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Inbred-Progeny Selection Is Predicted to Be Inferior to Half-Sib Selection for Three Maize Populations

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Abstract

Historically, inbred progeny selection has been promoted as an effective means of improving both inbred and outbred performance, and in some cases as being superior to other methods. Advances in theory and new estimates of genotypic covariance components have allowed us to make better predictions of gain from inbred progeny selection than previously available. We developed predicted gain equations using a full model, based on new theory and estimates, and a reduced model, which contained only the additive genetic variance in the numerator, for three maize (*Zea mays* L.) populations, BS13(S)C0, BSCB1(R)C13, and 3L Comp (HS-$S_1)_{S1}$Outbred progeny selection was superior to inbred progeny selection for plant height and grain yield when the response unit was the outbred population. Inbred progeny selection was superior for plant height in both populations and more effective for grain yield in BS13(S)C0 in inbred response units. Negative estimates of the covariance parameter D_1 reduced predicted gain for inbred progeny selection in the full model in comparison to the reduced model when D_1 was ignored.

Disciplines

Agricultural Science | Agriculture | Agronomy and Crop Sciences | Plant Breeding and Genetics

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ABSTRACT

Historically, inbred progeny selection has been promoted as an effective means of improving both inbred and outbred performance, and in some cases as being superior to other methods. Advances in theory and new estimates of genotypic covariance components have allowed us to make better predictions of gain from inbred progeny selection than previously available. We developed predicted gain equations using a full model, based on new theory and estimates, and a reduced model, which contained only the additive genetic variance in the numerator, for three maize (*Zea mays* L.) populations, BS13(S)C0, BSCB1(R)C13, and 3L Comp (HS-S$_1$)$_{S1}$. Outbred progeny selection was superior to inbred progeny selection for plant height and grain yield when the response unit was the outbred population. Inbred progeny selection was superior for plant height in both populations and more effective for grain yield in BS13(S)C0 in inbred response units. Negative estimates of the covariance parameter D_1 reduced predicted gain for inbred progeny selection in the full model in comparison to the reduced model when D_1 was ignored.

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Inbred–progeny recurrent selection was shown to be a superior method to mass selection and half–sib recurrent selection based on theoretical arguments by numerous authors over an approximately 20-yr period (Comstock, 1964;Horner et al., 1969; Eberhart, 1970;Choo and Kannenberg, 1979;Wricke, 1976;Wright, 1980;Cockerham and Matzinger, 1985). In contrast to theoretical predictions, inbred–progeny selection has not been demonstrated to be universally superior based on empirical work (Lamkey, 1992; Coors, 1999) nor has it been widely adopted in industrial maize (*Zea mays* L.) breeding programs, where the vast majority of performance evaluations have been based on testcross performance for decades (Hallauer et al., 1988).

The predicted superiority of inbred–progeny selection, at least in maize, appears to have been initiated in public-sector efforts to promote population improvement as opposed to repeated resampling of the same germplasm base (Comstock, 1964). The goal of public sector workers was to convince corn breeders of the value of continuous improvement of a common germplasm base through repeated selection and recombination to improve the performance of maize hybrids (A.R. Hallauer, personal communication, 2008). The result was a wave of theoretical studies espousing the virtues of recurrent selection methods to improve testcross

performance. Most of these studies focused on the comparison among inbred-progeny selection, mass selection, and half-sib methods on the basis of population per se performance as opposed to testcross performance (Comstock, 1964; Horner et al., 1969; Eberhart, 1970, 1972; Wricke, 1976; Choo and Kannenberg, 1979; Wright, 1980; Cockerham and Matzinger, 1985). A tacit assumption was that improvement of population per se performance was equivalent to improvement of testcross performance. Even in the study by Wright (1980) in which lengthy theory was presented for choosing the tester that would maximize selection response, selection methods were compared on the basis of response in the panmictic population per se and not on testcross performance. In addition to the failure in the literature to connect selection response in populations to response in testcross performance, it also appears that the theory used in the aforementioned studies was somewhat incomplete.

