + 2\left(\Delta_{\ddot{X}+\ddot{Y}} - \delta_{\ddot{X}\ddot{Y}}\right)\sigma_D^2 + 2\left(\gamma_{\ddot{X}Y} + \gamma_{X\ddot{Y}}\right)D_1 + \delta_{\ddot{X}\ddot{Y}}D_2^{\star} + \left(\Delta_{\ddot{X}\cdot\ddot{Y}} - F_{\ddot{X}}F_{\ddot{Y}}\right)H^{\star}$$

where σ_A^2 is additive variance; σ_D^2 dominance variance; D_1 covariance between additive effects and homozygous dominance deviations; $D_2^{\star}$ variance of homozygous dominance deviations; $H^{\star}$ the sum of homozygous dominance deviations, squared; and θ_{XY}, $\Delta_{\ddot{X}+\ddot{Y}}$, $\delta_{\ddot{X}Y}$, $\gamma_{\ddot{X}Y}$, $\gamma_{X\ddot{Y}}$, $\Delta_{\ddot{X}\cdot\ddot{Y}}$, $F_{\ddot{X}}$, and $F_{\ddot{Y}}$ the probabilities

of identity by descent for two, three, or four alleles (Cockerham, 1983). The variance and covariance parameters in this equation are collectively referred to as genetic covariance parameters. Cockerham (1971) describes the calculation of the 15 probabilities of identity by descent for two, three, and four alleles, which can be reduced to the eight descent measures in the expression of covariances between inbred relatives. The eight probabilities determine the coefficients for each of the five genetic covariance parameters (σ_A^2, σ_D^2, D_1, $D_2^\star$, $H^\star$). For our study, we had five generations of inbreeding within each independent line and thus 10 covariances among the generations and 5 variances. The coefficients used for the genetic covariance parameters for each of the 15 (co)variances are listed in Table 1. The coefficients were calculated based on the reports of Cockerham (1971, 1983) as well as Cockerham and Matzinger (1985).

Influence of Inbreeding

It should be emphasized that under the Harris (1964) model, inbreeding does not change any of the population-specific genetic covariance parameters, but it does change the relative contributions of the parameters to genotypic (co)variances. To outline the changes induced by inbreeding it is necessary to outline the genetic makeup of an individual.

Falconer and Mackay (1996) define the genetic value of an individual as

$$G = A + D$$

where G is the genotypic value of an individual, A the breeding value of an individual, and D the difference between the genotypic value and the breeding value of an individual.

G, A, and D from the Falconer and Mackay model are estimators of the actual genetic effects in the Harris model. G, A, and D are observed values, and their expected values change in accordance to the reference population.

Table 1. Coefficients for genotypic covariance components for the 15 covariance expressions relating five generations of inbreeding.

	Component				
Covariance	σ_A^2	σ_D^2	D_1	$D_2^\star$	$H^\star$
Cov(S_1, S_1)	1.000	0.250	1.000	0.125	0.000
Cov(S_1, S_3)	1.000	0.063	1.370	0.219	0.000
Cov(S_1, S_5)	1.000	0.016	1.469	0.242	0.000
Cov(S_1, S_1-TC)†	0.500	0.000	0.250	0.000	0.000
Cov(S_1, S5-TC)	0.500	0.000	0.250	0.000	0.000
Cov(S_3, S_3)	1.750	0.063	3.250	0.781	0.047
Cov(S_3, S_5)	1.750	0.016	3.344	0.805	0.012
Cov(S_3, S_1-TC)	0.500	0.000	0.438	0.000	0.000
Cov(S_3, S_5-TC)	0.875	0.000	0.813	0.000	0.000
Cov(S_5, S_5)	1.940	0.016	3.810	0.945	0.015
Cov(S_5, S_1-TC)	0.500	0.000	0.484	0.000	0.000
Cov(S_5, S_5-TC)	0.969	0.000	0.953	0.000	0.000
Cov(S_1-TC, S_1-TC)	0.250	0.000	0.000	0.000	0.000
Cov(S_1-TC, S_5-TC)	0.250	0.000	0.000	0.000	0.000
Cov(S_5-TC, S_5-TC)	0.484	0.000	0.000	0.000	0.000

†S_1-TC is the S_1 generation topcrossed the population, S_5-TC is the S_5 generation topcrossed to the population.

Following the Harris (1964) model, the values of G, A, and D are consistently defined with respect to a panmictic reference population and are thus independent of inbreeding. Inbreeding changes the expected values, variances, and covariances between G, A, and D (Table 2). In addition, inbreeding introduces additional genetic covariance parameters into the expected values, variances, and covariances where the degree of change between a noninbred individual and an inbred individual is determined largely by D_1, $D_2^\star$, and $H^\star$. The utility of Harris's model (1964) is the ability to describe the covariance between any two individuals regardless of their respective F values, which is not possible with the Fisherian model.

