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Testcross additive and dominance effects in best linear unbiased prediction of maize single-cross performance

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Abstract Best linear unbiased prediction (BLUP) has been found to be useful in maize (*Zea mays* L.) breeding. The advantage of including both testcross additive and dominance effects (Intralocus Model) in BLUP, rather than only testcross additive effects (Additive Model), has not been clearly demonstrated. The objective of this study was to compare the usefulness of Intralocus and Additive Models for BLUP of maize single-cross performance. Multilocation data from 1990 to 1995 were obtained from the hybrid testing program of Limagrain Genetics. Grain yield, moisture, stalk lodging, and root lodging of untested single crosses were predicted from (1) the performance of tested single crosses and (2) known genetic relationships among the parental inbreds. Correlations between predicted and observed performance were obtained with a delete-one cross-validation procedure. For the Intralocus Model, the correlations ranged from 0.50 to 0.66 for yield, 0.88 to 0.94 for moisture, 0.47 to 0.69 for stalk lodging, and 0.31 to 0.45 for root lodging. The BLUP procedure was consistently more effective with the Intralocus Model than with the Additive Model. When the Additive Model was used instead of the Intralocus Model, the reductions in the correlation were largest for root lodging (0.06–0.35), smallest for moisture (0.00–0.02), and intermediate for yield (0.02–0.06) and stalk lodging (0.02–0.08). The ratio of dominance variance (v_D) to total genetic variance (v_G) was highest for root lodging (0.47) and lowest for moisture (0.10). The Additive Model may be used if prior information indicates that V_D for a given trait has little contribution to V_G. Otherwise, the continued use of the Intralocus Model for BLUP of single-cross performance is recommended.

Key words Additive variance · Dominance · Maize · Best linear unbiased prediction

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Introduction

Best linear unbiased prediction (BLUP) has been found to be useful for predicting the performance of untested maize (*Zea mays* L.) single crosses (Bernardo 1994, 1995, 1996). Because of limited resources, maize breeders are unable to test all possible combinations between inbreds from two complementary heterotic groups that comprise a heterotic pattern. For example, a breeder may test only a few hundred, but not all 2500 single-cross combinations between 50 inbreds in Heterotic Group 1 and 50 inbreds in Heterotic Group 2. In the BLUP procedure, the performance of untested single crosses is predicted from (1) the performance of tested single crosses and (2) known genetic relationships among the parental inbreds. In a large-scale study, correlations between predicted and observed performance of 4099 tested single crosses in 16 heterotic patterns ranged from 0.43 to 0.76 for grain yield, 0.75 to 0.93 for grain moisture, 0.30 to 0.74 for stalk lodging, and 0.16 to 0.53 for root lodging (Bernardo 1996). The correlations, especially for lodging traits, increased as larger numbers of single crosses were available in a given heterotic pattern. These results indicate that BLUP is useful for the routine identification of superior single crosses prior to field testing.

The importance of both testcross additive and dominance effects for maize grain yield has long been recognized, and in empirical studies dominance variance (V_D) has constituted an average of 38% of the total genetic variance (V_G) for yield (Hallauer and Miranda 1981). Testcross additive and dominance effects were both included in the model for large-scale BLUP of maize single-cross performance (Bernardo 1996). In two preliminary studies, Bernardo (1994, 1995) compared correlations between predicted and observed yield when (1) both testcross additive and dominance effects (i.e., Intralocus Model) and (2) only testcross additive effects (i.e., Additive Model) were included in BLUP. The correlations obtained with the Intralocus Model were only approximately 0.01 greater than those obtained with the Additive Model, indicating that dominance effects had little impact in the predictions. But in the two preliminary studies, V_D comprised only 6 to 10% of V_G. Because of the (1) small number of single crosses (54 and 67) and (2) atypical proportion of V_G accounted for by V_D in these two studies, generalizing the results regarding the usefulness of Intralocus versus Additive Models to other datasets is difficult. Also, the usefulness of each genetic model has not been compared for traits other than yield.