Early forms of predicted selection response for inbred-progeny selection such as those given by Comstock (1964), Sprague (1966), and Empig et al. (1981) were technically correct, but the theory did not exist to estimate the correct covariance components for the numerator of the predicted selection response. In absence of empirical estimates, several authors relied on single-locus, two-allele models with no overdominance and environmental variance generated to match a desired heritability (Comstock, 1964; Horner et al., 1969; Wricke, 1976; Choo and Kannenberg, 1979). Under these simple conditions, inbred-progeny selection always had the highest expected response to selection (for population per se performance). The assumption of no overdominance was well founded in the best studies of the day suggesting that in fact the average degree of dominance for genes controlling grain yield in maize was less than 1.0 (Gardner and Lonnquist, 1959; Moll et al., 1964; Han and Hallauer, 1989). However, none of the authors promoting inbred-progeny selection considered that pseudo-overdominance could impact selection response in the same way as true overdominance. Wright (1980) took a step forward and included numerous genetic models including overdominance and epistasis and still found that inbred progeny recurrent selection had the highest predicted response to selection. To move beyond purely theoretical models based on one- or two-locus gene effects, a variety of attempts were made to approximate predicted selection response using biased estimators of the correct numerator-covariance in predicted selection response by Eckebil et al. (1977) and Jan-orn et al. (1976) in sorghum [*Sorghum bicolor* (L.) Moench] and by Eberhart (1970, 1972) in maize. Eckebil et al. (1977) and Eberhart (1970) recognized that their estimators were still biased, while Jan-orn et al. (1976) presented an estimator with some of the bias removed, but did not comment directly on whether they expected their estimator to be completely or partially

unbiased. The three biased estimators of predicted selection response still provided very favorable predictions of inbred-progeny selection methods.

Cornelius and Dudley (1976) provided the first unbiased estimators of predicted selection response known to the authors for inbred-progeny selection, and did so for selection based on general combining ability or line per se performance and predicted response in both general combining ability and line per se performance in a maize population. The unbiased estimation of predicted response presented by Cornelius and Dudley (1976) required five genotypic covariance components. However, it has been very difficult to obtain mating designs for estimating these components (Edwards and Lamkey, 2002; Wardyn et al., 2007) because of multicollinearity among estimators of the different components (Cornelius and Van Sanford, 1988; Wright and Cockerham, 1986). As such, the covariance estimators of Cornelius and Dudley (1976) had high standard errors and some components were outside the parameter space (Cornelius and Dudley, 1976; Cornelius, 1988). Bradshaw (1983) pointed out that the covariance between S_1 line performance and half-sib or full-sib families derived from the parent of the S_1 line provided an unbiased estimator of the numerator of predicted selection response for S_1 selection. This estimator was much simpler than the theory of Cornelius and Dudley (1976), although not nearly as general. Unfortunately, to the knowledge of the authors, the relatively straightforward approach of Bradshaw (1983) has not been widely used. Cockerham and Matzinger (1985) provided additional predicted selection response equations for inbred progeny selection, but still provided very little in the way of guidance as to how to estimate the required genotypic covariance components. In the absence of empirical estimators, Cockerham and Matzinger (1985) plugged in an arbitrary two-locus model and concluded, as many had in the past, that inbred-progeny selection was probably the most effective method for improving populations. Coors (1988) provided all required estimators for predicted selection response from S_1–progeny selection in a maize population, but it does not appear these estimators have been used in published predictions of selection response.

Following the collective experiences and theoretical observations of many of the studies cited, particularly Cornelius and Dudley (1976), Cornelius (1988), Cockerham (1983) Wright and Cockerham (1986), Lynch (1988), and Coors (1988), two studies were attempted to obtain estimators of covariance components for inbred relatives in two maize populations (Edwards and Lamkey, 2002; Wardyn et al., 2007). These two studies produced estimators of all five necessary genotypic covariance components required for prediction of selection response with much less collinearity among components than the estimators of Cornelius and Dudley (1976) and smaller relative

standard errors. The objectives of this paper were to use these estimates to answer the following two questions: (i) does inbred-progeny recurrent selection have higher predicted selection response than half-sib selection? and (ii) what is the impact of using a biased estimator of predicted response to inbred-progeny selection?

MATERIALS AND METHODS
Genetic Model
The assumed model for this investigation was a single locus model (Fisher, 1918; Harris, 1964):

$$g_{ij} = \mu + \alpha_i + \alpha_j + \delta_{ij} \qquad [1]$$

where g_{ij} = genotypic value of individual with genotype A_iA_j; μ = population mean; α_i = additive effect of ith allele, and δ_{ij} = dominance deviation.