Data Analysis

Grain yield, grain moisture, plant height, ear height, days to midsilk, and days to midpollen were the traits analyzed. All traits were analyzed using a mixed linear model of the form

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

where β is the vector of fixed effects, $\mathbf{u}$ the vector of random effects, $\mathbf{e}$ the vector of residuals, $\mathbf{X}$ the incidence matrix relating observations to fixed effects, and $\mathbf{Z}$ the incidence matrix relating observations to random effects.

Each trait and environment was analyzed individually to obtain single-location estimates of variance components for each trait. Generation, replicate within generation, lattice rows, and lattice columns were fit as fixed effects. The random effects were individual inbred generations within lines with lines considered as independent subjects. Each line had an associated random-effect vector, $\mathbf{u}_i$, with five elements for the five generations of inbreeding. The random-effect vectors, $\mathbf{u}_i$, (i = 1 … 200) for all 200 lines had equivalent variance–covariance matrices, which were

$$\mathrm{Var}(\mathbf{u}_i) = \sigma_A^2\mathbf{A}_1 + \sigma_D^2\mathbf{A}_2 + D_1\mathbf{A}_3 + D_2^\star\mathbf{A}_4 + H^\star\mathbf{A}_5$$

where $\mathbf{A}_1$ … $\mathbf{A}_5$ are 5 × 5 matrices containing coefficients for the contributions of individual covariance components to the (co)variances between generations, and σ^2_A, σ^2_D, D_1, $D_2^\star$, and $H^\star$ are genotypic covariance components

In addition to the single-environment model, a multienvironment model was fit for each trait. Environments (location–year combinations) and replications within environments

Table 2. Expectations [E(•)], variances [V(•)], and covariances [C(•)] for genotypic values (*G*), breeding values (*A*), and dominance deviations (*D*) of noninbred (*F* = 0) and inbred (*F* = 1) individuals from Edwards and Lamkey (2002).

Value	Noninbred	Inbred
G	$\alpha_i + \alpha_j + \delta_{ij}$	$2\alpha_i + \delta_{ii}$
A	$\alpha_i + \alpha_j$	$2\alpha_i$
D	δ_{ij}	δ_{ii}
E(G)	0	$\Sigma p_i\delta_{ii}$
E(A)	0	0
E(D)	0	$\Sigma p_i\delta_{ii}$
V(G)	$\sigma_A^2 + \sigma_D^2$	$2\sigma_A^2 + 4D_1 + D_2^\star$
V(A)	σ_A^2	$2\sigma_A^2$
V(D)	σ_D^2	$D_2^\star$
C(G,A)	σ_A^2	$2(\sigma_A^2 + D_1)$
C(G,D)	σ_D^2	$2D_1 + D_2^\star$
C(A,D)	0	$2D_1$

were fit as fixed effects. Environments were considered fixed as they were not of primary interest in this study. For grain yield and grain moisture, lattice rows and columns were fit as fixed effects. Only lattice rows were fitted for plant height and ear height. The random effects in the combined analysis were individual inbred generations within environments and lines, so that each line had an associated vector of random effects, $\mathbf{u}_i$, which contained 30 elements corresponding to random effects for each generation of inbreeding within each environment. As in the single-location model, each of the 200 lines was considered as an independent subject. The variance–covariance matrix of the 30-element line vectors in the combined model was similar to the single-location model except that common-environment covariances were introduced to model genotype-by-environment interaction. The covariance between any two generations of inbreeding of the same line grown in different environments is a function of only the main-effect components, σ^2_A, σ^2_D, D_1, $D_2^\star$, $H^\star$. However, the covariance between any two generations of inbreeding of the same line grown in the same environment includes both the main-effect components, σ^2_A, σ^2_D, D_1, $D_2^\star$, $H^\star$, plus the common-environment covariances, which are denoted with an "E" in their subscripts (σ^2_{AE}, σ^2_{DE}, D_{1E}, $D_{2E}^\star$, $H_E^\star$) (Henderson, 1984). The common-environment covariances are equivalent to classical genotype-by-environment interaction variances, i.e., our common-environment covariance, σ^2_{AE}, is equivalent to additive effect by environment interaction. Our components are technically common-environment covariances because of the way the linear model was specified, namely, with one random effect for each environment for a generation of inbreeding of a particular line as opposed to a genetic main effect plus an interaction effect for each environment. Our specification reduces the size and computational complexity of the model and, in fact, was required to avoid an error in a version of SAS prior to SAS version 9 (SAS Institute, 2002). Because they are equivalent to genotype by environment interaction components, we will refer to them as such in results and discussion to remain consistent with plant breeding literature. The structure of the 30 × 30 variance–covariance matrices for individual lines in the multienvironment model was