The objective of this study was to compare the usefulness of Intralocus and Additive Models for BLUP of maize single-cross performance in large datasets wherein V_D accounted for a substantial proportion (≈30% or more) of V_G for grain yield.

Materials and methods

Data sets

A total of 332 inbreds were assigned to seven different heterotic groups, arbitrarily designated A, B, C, D, E, F, and G. From pedigree records, coefficients of coancestry among inbreds were obtained by tabular analysis (Emik and Terrill 1949) that included modifications to accommodate (1) complete inbreeding of parental inbreds and progeny and (2) nonequal parental contributions for inbreds obtained by backcrossing. The number of inbreds and average coefficient of coancestry (in parentheses) in each heterotic group were: 32 (0.124) in A; 50 (0.079) in B; 66 (0.193) in C; 34 (0.089) in D; 60 (0.064) in E; 53 (0.040) in F; and 37 (0.107) in G. The heterotic groups A and B were related to the Iowa Stiff Stalk Synthetic (BSSS) population, whereas the other heterotic groups were unrelated to BSSS.

Single-cross predictions were obtained with performance data from the regular hybrid testing program of Limagrain Genetics. Seven different cross combinations (i.e., heterotic patterns) between the heterotic groups were considered. The hybrid performance data set comprised the results from multilocation yield trials conducted by Limagrain Genetics from 1990 to 1995. Each multilocation yield trial was conducted at 2–16 locations in Illinois, Iowa, Wisconsin, Minnesota, and Indiana (USA), Ontario (Canada), southwest France, or northern Italy in a randomized complete block design with one or two replicates at each location. The resulting dataset was highly unbalanced across multilocation trials but, disregarding occasional missing plots at individual locations, balanced within multilocation trials. The performance at each individual location was not considered. Rather, each data point was the average performance of a single cross or check hybrid at several locations in a multilocation yield trial. Data were recorded for grain yield (quintals ha^{-1} at 15.5% moisture) and the percentage of grain moisture, stalk lodging, and root lodging.

Estimation of genetic variances, residual variances, and yield trial effects

Data analyses were performed separately for each heterotic pattern. Assume n single crosses were made between n_1 inbreds from Group 1 and n_2 inbreds from Group 2. The single crosses, along with n_C check hybrids, were evaluated in t different yield trials resulting in p total data points. In the mixed-model equations (MME) for single-cross prediction, the linear model assuming negligible epistasis was:

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}_0\mathbf{c} + \mathbf{Z}_1\mathbf{a}_1 + \mathbf{Z}_2\mathbf{a}_2 + \mathbf{Z}\mathbf{d} + \mathbf{e}$$

where: $\mathbf{y} = p \times 1$ vector of observed performance for a given trait (i.e., hybrid by multilocation trial means); $\beta = t \times 1$ vector of yield trial effects; $\mathbf{c} = n_C \times 1$ vector of check hybrid effects; $\mathbf{a}_1 = n_1 \times 1$ vector of testcross additive effects of Group 1 inbreds; $\mathbf{a}_2 = n_2 \times 1$ vector of testcross additive effects of Group 2 inbreds; $\mathbf{d} = n \times 1$ vector of dominance effects; $\mathbf{e} = p \times 1$ vector of residual effects; and $\mathbf{X}$, $\mathbf{Z}_0$, $\mathbf{Z}_1$, $\mathbf{Z}_2$, and $\mathbf{Z}$ were incidence matrices of 1's and 0's relating $\mathbf{y}$ to β, $\mathbf{c}$, $\mathbf{a}_1$, $\mathbf{a}_2$, and $\mathbf{d}$, respectively. Multilocation yield trial effects were considered fixed, whereas all other effects in the model were considered random.