Harris (1964) developed genotypic-covariances for any level of inbreeding from the basic single-locus model. Previously, genotypic covariances between related individuals had been described in general terms only for noninbred individuals (Fisher, 1918; Kempthorne, 1954; Malecot, 1969). Covariances between noninbred individuals required only the two covariance components, σ^2_A and σ^2_D, whereas five components are required for covariances individuals with general levels of inbreeding (Harris, 1964). The additional components, D_1, $D_2^\star$, and $H^\star$, are related directly to the homozygous dominance deviations, the basis for inbreeding depression (Table 1). The component $D_2^\star$ is the variance of the homozygous dominance deviations, which parallels the dominance variance, σ^2_D, except that $D_2^\star$ is defined strictly for dominance deviations in individuals with alleles identical by descent. Dominance deviations exist between alleles that are identical by descent because the additive effects are defined with respect to noninbred individuals, and hence, do not predict the genotypic value of an inbred individual in Harris' (1964) parameterization. The component $H^\star$ is equivalent to the sum (over loci) of homozygous dominance deviations, squared, and in general contributes little to the covariances between related individuals (Cockerham, 1983). The term D_1 is the covariance between additive effects and homozygous dominance deviations and is unique among genotypic covariance components in that it can be positive or negative. Interpretation of the component D_1 is difficult, but perhaps the most important implication of the component is its contribution to the covariance between inbred and outbred performance (Edwards and Lamkey, 2002, 2003; Edwards, 2008). Collecting all five components into a single expression

for the covariance between individuals X and Y produced (Harris, 1964; Cockerham, 1983; Cockerham and Weir, 1984; Wright and Cockerham, 1986):

$$Cov(X,Y) = 2\theta_{XY}\sigma^2_A + \left(\Delta_{\ddot{X}+\ddot{Y}} - \delta_{\ddot{X}\ddot{Y}}\right)\sigma^2_D + 2\left(\gamma_{\ddot{X}Y} + \gamma_{X\ddot{Y}}\right)D_1$$
$$+ \delta_{\ddot{X}\ddot{Y}}D_2^\star + \left(\Delta_{\ddot{X}\ddot{Y}} - F_X F_Y\right)H^\star \qquad [2]$$

where θ_{XY}, $\Delta_{\ddot{X}+\ddot{Y}}$, $\delta_{\ddot{X}\ddot{Y}}$, $\gamma_{\ddot{X}Y}$, $\gamma_{X\ddot{Y}}$, $\Delta_{\ddot{X}\ddot{Y}}$, F_X, and F_Y are identity by descent probabilities for two, three, or four alleles (Harris, 1964; Cockerham, 1971; Table 2). Identity by descent probabilities are nonmutually exclusive probabilities of combinations of two, three, or four alleles being identical by descent and were described in detail by Cockerham (1971) as functions of 15 mutually exclusive identity states. The probabilities θ_{XY}, F_X, and F_Y are the more commonly known co-ancestry coefficients between X and Y (θ_{XY}) and the inbreeding coefficients of X and Y (F_X and F_Y). All the identity-by-descent probabilities are defined in Table 2.

Genetic Gain
Genetic gain was predicted for four recurrent selection methods:
1. HS: half-sib selection with a selection unit obtained by harvesting seed from a single individual with male gametes sampled randomly from the population with recombination of half-sib seed;
2. HS-S_1: half-sib progeny of an S_1 line selection with a selection unit developed by self-pollinating a single individual to produce an S_1 line followed by topcrossing the S_1 line to the population per se as male with recombination of remnant S_1 seed;
3. S_1: S_1–progeny selection with a selection unit developed by harvesting the self-pollinated seed of a single noninbred individual with recombination of remnant S_1 seed;
4. S_2: S_2–progeny selection with a selection unit developed by self-pollinating a single individual within an S_1 line to produce an S_2 family of individuals with $F = 0.75$ with recombination of remnant S_2 seed.

Response was computed for individuals in the recombined population with inbreeding coefficients of $F = 0$, $F = 0.5$, and $F = 0.75$ corresponding to zero, one, or two generations of self-pollination. Predicted genetic gains were obtained from the genetic gain equation used in Edwards (2008):

$$\Delta G = pi\frac{\sigma_{C,O}}{\sigma_P} \qquad [3]$$

where $\sigma_{C,O}$ = covariance between candidates and offspring; σ_P = phenotypic standard deviation of candidates; p = parental control; and i = standardized selection differential.