$$\mathrm{V}(\mathbf{u}_i) = \mathbf{J}_6 \otimes \left[\sigma^2_A \mathbf{A}_1 + \sigma^2_D \mathbf{A}_2 + D_1 \mathbf{A}_3 + D_2^\star \mathbf{A}_4 + H^\star \mathbf{A}_5\right] + \mathbf{I}_6 \otimes \left[\sigma^2_{AE} \mathbf{A}_1 + \sigma^2_{DE} \mathbf{A}_2 + D_{1E} \mathbf{A}_3 + D_{2E}^\star \mathbf{A}_4 + H_E^\star \mathbf{A}_5\right]$$

where $\mathbf{J}_6$ is a 6 × 6 matrix of ones; $\mathbf{I}_6$ is a 6 × 6 identity matrix; ⊗ is the direct product operator; $\mathbf{A}_1 \ldots \mathbf{A}_5$ are the 5 × 5 coefficient matrices; σ^2_A, σ^2_D, D_1, $D_2^\star$, and $H^\star$ are genotypic covariance components; and σ^2_{AE}, σ^2_{DE}, D_{1E}, $D_{2E}^\star$, and $H_E^\star$ are common environment covariances.

Restricted maximum likelihood (REML) estimators were obtained for all genotypic covariance components in both the single-location analyses and the combined analyses for all traits using the mixed procedure in SAS version 9 (SAS Institute, 2002). Because the exact sampling distribution of variance components is unknown, we relied on the asymptotic large-sample variance–covariance matrix of the vector of covariance parameters obtained directly from the mixed procedure. From this, standard errors were attached to each estimate and significance was assigned at the 0.05 level if the estimate was more than two standard errors away from zero. This asymptotic variance covariance matrix was also used to calculate the correlations among the genetic covariance parameters. Error variances were found to be heterogeneous by generation and were fit accordingly in the analysis.

Correlations between G, A, and D for inbred individuals were calculated as

$$r_{G,A} = \frac{2\left(\sigma^2_A + D_1\right)}{\sqrt{2\sigma^2_A\left(2\sigma^2_A + 4D_1 + D_2^\star\right)}}$$

$$r_{G,D} = \frac{2D_1 + D_2^\star}{\sqrt{D_2^\star\left(2\sigma^2_A + 4D_1 + D_2^\star\right)}}$$

and

$$r_{A,D} = \frac{2D_1}{\sqrt{2\sigma^2_A D_2^\star}}$$

as reported by Edwards and Lamkey (2002) and equivalent to the report of Cornelius (1988). By definition, A and D are independent in noninbred individuals, and the correlations between G and A and D were calculated as

$$r_{G,A} = \frac{\sigma^2_A}{\sqrt{\sigma^2_A\left(\sigma^2_A + \sigma^2_D\right)}} \text{ and}$$

$$r_{G,D} = \frac{\sigma^2_D}{\sqrt{\sigma^2_D\left(\sigma^2_A + \sigma^2_D\right)}}$$

(Edwards and Lamkey, 2002).

Predicted genetic variances and covariances were calculated as linear combinations of estimated genetic covariance parameters. The standard errors for the predictions were calculated as a linear function of the asymptotic standard errors of the genetic covariance parameters.

RESULTS

Genetic Variances

All five genetic main effect covariance parameters were significantly different from zero for all traits (Table 3) with the exception of D_1 and $H^\star$ for midpollen and $\sigma_D{}^2$ for midsilk. Grain yield differed from all other traits in that the estimate of dominance variance was larger than the estimate of additive variance. The covariance between additive effects and homozygous dominance effects (D_1) was negative for all traits with the exception of the flowering traits. Furthermore, $H^\star$ was significantly greater than zero for all traits, although the standard errors were relatively large. For grain yield, the genotype-by-environment interaction components were all significantly different from zero and accounted for a large portion of the total genetic variance. The genotype-by-environment interaction components for the plant height traits and days to midsilk were relatively small in comparison to the other components.

In all environments except Rippey, the additive variance was less than the dominance variance for grain yield (Fig. 2). The additive variance for plant height was larger than the dominance variance at all locations with the exception of Carroll 2004, where the two variances were