Assume *i* and *i′* were two inbreds from Group 1 whereas *j* and *j′* were two inbreds from Group 2. The covariance between $i \times j$ and $i' \times j'$ was (Stuber and Cockerham 1966):

$$\mathrm{Cov}\,[(i \times j),\, (i' \times j')] = f_{ii'}\, V_{A(1)} + f_{jj'}\, V_{A(2)} + f_{ii'}\, f_{jj'}\, V_D$$

where: $V_{A(1)}$ = summed (across loci) testcross additive variance of alleles from Group 1; $V_{A(2)}$ = summed (across loci) testcross additive variance of alleles from Group 2; V_D = summed (across loci) dominance variance of paired Group 1 and Group 2 alleles; $f_{ii'}$ = coefficient of coancestry between inbreds *i* and *i′*; and $f_{jj'}$ = coefficient of coancestry between inbreds *j* and *j′*. The random effect vectors $\mathbf{c}$, $\mathbf{a}_1$, $\mathbf{a}_2$, $\mathbf{d}$, and $\mathbf{e}$ had zero means and the following covariances:

$$\mathrm{Var}\begin{bmatrix}\mathbf{c}\\ \mathbf{a}_1\\ \mathbf{a}_2\\ \mathbf{d}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{I}V_C & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{A}_1V_{A(1)} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{A}_2V_{A(2)} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{D}V_D & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R}V_R\end{bmatrix}$$

where V_C = variance among check hybrids and V_R = residual variance.

The matrix elements were equal to $f_{ii'}$ in $\mathbf{A}_1$, $f_{jj'}$ in $\mathbf{A}_2$, and $f_{ii'}\,f_{jj'}$ in $\mathbf{D}$. The check hybrids were assumed to be unrelated and the covariance of c was $\mathbf{I}V_C$, where $\mathbf{I}$ was an identity matrix. In $\mathbf{R}$, the off-diagonal elements were assumed to be zero, and the kth diagonal element was the reciprocal of the number of observations (locations) for the kth data point in $\mathbf{y}$. For example, if the first element in y was the average performance of a single cross in a trial at four locations, the first diagonal element in $\mathbf{R}$ was 1/4.

Solutions to β, $\mathbf{c}$, $\mathbf{a}_1$, $\mathbf{a}_2$, and d were obtained by solving the following MME (Henderson 1985):

$$\begin{bmatrix}\beta\\ \mathbf{c}\\ \mathbf{a}_1\\ \mathbf{a}_2\\ \mathbf{d}\end{bmatrix} = \begin{bmatrix}\mathbf{X'R^{-1}X} & \mathbf{X'R^{-1}Z_0} & \mathbf{X'R^{-1}Z_1} & \mathbf{X'R^{-1}Z_2} & \mathbf{X'R^{-1}Z}\\ \mathbf{Z_0'R^{-1}X} & \mathbf{Z_0'R^{-1}Z_0+V_0} & \mathbf{Z_0'R^{-1}Z_1} & \mathbf{Z_0'R^{-1}Z_2} & \mathbf{Z_0'R^{-1}Z}\\ \mathbf{Z_1'R^{-1}X} & \mathbf{Z_1'R^{-1}Z_0} & \mathbf{Z_1'R^{-1}Z_1+V_1} & \mathbf{Z_1'R^{-1}Z_2} & \mathbf{Z_1'R^{-1}Z}\\ \mathbf{Z_2'R^{-1}X} & \mathbf{Z_2'R^{-1}Z_0} & \mathbf{Z_2'R^{-1}Z_1} & \mathbf{Z_2'R^{-1}Z_2+V_2} & \mathbf{Z_2'R^{-1}Z}\\ \mathbf{Z'R^{-1}X} & \mathbf{Z'R^{-1}Z_0} & \mathbf{Z'R^{-1}Z_1} & \mathbf{Z'R^{-1}Z_2} & \mathbf{Z'R^{-1}Z+V3}\end{bmatrix}^{-}\begin{bmatrix}\mathbf{X'R^{-1}y}\\ \mathbf{Z_0'R^{-1}y}\\ \mathbf{Z_1'R^{-1}y}\\ \mathbf{Z_2'R^{-1}y}\\ \mathbf{Z'R^{-1}y}\end{bmatrix}$$