Table 1. Genotypic covariance components for inbred relatives, their definitions, and coefficients in the general genotypic covariance between individuals X and Y.

Component	Expectation	Coefficient	Description
σ^2_A	$\sum_i p_i \alpha_i^2$	$2\theta_{XY}$	Additive variance
σ^2_D	$\sum_i p_i p_j \delta_{ij}^2$	$2(\Delta_{\ddot{X}+\ddot{Y}} - \delta_{\ddot{X}\ddot{Y}})$	Dominance variance
D_1	$\sum_i p_i \alpha_i \delta_{ii}$	$2(\gamma_{X\ddot{Y}} + \gamma_{\ddot{X}Y})$	Covariance between additive effects and homozygous dominance deviations
$D_2^\star$	$\sum_i p_i \delta_{ii}^2 - (\sum_i p_i \delta_{ii})^2$	$\delta_{\ddot{X}\ddot{Y}}$	Variance of homozygous dominance deviations
$H^\star$	$(\sum_i p_i \delta_{ii})^2$	$\Delta_{\ddot{X}\ddot{Y}} - F_X F_Y$	Sum of homozygous dominance deviations (inbreeding depression), squared

Table 2. Identity by descent probabilities required for covariances between inbred relatives for two individuals. Individual X had alleles X_1 and X_2 and individual Y had alleles Y_1 and Y_2. Each identity by descent probability is an average probability of identity of the allelic equivalencies shown in the second column. Notation for components was obtained from Cockerham (1971).

Measure	Equivalent sets of alleles
F_X	$X_1 \equiv X_2$
F_Y	$Y_1 \equiv Y_2$
θ_{XY}	$X_1 \equiv Y_1$ or $X_1 \equiv Y_2$ or $X_2 \equiv Y_1$ or $X_2 \equiv Y_2$
$\gamma_{\ddot{X}Y}$	$X_1 \equiv X_2 \equiv Y_1$ or $X_1 \equiv X_2 \equiv Y_2$
$\gamma_{X\ddot{Y}}$	$Y_1 \equiv Y_2 \equiv X_1$ or $Y_1 \equiv Y_2 \equiv X_2$
$\Delta_{\ddot{X}\ddot{Y}}$	$X_1 \equiv X_2,\ Y_1 \equiv Y_2$
$\Delta_{\ddot{X}+\ddot{Y}}$	$X_1 \equiv Y_1,\ X_2 \equiv Y_2$ or $X_1 \equiv Y_2,\ X_2 \equiv Y_1$
$\delta_{\ddot{X}\ddot{Y}}$	$X_1 \equiv X_2 \equiv Y_1 \equiv Y_2$

The standardized selection differential, i, was held constant at 1.755 corresponding to a selection intensity of 10%. The value of parental control, p, was 2 for all methods because remnant seed used for recombination was obtained from selected families only. Formulas were obtained directly from Tables 3, 4, and 5 in Edwards (2008) for the four selection methods and three levels of inbreeding in the recombined population. The half-sib methods corresponded to the methods half-sib-1 (one generation of outcrossing) and Half-sib-TS (topcross with recombination of selfed seed) in Table 4 of Edwards (2008). The self progeny selection methods corresponded to the Self-progeny–1 method (one generation of selfing for seed production) in Table 4 of Edwards (2008) with inbreeding coefficients of 0 and 0.5 for the parent (F_P) and 0.5 and 0.75 for individuals in candidate families (F_C). Substitution of these parameters into Tables 3 and 5 of Edwards (2008) resulted in formulae for the numerator covariance of predicted genetic gain in Table 3. The genetic contribution to the phenotypic variance used in obtaining the denominator of predicted gain was obtained from Table 6 in Edwards (2008). The full phenotypic variance for the denominator of predicted gain was computed on a family-mean basis assuming the number of replications and locations used in the studies in which variance components were originally estimated. In addition to the full genetic model, genetic gain was estimated from a reduced genetic model in which the numerator covariance, $\sigma_{C,O}$, contained only

additive genetic variance (with appropriate coefficient). The reduced model reflected the effect of ignoring the covariance parameter D_1. A third set of predictions was obtained from a repeatability model (based on family-mean basis repeatability) in which genetic variance among selection candidates was substituted for the numerator covariance, $\sigma_{C,O}$, and the same denominator as the previous two models was used.