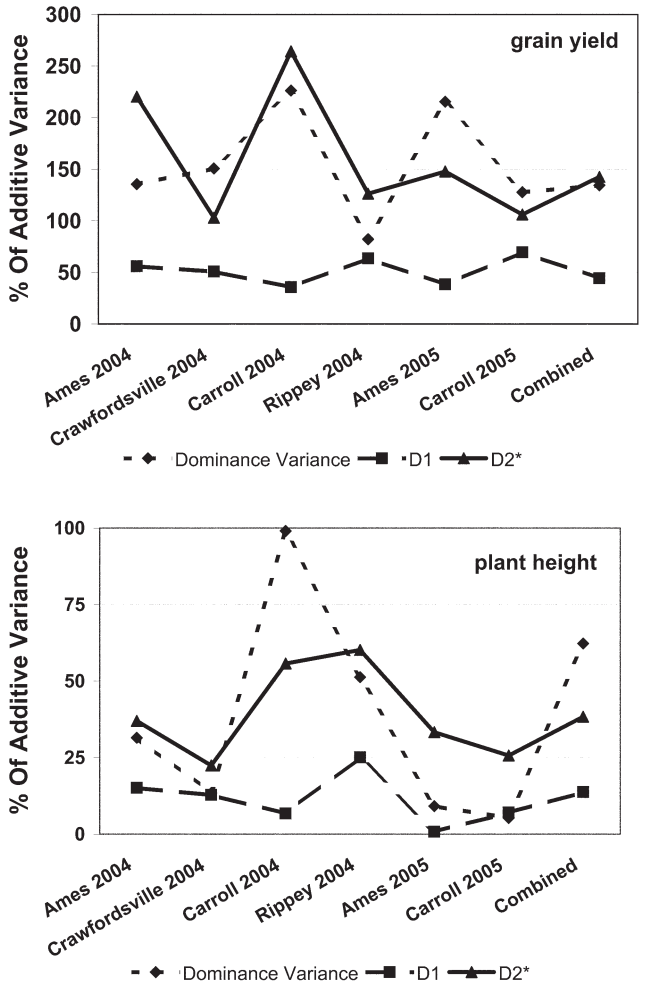

Figure 2. Values of the σ_D^2, D_1, and D_2^* expressed as a relative percentage of the respective σ_A^2 for six environments and the combined analysis for grain yield and plant height.

nearly equal. For both traits, the relative values of the parameters showed variation across environments. The Rippey environment appears to be unique in that it had a negative estimate of $H^\star$ for plant height and contains extreme values for $D_2^\star$ and D_1 for grain yield.

Genetic variances were predicted for each generation based on the estimates of the genetic covariance parameters and compared to the observed genetic variances for each generation (Fig. 3). The model accurately predicted variances of both outbred generations for all traits. The model differed most often from the observed values in the S_3 and S_1 generation. The only difference larger than two standard deviations between the observed and predicted values was for grain moisture in the S_3 generation, where the predicted value was 5.04 g kg^{-1} and the observed value was 3.93 g kg^{-1}.

Correlations

For noninbred individuals, the correlation between *G* and *A* was greater than the correlation between *G* and *D* for all traits with the exception of grain yield (Table 4). The correlation between *G* and *A* for grain yield was 0.65, whereas this correlation ranged from 0.78 to 0.84 for the remaining traits. Grain yield also differed in that the correlation between *G* and *D* in noninbred individuals for grain yield was 0.75, but for all other traits was between 0.55 and 0.62. Correlations between *A* and *D* in inbred individuals were found to be negative for grain moisture, grain yield, plant height, and ear height with a range of −0.31 for plant height to −0.59 for ear height. For inbred individuals, silk date was unique as the correlation of *G* with both *A* and *D* was greater than 0.70. In addition, silk date also had a high positive correlation between *A* and *D* in inbred individuals.

DISCUSSION

Comparison to BS13

Edwards and Lamkey (2002) reported genetic covariance estimates for the maize population BS13(S)C0. It was derived from a maize population that was subjected to seven cycles of half-sib selection with Ia13 used as a tester (see Edwards and Lamkey, 2002 for details concerning formation of BS13(S)C0). These estimates were the first significant published estimates of $D_2^\star$ and $H^\star$ in any crop species. Their breeding design differed from the current design in that they evaluated four inbred generations as well as outbred progeny from the S_1 generation. When compared to estimates obtained from BSCB1(*R*)C13, the relative proportions of the genetic covariance parameters are strikingly similar (Table 5). In terms of grain yield, more genetic variance was found in BSCB1, but there was also more inbreeding depression found in BSCB1(*R*)C13. What is of more importance is the relative values of σ_A^2, σ_D^2, and D_1. In both populations, σ_D^2 was larger than σ_A^2 and D_1 was negative. The absolute value of D_1 was nearly half the value of

Table 3. Genetic covariance parameters for BSCB1(*R*)C13 for grain yield, grain moisture, plant height, ear height, days to midsilk, and days to midpollen, for a combined analysis over four locations in 2004 and two locations in 2005.