$$= \begin{bmatrix}\mathbf{C_{00}} & \mathbf{C_{01}} & \mathbf{C_{02}} & \mathbf{C_{03}} & \mathbf{C_{04}}\\ \mathbf{C_{10}} & \mathbf{C_{11}} & \mathbf{C_{12}} & \mathbf{C_{13}} & \mathbf{C_{14}}\\ \mathbf{C_{20}} & \mathbf{C_{21}} & \mathbf{C_{22}} & \mathbf{C_{23}} & \mathbf{C_{24}}\\ \mathbf{C_{30}} & \mathbf{C_{31}} & \mathbf{C_{32}} & \mathbf{C_{33}} & \mathbf{C_{34}}\\ \mathbf{C_{40}} & \mathbf{C_{41}} & \mathbf{C_{42}} & \mathbf{C_{43}} & \mathbf{C_{44}}\end{bmatrix}\begin{bmatrix}\mathbf{X'R^{-1}y}\\ \mathbf{Z_0'R^{-1}y}\\ \mathbf{Z_1'R^{-1}y}\\ \mathbf{Z_2'R^{-1}y}\\ \mathbf{Z'R^{-1}y}\end{bmatrix}$$

where: $\mathbf{V_0} = \mathbf{I}\, V_R/V_C$; $\mathbf{V_1} = \mathbf{A_1}^{-1}\, V_R/V_{A(1)}$; $\mathbf{V_2} = \mathbf{A_2}^{-1}\, V_R/V_{A(2)}$; $\mathbf{V_3} = \mathbf{D}^{-1}\, V_R/V_D$; and the "–" sign as a superscript denotes a generalized inverse. Restricted maximum likelihood (REML) estimates of residual and genetic variances were obtained by iterating on (Henderson 1984, 1985):

$$V_R = [\mathbf{y}'\mathbf{R}^{-1}\mathbf{y} - (\text{solution vector})'\ (\text{right-hand side vector})] / [p - \text{rank}\,(X)]$$

$$V_C = (\mathbf{c}'\mathbf{c} + V_R\ \text{tr}\ \mathbf{C_{11}})/n_c$$

$$V_{A(1)} = (\mathbf{a_1}'\mathbf{A_1}^{-1}\mathbf{a_1} + V_R\ \text{tr}\ \mathbf{A_1}^{-1}\ \mathbf{C_{22}})/n_1$$

$$V_{A(2)} = (\mathbf{a_2}'\mathbf{A_2}^{-1}\mathbf{a_2} + V_R\ \text{tr}\ \mathbf{A_2}^{-1}\ \mathbf{C_{33}})/n_2$$

$$V_D = (\mathbf{d}'\mathbf{D}^{-1}\mathbf{d} + V_R\ \text{tr}\ \mathbf{D}^{-1}\ \mathbf{C_{44}})/n$$

where tr = trace operator, i.e., sum of the diagonal elements of a matrix.

Comparison of Intralocus and Additive Models

For each heterotic pattern, the performance of the $(n_1n_2 - n) = m$ untested single crosses was predicted from the performance of the n tested single crosses. Let $\mathbf{y_P}$ be an $n \times 1$ vector of average performance of tested single crosses, corrected for yield trial effects (i.e., β from the solution of the MME):

$$\mathbf{y_P} = (\mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z})^{-1}\ \mathbf{Z}'\mathbf{R}^{-1}(\mathbf{y} - \mathbf{X}\beta).$$

For the Intralocus and Additive Models, the performance for each trait of the untested single crosses was predicted as:

$$\mathbf{y_M} = \mathbf{C_{MP}}\ \mathbf{C_{PP}^{-1}}\ \mathbf{y_P}$$

where: $\mathbf{y_M}$ = $m \times 1$ vector of predicted performance of the untested single crosses; $\mathbf{C_{MP}}$ = $m \times n$ matrix of genetic covariances between the untested single crosses and the tested single crosses; and $\mathbf{C_{PP}}$ = $n \times n$ phenotypic variance-covariance matrix among the tested single crosses. Depending on the genetic model, the elements of $\mathbf{C_{MP}}$ and $\mathbf{C_{PP}}$ [i.e., covariances between single crosses $(i \times j)$ and $(i' \times j')$] were calculated as:

1. *Intralocus Model*:
   $\text{Cov}\,[(i \times j), (i' \times j')] = f_{ii'}\, V_{A(1)} + f_{jj'}\, V_{A(2)} + f_{ii'}\, f_{jj'}\, V_D$
2. *Additive Model*:
   $\text{Cov}\,[(i \times j), (i' \times j')] = f_{ii'}\, V_{A(1)} + f_{jj'}\, V_{A(2)}$

For both models, the quantity V_R/(kth diagonal element of the diagonal $\mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z}$ matrix) was added to the kth diagonal element of $\mathbf{C_{PP}}$.