Parameter Estimates

Estimates of all parameters needed for predicting genetic gain for all four methods of selection and three levels of inbreeding in the recombined population were available for two maize populations, BSCB1(R)C13, a member of the non-stiff stalk heterotic pattern (Wardyn et al., 2007), and BS13(S)C0, a member of the stiff stalk heterotic pattern (Edwards and Lamkey, 2002) (Table 4). In addition, Coors (1988) provided sufficient parameters from the 3L Comp (HS-S$_1$)$_{S1}$ population, a narrow based synthetic derived by intermating three inbred lines, to predict gain from half-sib and S$_1$ selection. Parameter estimates in 3L Comp (HS-S$_1$)$_{S1}$ were $\hat{\sigma}_A^2 = 293 \pm 59$, $\hat{D}_1 = -309 \pm 126$, $\hat{\sigma}_{P(HS)}^2 = 231 \pm 12$, and $\hat{\sigma}_{P(S_1)}^2 = 369 \pm 21$ (Coors, 1988). Phenotypic variances, $\hat{\sigma}_{P(HS)}^2$ and $\hat{\sigma}_{P(S_1)}^2$, in Coors (1988) were total phenotypic variances for half-sib and S$_1$ progeny on an entry mean basis. Epistasis was assumed to be negligible in BS13SC(0) and 3L Comp (HS-S$_1$)$_{S1}$ (Coors, 1988; Edwards and Lamkey, 2002) and additive by additive epistasis was found to be nonsignificant in BSCB1RC(13) (unpublished data).

RESULTS
Theory

The two half-sib methods differed by a factor of two, with recombination of S$_1$ seed resulting in twice the predicted gain as recombination of half-sib seed. However, prediction of genetic gain based on repeatability alone did not reflect this difference (Table 5). Table 3 revealed some important patterns with respect to the impact of inbreeding on the numerator covariance of the genetic gain equation. First, in the case of half-sib selection and noninbred response ($F = 0$), only additive genetic variance contributed to the numerator. The contribution of the covariance component D_1 was dependent on inbreeding in both the candidates for selection and the recombined population. If response was measured in inbred individuals in the recombined population, D_1 contributed to the numerator for all methods. If response was measured in noninbred individuals in the recombined population ($F = 0$ in Table 5), D_1 only contributed to selection response for the inbred methods. In effect, D_1 contributed to any predicted response in which either the selection candidates or response units were inbred. The component $D_2\star$, the variance of homozygous dominance deviations, contributed only when both selection units and response units were inbred.

Table 3. Genetic components of the numerator covariance and denominator genetic variance in the genetic gain equation for four methods of recurrent selection. For the half-sib methods, half-sib refers to traditional half-sib selection with recombination of remnant half-sib seed and half-sib S$_1$ refers to producing half-sib families by topcrossing S$_1$ lines to the base population and recombining remnant S$_1$ seed. The inbreeding coefficient in the numerator covariance is the inbreeding coefficient of individuals derived by self-pollination in the recombined population. The full genetic gain equation was given in the materials and methods.

Method	Numerator covariance	Denominator genetic variance
Half-sib	$\frac{1}{4}\sigma_A^2 + \frac{1}{4}FD_1$	$\frac{1}{4}\sigma_A^2$
Half-sib S$_1$	$\frac{1}{2}\sigma_A^2 + \frac{1}{2}FD_1$	$\frac{1}{2}\sigma_A^2$
S$_1$	$\sigma_A^2 + (\frac{1}{2}+F)D_1 + \frac{1}{4}FD_2^*$	$\sigma_A^2 + \frac{1}{4}\sigma_D^2 + D_1 + \frac{1}{8}D_2^*$
S$_2$	$\frac{3}{2}\sigma_A^2 + (\frac{5}{4}+\frac{3}{2}F)D_1 + \frac{5}{8}FD_2^*$	$\frac{3}{2}\sigma_A^2 + \frac{1}{8}\sigma_D^2 + \frac{5}{2}D_1 + \frac{9}{16}D_2^* + \frac{1}{16}H^*$

Predicted Gain

Predicted gain was greater for inbred methods than either of the half-sib methods in both the reduced model and the repeatability model for both traits for all three populations (Table 5). Furthermore, the predicted gains did not change as inbreeding in the response units varied in the reduced model or repeatability model because these reduced models ignore changes in genetic covariance parameters introduced by inbreeding in the recombined population.