Component	Grain yield	Grain moisture	Plant height	Ear height	Midpollen	Midsilk
	Mg^2 ha^{-2}	g^2 kg^{-2}	cm^2	cm^2	days^2	days^2
σ_A^2	0.61 ± 0.06	2.78 ± 0.21	138 ± 11	119 ± 9	1.41 ± 0.14	1.58 ± 0.15
σ_D^2	0.82 ± 0.15	1.55 ± 0.26	86 ± 18	51 ± 11	0.82 ± 0.31	0.67 ± 0.38
D_1	−0.27 ± 0.05	−0.52 ± 0.12	−19 ± 6	−29 ± 5	0.06 ± 0.08	0.36 ± 0.10
D_2^*	0.87 ± 0.14	1.36 ± 0.22	53 ± 10	40 ± 8	0.64 ± 0.18	1.14 ± 0.27
H^*	6.21 ± 1.46	14.91 ± 4.51	729 ± 201	407 ± 129	2.25 ± 2.42	12.41 ± 5.12
σ^2_{AE}	0.25 ± 0.02	0.35 ± 0.03	7 ± 2	8 ± 2	0.14 ± 0.04	0.19 ± 0.05
σ^2_{DE}	0.22 ± 0.07	0.58 ± 0.11	−1 ± 9	7 ± 7	−0.29 ± 0.17	0.00 ± 0.24
D_{1E}	−0.16 ± 0.03	−0.08 ± 0.03	−2 ± 2	−4 ± 2	−0.13 ± 0.05	−0.06 ± 0.06
D_{2E}^*	0.40 ± 0.07	0.39 ± 0.09	5 ± 6	11 ± 5	0.47 ± 0.16	0.41 ± 0.20
H_E^*	2.46 ± 0.72	21.5 ± 2.01	140 ± 82	60 ± 52	1.13 ± 1.66	0.38 ± 2.87

σ_A^2 in both populations. Thus it appears that for grain yield, the genetic variance structures of these two populations are similar. For grain yield, grain moisture, plant height, and ear height, BSCB1(*R*)C13 showed more inbreeding depression as the estimate of $H^\star$ was greater. The estimates of $D_2^\star$ give an indication of the variance of dominance deviations of inbred lines, i.e., the difference between inbred per se performance and performance of outbred progeny of the same inbred line. BS13 showed relatively more variation in inbred dominance deviations for plant height, ear height, and grain moisture than BSCB1(*R*)C13 (Table 5).

Both of the populations for which parameter estimates are available, BS13(S)C0 and BSCB1(*R*)C13, were selected for grain yield and grain moisture with a greater emphasis placed on grain yield. BS13(S)C0 was initially put through 7 cycles of half-sib selection, and BSCB1(*R*)C13 has undergone 13 cycles of reciprocal improvement with the BSSS(R) population (Penny and Eberhart, 1971; Lamkey et al., 1991; Keeratinijakel and Lamkey, 1993; Schnicker and Lamkey, 1993; Holthaus and Lamkey, 1995). Given observed covariance parameter estimates for grain yield in these two popluations, it appears that selection has produced similar genotypic covariance structures in two populations that differ in their genetic background. Of greatest concern are the large negative values of D_1 found in both populations for grain yield. A large negative value of D_1 indicates that simultaneous improvement of both inbred and outbred performance will be difficult. What would be of great interest in future studies is data on the genetic covariance parameters in an unselected maize population as it is impossible to separate the effects of genetic drift from selection in these two populations.