A cross-validation procedure was performed to evaluate the usefulness of the Intralocus and Additive Models for predicting single-cross performance. Given n tested single crosses, the data for the first single cross were disregarded and predicted, for both the Intralocus and Additive Models, from the remaining $n - 1$ single crosses. The performance of the 2nd, 3rd, ..., nth single cross was likewise predicted from the remaining $n - 1$ single crosses. The correlation between the predicted and observed performance (sample size of n) was calculated for each trait as an indication of the effectiveness of each genetic model.

All the necessary computations were done with a modified version of *lgHYPER©*, a proprietary FORTRAN 77 program written by the author for Limagrain Genetics.

Results and discussion

Means and genetic variances

Different testing locations were used for each heterotic pattern, and the differences in means of yield trial effects did not necessarily reflect the relative yield potential and maturity of each heterotic pattern (Table 1). Across heterotic patterns, mean stalk lodging varied from 4.6% in C × D to 6.5% in A×G, whereas mean root lodging varied from 2.8% in B × E to 4.1% in C × D.

Genetic variances due to testcross additive effects [$V_{A(1)}$ and $V_{A(2)}$] as well as dominance effects (V_D) were important for yield (Table 1). The ratio of V_D to total genetic variance [$V_G = V_{A(1)} + V_{A(2)} + V_D$] ranged from 0.29 in B × G to 0.52 in A × G, with an average of 0.41 across the seven heterotic patterns. Asymptotic variances have been proposed but found to be unreliable (Chang 1988) as measures of precision of REML estimates of variances. Hence, information on the precision of the $V_{A(1)}$, $V_{A(2)}$, V_D, and V_D/V_G estimates was not available. Nevertheless, the V_D/V_G ratios for yield in this study were comparable with the average V_D/V_G ratio of 0.38 reported by Hallauer and Miranda (1981) from summaries of results from 82 empirical studies in maize. The V_D/V_G ratios in this study indicated that, in addition to testcross additive effects, dominance effects are necessary for the characterization of genetic variability for yield in maize.

For moisture, V_D/V_G ranged from 0.05 in C × D to 0.15 in A × G, with an average of 0.10 across the seven heterotic patterns (Table 1). Thus, the importance of dominance relative to testcross additive effects was less for moisture than for yield. Hallauer and Miranda (1981) also drew the same conclusion, but they reported a higher average V_D/V_G ratio of 0.19. For lodging traits, Hallauer and Miranda (1981) found that estimates of V_D were few and often negative. In this study, V_D/V_G for stalk lodging varied from 0.05 in B × G to 0.39 for B × F, with an average of 0.26. The V_D/V_G values for root lodging ranged from 0.17 in B × F to 0.81 in B × E, with an average of 0.47. These V_D/V_G ratios indicated that testcross additive and dominance effects both determine stalk and root lodging performance of maize single crosses.

Correlation between predicted and observed performance: Intralocus versus Additive Models

In the cross-validation procedure, predicted single-cross performance was compared with observed performance but not with the true, unknown genetic values. Even if the correlation between predicted and true genetic values is 1, the correlation between predicted and observed performance cannot be greater than the square root of heritability (Bernardo 1996). Hence, the square root of heritability (Table 2) sets a theoretical upper bound on the correlation between predicted and observed performance and should be the reference in interpreting the correlations obtained with the cross-validation procedure.