Contrary to results found from the reduced model, the inbreeding level at which response was measured had a profound impact on the predicted gains when the full model was used (Table 5). When the response was measured in noninbred individuals in the recombined population, half-sib selection with recombination of S_1 seed was superior to both forms of inbred progeny selection for grain yield in all three populations (Table 5). However, half-sib selection with recombination of half-sib seed was inferior to all other methods for grain yield in all three populations with response measured in noninbred individuals. When response was measured in inbred individuals in the recombined population, inbred selection methods had a clear advantage over both half-sib methods at $F = 0.75$ in BSCB1(R)C13 and BS13(S)C0 (Table 5). At $F = 0.5$, both inbred methods were better than both half-sib methods in BS13(S)C0, but comparable to half-sib selection with recombination of S_1 seed in BSCB1(R)C13. In the 3L Comp $(HS-S_1)_{S1}$ population, progress from S_2 selection was unestimable. Under the full model in this population, gain from S_1 selection was intermediate to the two half-sib methods for response in noninbred individuals, but clearly inferior to half-sib methods for response in individuals with $F = 0.5$.

For plant height, the differences among methods were smaller in magnitude and less consistent. Half-sib selection did not have the clear advantage seen for grain yield for response in noninbred individuals (based on the full model) nor did inbred methods show a strong advantage for response in inbred individuals (Table 5). The exception was the advantage of S_2 selection when evaluating response in individuals with $F = 0.75$ in the recombined population, in which case S_2 selection had a clear advantage. The clearest trend for plant height was the inferiority of half-sib selection with recombination of half-sib seed.

DISCUSSION

Our predictions of response to inbred progeny selection in three maize populations did not show the advantages over half-sib methods predicted by earlier authors. In the late 1960s and 1970s, when theoretical comparisons among inbred and outbred progeny recurrent selection methods were of great interest, estimation methods were

Table 4. Genetic covariance parameter estimates for BSCB1(R)C13 (Wardyn et al. 2007) and BS13(S)C0 (Edwards and Lamkey, 2002). Error variances for half-sib progeny ($\sigma^2_{E(HS)}$), S_1 lines, and S_2 lines, and standard errors were obtained directly from the same analyses used in Wardyn et al. (2007) and Edwards and Lamkey (2002), but were not published in those reports.

	Grain yield		Plant height	
Component	BSCB1(R)C13	BS13(S)C0	BSCB1(R)C13	BS13(S)C0
	——— Mg ha^{-1} ———		——— cm^2 ———	
σ^2_A	0.61 ± 0.06	0.29 ± 0.05	138 ± 11	208 ± 23
σ^2_D	0.82 ± 0.15	0.32 ± 0.09	86 ± 18	64 ± 21
D_1	−0.27 ± 0.05	−0.18 ± 0.06	−19 ± 6	−76 ± 18
D_2^*	0.87 ± 0.14	0.85 ± 0.19[†]	53 ± 10	194 ± 47
H^*	6.21 ± 1.46	1.55 ± 0.48	729 ± 201	661 ± 149
σ^2_{AE}	0.25 ± 0.02	0.12 ± 0.04	7 ± 2	7 ± 5
σ^2_{DE}	0.22 ± 0.07	0.11 ± 0.06	−1 ± 9	9 ± 9
D_{1E}	−0.16 ± 0.03	−0.11 ± 0.04	−2 ± 2	0 ± 6
D_{2E}^*	0.40 ± 0.07	0.33 ± 0.11	5 ± 6	3 ± 15
H_E^*	2.46 ± 0.72	0.54 ± 0.29	140 ± 82	128 ± 45
$\sigma^2_{E(HS)}$	0.32 ± 0.01	0.37 ± 0.02	37 ± 2	56 ± 4
$\sigma^2_{E(S_1)}$	0.34 ± 0.01	0.29 ± 0.02	58 ± 3	57 ± 4
$\sigma^2_{E(S_2)}$	0.32 ± 0.02	0.27 ± 0.03	61 ± 3	52 ± 6