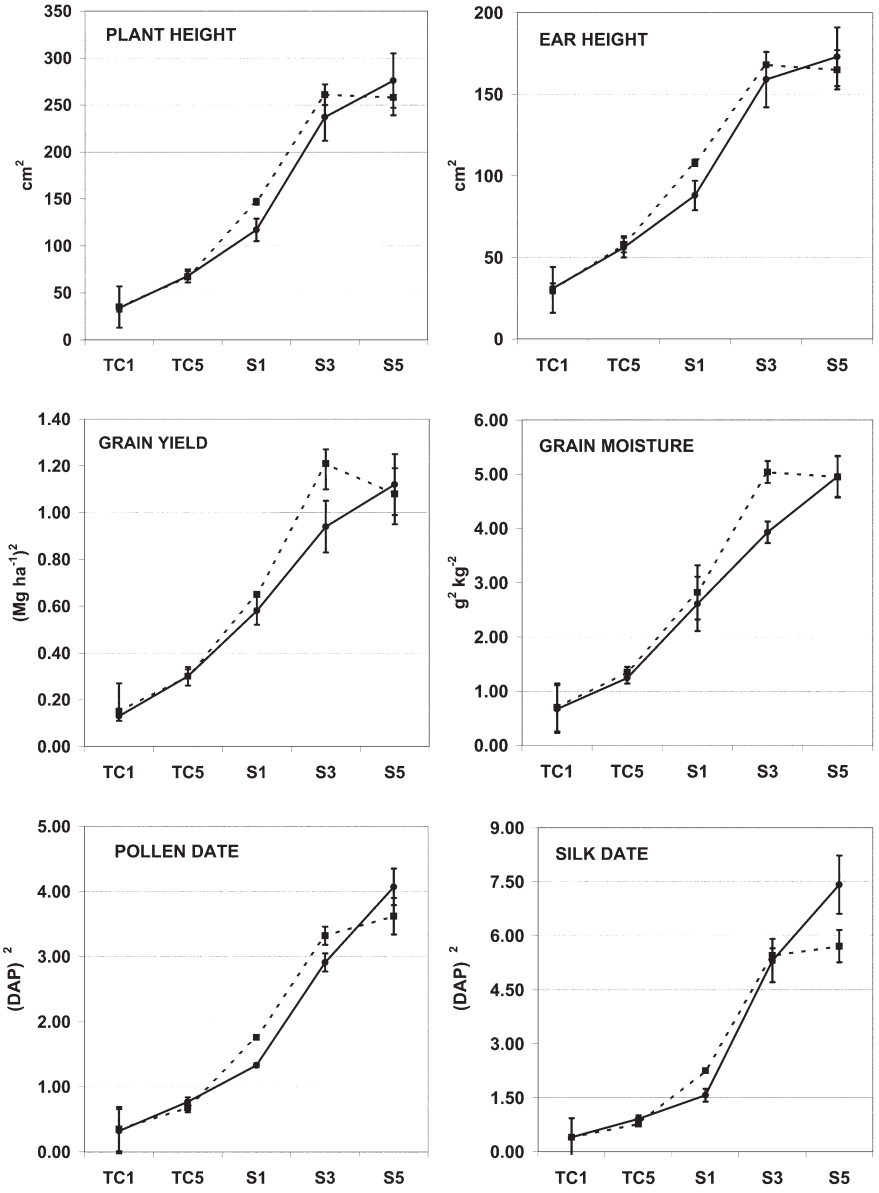

Figure 3. Line graphs representing the comparison of observed (solid lines) genetic variances and predicted (dotted lines) genetic variances using the estimated genetic covariance parameters for plant height, ear height, grain yield, grain moisture, days to mid pollen (pollen date measured in days after planting [DAP]) and days to midsilk (silk date, measured in DAP) versus generation of inbreeding. Generations: TC1, topcrosses of S_1 lines; TC5, topcrosses of S_5 generation. S_1, S_3, and S_5 are the inbred generations per se. Standard error bars represent one standard deviation.

Design and Estimation Issues

The mating design used in this study was developed based on previous suggestions made by several researchers. Lynch (1988) suggested that a large (over 100) number of lines be evaluated and an effort be made to accurately estimate the additive genetic variance. Cornelius (1988) recommended that outbred progenies from early in the inbreeding process be used to separate the additive and dominance components of genetic variance. We have satisfied Lynch's (1988) suggestion by evaluating 200 lines in each of five generations, and we have satisfied the second suggestion by testing the S_1 topcross generation as this will give us a clean estimate of the additive genetic variance. Edwards and Lamkey (2002) suggested including outbred progenies of inbred generations as a means of reducing correlations between parameters. Thus we included the S_5 topcross generation. In actuality, the inclusion of this generation serves another purpose as well. By inclusion of both the S_5 and S_5 topcross generations we were able to separate inbred dominance deviations from inbred breeding values. To our knowledge, this has not been previously done in any maize population. In all, we evaluated 200 lines in five generations: S_1, S_3, S_5, S_1 topcross, and S_5 topcross (Fig. 1).

Table 4. Correlations between genotypic values (*G*), breeding values (*A*), and dominance deviations (*D*) in both inbred and noninbred individuals in BSCB1(*R*)C13.

	Noninbred individuals		Inbred individuals		
Trait	*r*(*G*,*A*)	*r*(*G*,*D*)	*r*(*G*,*A*)	*r*(*G*,*D*)	*r*(*A*,*D*)
Grain yield	0.65	0.75	0.61	0.35	−0.52
Grain moisture	0.80	0.60	0.87	0.12	−0.37
Plant height	0.78	0.62	0.90	0.13	−0.31
Ear height	0.84	0.55	0.92	−0.22	−0.59
Midpollen	0.80	0.61	0.91	0.49	0.09
Midsilk	0.84	0.55	0.91	0.72	0.38

The S_1 generation was included in the design based on suggestions made by Cockerham (1983), because progenies from early generations of inbreeding provide information to estimate σ_D^2. We also included outbred progenies of the S_1 generation to separate the σ_A^2 and σ_D^2 components of genetic variance and in essence to separate breeding values and dominance deviations in noninbred individuals. The S_3 generation was included to provide more information on $H^\star$, as it only contributes to the variance of inbred generations and the covariances between inbred generations (Table 1). A shortcoming of our design is that we do not have independent estimates of all five parameters which resulted in multicollinearity among the estimators. We have quantified this multicollinearity via a correlation matrix for grain yield computed from the asymptotic covariance matrix of the estimates:

$$\begin{array}{c} \\ \sigma_A^2 \\ \sigma_D^2 \\ D_1 \\ D_2^\star \\ H^\star \end{array} \begin{array}{c} \begin{array}{ccccc} \sigma_A^2 & \sigma_D^2 & D_1 & D_2^\star & H^\star \end{array} \\ \begin{bmatrix} 1 & & & & \\ -0.01 & 1 & & & \\ -0.62 & -0.07 & 1 & & \\ 0.27 & -0.08 & -0.64 & 1 & \\ -0.05 & -0.05 & -0.04 & -0.22 & 1 \end{bmatrix} \end{array}$$