For the Intralocus Model, the correlation between predicted and observed performance ranged from 0.50 to 0.66 for yield, 0.88 to 0.94 for moisture, 0.47 to 0.69 for stalk lodging, and 0.31 to 0.45 for root lodging (Table 2). Across heterotic patterns, the correlation coefficients for the Intralocus Model were significantly different (P=0.05) from zero for all four traits. The correlations between predicted and observed yield were 68% to 84% of their corresponding upper bounds, and seemed sufficiently high for pick-

Table 1 Means and genetic variances for yield (quintals ha^{-1}), moisture (%), stalk lodging (%), and root lodging (%) in seven heterotic patterns (Group 1 × Group 2) in maize

Group 1	Group 2	Number of single crosses		Yield	Moisture	Stalk lodging	Root lodging
A	E	232	Mean[a]	91.3	21.4	5.9	3.1
			$V_{A(1)}$	9.26	2.67	6.77	0.33
			$V_{A(2)}$	6.79	2.27	1.54	6.50
			V_D	16.09	0.49	4.31	10.25
			V_D/V_G	0.50	0.09	0.34	0.60
A	F	206	Mean	92.0	22.3	5.4	3.8
			$V_{A(1)}$	19.23	2.72	4.80	1.58
			$V_{A(2)}$	1.79	2.60	0.59	3.04
			V_D	17.91	0.76	2.17	3.79
			V_D/V_G	0.46	0.13	0.29	0.45
A	G	159	Mean	92.4	22.4	6.5	3.7
			$V_{A(1)}$	9.97	2.45	3.17	1.68
			$V_{A(2)}$	5.43	2.26	1.23	3.78
			V_D	16.41	0.80	2.60	4.43
			V_D/V_G	0.52	0.15	0.37	0.45
B	E	301	Mean	93.9	23.0	5.8	2.8
			$V_{A(1)}$	11.30	2.75	2.19	4.60
			$V_{A(2)}$	12.03	1.94	4.53	4.41
			V_D	11.24	0.52	3.23	38.07
			V_D/V_G	0.33	0.10	0.32	0.81
B	F	311	Mean	93.4	23.3	5.0	3.1
			$V_{A(1)}$	12.71	3.43	1.30	1.56
			$V_{A(2)}$	4.44	2.92	1.11	5.30
			V_D	10.72	0.46	1.54	1.43
			V_D/V_G	0.38	0.07	0.39	0.17
B	G	208	Mean	93.9	23.8	6.1	3.4
			$V_{A(1)}$	19.86	4.12	1.46	1.93
			$V_{A(2)}$	10.78	2.52	8.16	2.67
			V_D	12.78	0.62	0.46	2.97
			V_D/V_G	0.29	0.09	0.05	0.39
C	D	352	Mean	92.6	24.1	4.6	4.1
			$V_{A(1)}$	5.12	1.43	1.02	1.05
			$V_{A(2)}$	14.86	1.48	1.22	3.92
			V_D	13.50	0.16	0.21	3.36
			V_D/V_G	0.40	0.05	0.09	0.40

[a] Mean, Average of fixed effects of multilocation trials for each heterotic pattern; $V_{A(1)}$, variance due to testcross additive effects of Group 1 inbreds; $V_{A(2)}$, variance due to testcross additive effects of Group 2 inbreds; V_D, variance due to dominance effects; and V_D/V_G, ratio of V_D to the total genetic variance ($V_G = V_{A(1)} + V_{A(2)} + V_D$)

the-winner schemes (Robson et al. 1967) that are characteristic of maize hybrid breeding programs. Based on the magnitudes of the correlations between predicted and observed trait values, BLUP of the performance of untested single crosses was most effective for moisture and least effective for root lodging.