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

not available for all required genotypic covariance components needed for predicted genetic gain. In the absence of estimators or mating designs to obtain estimators, early authors resorted to generating components based on single-locus genetic models with two alleles and little or no overdominance. The genotypic covariance structures generated under such simple models were clearly quite different from the genotypic covariance structures observed empirically in the three populations used in our study. Genetically, one difference may be due to assumed levels of overdominance. Early authors assumed that overdominance was not important, whereas Edwards and Lamkey (2002) estimated the average degree of dominance for grain yield to be 2.65 (where zero equals no dominance and 1.0 equals complete dominance) in BS13(S)C0 based on their estimates of genotypic covariance components. The number of alleles and distribution of allele frequencies can also influence covariance components (Cornelius, 1988). Epistasis may also play a role. Theoretical studies of expected gain before 1980 were based solely on single-locus models and thus assumed that epistasis did not exist. However, if epistasis does exist, epistatic effects influence the estimators of covariance components derived from single-locus models because of partial confounding of single-locus and epistatic gene effects (Cheverud and Routman, 1995). Therefore, if epistasis was important in the populations used to obtain estimated covariance component estimators for this study, the observed covariance structures could be quite different from theoretical expectations based on single-locus models because of the

Table 5. Predicted genetic gain for S$_1$, S$_2$, and half-sib selection methods based on current estimates of genotypic covariance parameters in three maize populations, BSCB1(R)C13 BS13(S)C0, and 3L Comp (HS-S$_1$)$_{S1}$ for grain yield and plant height for three methods of calculating heritability: full genotypic covariance model, a reduced genetic model which includes only σ^2_A in the numerator, and repeatability on a family mean basis.

Selection unit	Response unit	BSCB1(R)C13			BS13(S)C0			3L Comp (HS-S$_1$)$_{S1}$		
		Full model[†]	Reduced model[‡]	Repeatability[§]	Full model	Reduced model	Repeatability	Full model	Reduced model	Repeatability
		Grain yield						Grain yield		
		———————— Mg ha^{-1} ————————						——— g plant^{-1} ———		
HS-HS	F = 0	0.62	0.62	0.62	0.37	0.37	0.37	8.46	8.46	8.46
HS-S$_1$	F = 0	1.23	1.23	0.62	0.75	0.75	0.37	16.92	16.92	8.46
S$_1$	F = 0	0.99	1.27	1.36	0.60	0.87	0.89	12.65	26.77	25.50
S$_2$	F = 0	0.89	1.40	1.88	0.46	0.94	1.30			
HS-HS	F = 0.5	0.48	0.62	0.62	0.26	0.37	0.37	4.00	8.46	8.46
HS-S$_1$	F = 0.5	0.96	1.23	0.62	0.52	0.75	0.37	8.00	16.92	8.46
S$_1$	F = 0.5	0.93	1.27	1.36	0.65	0.87	0.89	–1.46	26.77	25.50
S$_2$	F = 0.5	0.99	1.40	1.88	0.74	0.94	1.30			
HS-HS	F = 0.75	0.41	0.62	0.62	0.20	0.37	0.37	1.77	8.46	8.46
HS-S$_1$	F = 0.75	0.82	1.23	0.62	0.40	0.75	0.37	3.54	16.92	8.46
S$_1$	F = 0.75	0.90	1.27	1.36	0.67	0.87	0.89	–8.52	26.77	25.50
S$_2$	F = 0.75	1.20	1.40	1.88	1.03	0.94	1.30			
		Plant height								
		———————— cm ————————								
HS-HS	F = 0	9.8	9.8	9.8	12.0	12.0	12.0			
HS-S$_1$	F = 0	19.7	19.7	9.8	24.0	24.0	12.0			
S$_1$	F = 0	18.2	19.6	20.9	22.2	27.2	22.5			
S$_2$	F = 0	20.2	22.8	27.1	22.4	32.2	29.0			
HS-HS	F = 0.5	9.2	9.8	9.8	9.8	12.0	12.0			
HS-S$_1$	F = 0.5	18.3	19.7	9.8	19.6	24.0	12.0			
S$_1$	F = 0.5	17.8	19.6	20.9	20.4	27.2	22.5			
S$_2$	F = 0.5	20.5	22.8	27.1	22.7	32.2	29.0			
HS-HS	F = 0.75	8.8	9.8	9.8	8.7	12.0	12.0			
HS-S$_1$	F = 0.75	17.6	19.7	9.8	17.4	24.0	12.0			
S$_1$	F = 0.75	17.6	19.6	20.9	19.5	27.2	22.5			
S$_2$	F = 0.75	21.4	22.8	27.1	25.9	32.2	29.0			

[†]Genetic gain equation including all genetic components as obtained from Edwards (2008).