Our experiment, when compared to the Edwards and Lamkey (2002) experiment, had smaller correlations between parameter estimates in all cases. Although the correlations are reduced from previous designs, our estimator of D_1 was still correlated with estimators of σ_A^2 and $D_2^\star$. In our design, the coefficients on D_1 change simultaneously with the coefficients on σ_A^2 and $D_2^\star$ and in the same direction:

$$\begin{aligned} \mathrm{Var}(S_1) &= \sigma_A^2 + 1D_1 + 0.125D_2^\star + 0.25\sigma_D^2 \\ \mathrm{Var}(S_5) &= 1.94\sigma_A^2 + 3.81D_1 + 0.945D_2^\star + 0.015H^\star + 0.016\sigma_D^2 \\ \mathrm{Var}(S_\infty) &= 2\sigma_A^2 + 4D_1 + 1D_2^\star \end{aligned}$$

Thus, estimators of D_1 are correlated with estimates of σ_A^2 and $D_2^\star$. New designs should seek to further reduce multicollinearity among estimators of D_1, σ_A^2, and $D_2^\star$.

In addition to the specific set of relatives used in this study, i.e., the mating design, development of single-locus covariance theory also assumes a highly idealized population in that deviations from Hardy–Weinberg equilibrium, effects of linkage, epistasis, and assortative mating are all ignored. Yet, these deviations are known to exist. Hinze et al. (2005) showed that 15 to 20% out of 105 simple sequence repeat loci genotyped in 30 individuals in several cycles of the BSCB1(*R*) population deviated from Hardy–Weinberg equilibrium, providing direct evidence that at least one assumption was violated. Obtaining an ideal population in which none of the model assumptions are violated is impossible. The practical alternative is to interpret estimates of studies such as these cautiously. In particular, the estimates simply do not reflect the effects of segregation of individual alleles at individual loci in an idealized population, but rather, estimates reflect segregation of chromosome segments in the population as it exists. In such context, variance component estimates might more accurately be interpreted as the effects of segregating chromosome segments, as opposed to being effects of individual alleles. A good example of such an interpretation in the classical literature comes from estimates of dominance variance before and after random mating of F_2 populations (Gardner and Lonnquist, 1959; Moll et al., 1964; Lonnquist, 1980; Han and Hallauer, 1989). Dominance variance was estimated in F_2 populations in linkage disequilibrium and reported as dominance variance without attempts to remove the bias. However, the authors also pointed out that these estimates were biased by linkage disequilibrium, as we admit our estimates are likely biased by various violations of assumptions. Clearly, advances are needed in estimation theory for these types of studies to handle issues such as assortative mating, linkage disequilibrium, and other deviations.

Role of Dominance

Previous estimates of σ_A^2 and σ_D^2 in maize have been reported in numerous studies, and the general result is that σ_A^2 is larger than σ_D^2, and many times much larger. This has been found to be true for all traits in maize (see Hallauer and Miranda Filho, 1988). The only consistent exception is grain yield in the BSSS population, where σ_D^2 is approximately equal to σ_A^2 (Hallauer and Miranda Filho, 1988). It was surprising that we found such a large proportion of dominance variance in BSCB1(*R*)C13 for grain yield, as previous estimates have shown additive variance to be larger than dominance variance (Hallauer, 1970). Hallauer (1970) estimated the additive and dominance variances for Cycle 0 and Cycle 4 of BSCB1. He found the dominance to additive variance ratio to be 0.40 in Cycle 0 and 0.77 in Cycle 4, although no statistical test is available for the ratio itself, given the large standard errors associated with the respective variance components the difference between these two ratios is most likely insignificant. We have evaluated BSCB1(*R*)C13 and estimated the dominance to additive variance ratio to be 1.34, a great deal larger than the estimates obtained from Cycles 0 and 4. Although our study and Hallauer's study estimated variance components using different methods,

it appears as though dominance variance is increasing in BSCB1(*R*) relative to the additive variance.