For the Additive Model, the correlation between predicted and observed performance ranged from 0.48 to 0.63 for yield, 0.86 to 0.92 for moisture, 0.47 to 0.68 for stalk lodging, and 0.07 to 0.35 for root lodging (Table 2). The correlation between predicted and observed root lodging in A × F (r=0.07) was not significantly different from zero (P=0.05). For the Additive Model, the correlations between predicted and observed yield were 65% to 79% of their corresponding upper bounds. However, the correlations between predicted and observed performance were consistently higher with the Intralocus Model than with the Additive Model (Table 2). When the simpler Additive Model was used instead of the Intralocus Model, the correlation between predicted and observed performance was reduced by 0.02 to 0.06 for yield, 0.00 to 0.02 for moisture, 0.00 to 0.08 for stalk lodging, and 0.06 to 0.35 for root lodging. Within each trait, no clear relationship was noted between V_D/V_G ratios and the reductions in the correlation caused by using the Additive Model instead of the Intralocus Model. But the results indicated that the usefulness of Intralocus versus Additive Models varied among traits. For moisture, the correlations between predicted and observed values were high (≈0.90) for either model. These high correlations, as well as the small differences in the correlation between predicted and observed performance when the two models were used, suggested that the Additive Model may be suitable for routine prediction of grain moisture of untested single crosses.

In contrast, correlations between predicted and observed root lodging were lowest among the four traits stud-

Table 2 Correlations between predicted and observed performance when dominance effects were included (Intralocus Model) and excluded (Additive Model) in best linear unbiased prediction of yield, moisture, stalk lodging, and root lodging in seven heterotic patterns of maize

Heterotic pattern	Genetic model	Correlation between predicted and observed performance			
		Yield	Moisture	Stalk lodging	Root lodging
A × E	Intralocus model	0.64	0.94	0.66	0.44
	Additive model	0.60	0.92	0.62	0.30
	Upper bound[a]	0.76	0.96	0.89	0.74
A × F	Intralocus model	0.54	0.89	0.60	0.42
	Additive model	0.52	0.88	0.52	0.07[NS]
	Upper bound	0.80	0.96	0.85	0.57
A × G	Intralocus model	0.60	0.93	0.58	0.45
	Additive model	0.54	0.91	0.54	0.31
	Upper bound	0.79	0.96	0.83	0.59
B × E	Intralocus model	0.64	0.89	0.62	0.45
	Additive model	0.62	0.87	0.59	0.32
	Upper bound	0.78	0.95	0.89	0.81
B × F	Intralocus model	0.50	0.92	0.54	0.33
	Additive model	0.48	0.91	0.51	0.14
	Upper bound	0.74	0.97	0.80	0.54
B × G	Intralocus model	0.66	0.88	0.69	0.41
	Additive model	0.61	0.86	0.68	0.35
	Upper bound	0.81	0.97	0.88	0.52
C × D	Intralocus model	0.66	0.89	0.47	0.31
	Additive model	0.63	0.89	0.47	0.22
	Upper bound	0.81	0.94	0.67	0.63

[NS] Not significantly different from zero at $P = 0.05$. All other correlation coefficients were significant

[a] Theoretical upper bound, equal to the square root of heritability, on the correlation between predicted and observed single-cross performance

ied, and the use of the Additive Model instead of the Intralocus Model resulted in large reductions in the effectiveness of BLUP. Hence, the continued use of the Intralocus Model for root lodging is suggested. For yield and stalk lodging, the superiority of the Intralocus Model over the Additive Model was less than that for root lodging but greater than that for moisture. In practice, the only added cost of using the Intralocus Model rather than the Additive Model is longer computing time, e.g., up to 24 h on a Pentium™ (Intel Corporation) machine for datasets typically encountered in a commercial maize hybrid breeding program (Bernardo 1996). However, computing time is cheap and is getting cheaper as faster processors, compilers, and computing algorithms are developed. Also, the correlations between predicted and observed performance for yield and stalk lodging were moderately high, but not as high as those for moisture. Hence, to maximize the correlation between predicted and observed trait values, the continued use of the Intralocus Model for yield and stalk lodging is justified.

In conclusion, the results of this study demonstrated that (1) testcross additive and dominance effects were both exploited in BLUP of the performance of untested single crosses, and (2) BLUP was consistently more effective with the Intralocus Model than with the Additive Model when V_D comprised a substantial proportion of V_G. The Additive Model may be used if prior information indicates that V_D for a given trait, such as grain moisture in maize, has little contribution to V_G. Otherwise, the continued use of the Intralocus Model for BLUP of single-cross performance is recommended.

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