[‡]Reduced genetic model equals the full model with only the σ^2_A term, with appropriate coefficient, in the numerator covariance.

[§]Repeatability model in which the ratio $\sigma_{C,O}/\sigma^2_P$ in the genetic gain equation is replaced with repeatability on a plot-mean basis.

influence of epistasis (even if epistasis is ignored in the estimation models).

While the body of theoretical literature that promoted inbred-progeny selection appeared to say much about expected response for population per se performance (i.e., improvement in performance of noninbred individuals in the population), much less has been said about improvement in performance of inbred lines. Our predictions showed that for inbred response units (i.e., inbred individuals derived from improved populations), inbred-progeny recurrent selection methods were approximately equivalent or superior to half-sib method in two of the three populations studied (BSCB1(R)C13 and BS13(S)C0). Thus, inbred-progeny selection may be considered a superior method if the objective is to improve inbred-progeny performance. However, the 3L Comp (HS-S$_1$)$_{S1}$ population

was an exception in that both half-sib methods had higher predicted response for partially inbred individuals than S$_1$ selection. However, if higher levels of inbreeding of candidates and response units could be evaluated in 3L Comp (HS-S$_1$)$_{S1}$, it is possible that inbred-progeny selection methods might have superiority over half-sib methods for improvement of inbred-progeny performance. In the two populations BSCB1(R)C13 and BS13(S)C0, our results demonstrated that half-sib methods were generally superior for improving noninbred individuals in the improved population and inbred-progeny methods were generally superior for improving inbred performance.

Beyond the numerical predictions of selection response we have presented, a better understanding of the underlying genetic principles in maize populations that limit the relationship between inbred and outbred performance is needed

to determine if the relationship can be manipulated. Previous authors who proposed that inbred-progeny recurrent selection would effectively improve outbred population performance generally assumed a single locus genetic model with partial or complete dominance (Eberhart, 1970; Comstock, 1964; Horner et al., 1969; Cockerham and Matzinger, 1985). However, overdominance, epistasis, and or linkage disequilibrium could all change these predictions profoundly, as could other possible genetic phenomena. Predicted response to inbred-progeny recurrent selection in all three populations that we studied was profoundly affected by negative estimates of the covariance parameter D_1, which is the covariance between homozygous dominance deviations and additive effects. Unfortunately, the fact that D_1 is negative is not very informative because of the lack of a good genetic interpretation of the parameter other than its mathematical definition. However, in two of the studies from which we obtained covariance parameters, the average degree of dominance of genes could be computed from the estimated covariance parameters. For grain yield, Edwards and Lamkey (2002) reported an average degree of dominance of 2.65 and the estimated value from components in Wardyn et al. (2007) was 3.84. These values were well in the range of overdominance, and provide a genetically interpretable parameter that may explain the low response predicted for inbred-progeny selection. Edwards and Lamkey (2002) hypothesized that the estimated high degree of dominance is most likely due to pseudo-overdominance caused by linkage disequilibrium, even though there was no way to resolve true overdominance from pseudo-overdominance. Thus, the presence of strong repulsion phase linkage disequilibrium may be a genetic factor that limits improvement in outbred performance from inbred-progeny selection and may affect the observed relationship between inbred and outbred performance in maize. Early authors who studied inbred progeny selection did so with the assumption that the true dominance coefficients of genes controlling grain yield were in the range of partial to complete dominance. However, it was also known that estimators of the average degree of dominance were strongly influenced by pseudo-overdominance because of biases in variance component estimates (Gardner and Lonnquist, 1959; Moll et al., 1964). The authors who studied inbred-progeny selection on the basis of the partial-to-complete dominance assumption thus had to assume that pseudo-overdominance impacted variance component estimation studies but did not have a similar effect on selection response patterns. Our work provides strong motivation for additional theoretical and empirical work on how linkage disequilibrium affects the relationship between inbred and outbred performance and selection response patterns.

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