We can only speculate as to why dominance variance is becoming more prominent in BSCB1(*R*), but several possible explanations do exist. If overdominant gene action is the cause, dominance variance would be larger than additive variance given recessive allele frequencies ranged between 0.2 and 0.8. Given the large amount of evidence against the overdominant hypothesis, we argue that this explanation is not sufficient. Under the dominance hypothesis (Crow, 2000) and a recessive allele frequency of less than 0.35, one would also observe more dominance variance than additive variance. Although this may in fact be the case in BSCB1(*R*)C13, it is an unlikely scenario given that recessive alleles with large phenotypic effects are eventually purged via selection. More likely causes of the increase in dominance variance within the population are drift and linkage disequilibrium. Drift alone has been shown theoretically to increase dominance variance with recessive alleles (Robertson, 1952). Edwards and Lamkey (2003) used genotypic covariance estimates in BS13(S)C13, which had similarities in structure to BSCB1(*R*)C13, to predict that genetic drift would increase the dominance variance within subpopulations derived from the base population. Linkage disquilibrium has been shown to increase following selection (Bulmer, 1971; Hospital and Chevalet, 1996) and drift (Avery and Hill, 1979). In classical studies, it has been shown that random mating of F_2 populations to reduce linkage disequilibrium tends to decrease the dominance variance (Gardner and Lonnquist, 1959; Moll et al., 1964; Lonnquist, 1980; Han and Hallauer, 1989). Conversely, increasing linkage disequilibrim could be expected to increase the magnitude of dominance variance. An increase in linkage disequilibrium within BSCB1(*R*)C13 may be expected based only on its finite size (i.e., drift) and its selection history. However, beyond effects of selection and drift acting independently, Hospital and Chevalet (1996) demonstrated that selection and drift acting in concert specifically lead to an increase in repulsion phase linkages within the population. Commercial maize breeders rarely employ recurrent selection and most often utilize F_2 populations to develop new inbreds. The use of F_2 populations has several advantages with regards to the genetic covariance parameters. When allele frequencies are equal, D_1 and D_2★ both equal zero, and when there are only two alleles per locus, H★ equals σ_D^2 (Cockerham, 1983). When D_1 equals zero, the additive and dominance effects within an individual are no longer correlated. The commercial maize industry is primarily concerned with the performance of an individual in a cross to an unrelated individual. In such crosses, D_1, D_2★, and H★ only influence inbred per se performance, as homozygous dominance deviations are assumed to be absent from a cross of two unrelated individuals. A much greater concern, however, to commercial maize breeders should be effects of the covariance structures that have been observed in two maize populations, BSCB1(*R*)C13 and BS13(S)C0 (Edwards and Lamkey, 2002), representing two different sides of a commonly used heterotic pattern. The observed covariance structures in our study and that of Edwards and Lamkey (2002) demonstrate the potential difficulty in simultaneously improving inbred performance and hybrid performance. More importantly, the increase in dominance variance in BSCB1(*R*)C13 suggests that repulsion phase linkage is increasing within the population. If in fact dominance variance is increasing in BSCB1(*R*) due to increasing repulsion phase linkage disequilibria, it suggests that long-term selection within a heterotic group may drive genotypic variance component structures in a direction that makes the population more difficult to improve. Clearly, much more work is needed in this area to understand the genetics of long-term selection and to determine how to maintain long-term response to selection.

Table 5. Genetic covariance parameters for BSCB1(*R*)C13 and BS13(S)C0 for grain yield, grain moisture, plant height, ear height, days to midsilk, and days to midpollen, for a combined analysis over six locations.

Component	Grain yield		Plant height		Midsilk	
	BSCB1(*R*)C13	BS13(S)C0	BSCB1(*R*)C13	BS13(S)C0	BSCB1(*R*)C13	BS13(S)C0
	Mg^2 ha^{-2}		cm^2		days^2	
σ^2_A	0.61 ± 0.06	0.29 ± 0.05	138 ± 11	208 ± 23	1.6 ± 0.2	4.1 ± 0.5
σ^2_D	0.82 ± 0.15	0.32 ± 0.09	86 ± 18	64 ± 21	0.7 ± 0.4	1.0 ± 0.4
D_1	–0.27 ± 0.05	–0.18 ± 0.06	–19 ± 6	–76 ± 18	0.4 ± 0.1	–1.0 ± 0.4
D_2★	0.87 ± 0.14	0.85 ± 0.19†	53 ± 10	194 ± 47	1.1 ± 0.3	1.7 ± 1.0
H★	6.21 ± 1.46	1.55 ± 0.48	729 ± 201	661 ± 149	12.4 ± 5.1	21.0 ± 4.2
	Grain moisture		Ear height		Midpollen	
	BSCB1(*R*)C13	BS13(S)C0	BSCB1(*R*)C13	BS13(S)C0	BSCB1(*R*)C13	BS13(S)C0
	g^2 kg^{-2}		cm^2		days^2	
σ^2_A	2.78 ± 0.21	5.20 ± 0.60	119 ± 9	149 ± 17	1.4 ± 0.1	2.1 ± 0.3
σ^2_D	1.55 ± 0.26	1.70 ± 0.70	51 ± 11	44 ± 14	0.8 ± 0.3	1.0 ± 0.4
D_1	–0.52 ± 0.12	–0.40 ± 0.40	–29 ± 5	–66 ± 13	0.1 ± 0.1	–0.3 ± 0.3
D_2	1.36 ± 0.22	2.90 ± 1.20	40 ± 8	147 ± 33	0.6 ± 0.2	0.6 ± 0.7
H★	14.91 ± 4.51	6.50 ± 4.80	407 ± 129	344 ± 89	2.3 ± 2.4	6.4 ± 2.1

†This standard error was incorrectly reported in Edwards and Lamkey (2002); 0.19 is the correct standard error.

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