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RESEARCH

General Combining Ability Model for Genomewide Selection in a Biparental Cross

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ABSTRACT

Genomewide selection within an A/B biparental cross is most advantageous if it could be effectively done before the cross is phenotyped. Our objectives were to determine if a general combining ability (GCA) model is useful for genomewide selection in an A/B cross, and to assess the influence of training population size (N_{GCA}), number of crosses pooled into the training population ($N_{\times}$), linkage disequilibrium (r^2), and heritability (h^2) on the prediction accuracy with the GCA model. The GCA model involved pooling 4 to 38 maize crosses with A and B as one of the parents into the training population for an A/B cross, whereas the same background (SB) model involved pooling crosses between random inbreds. Across 30 A/B test populations, the mean response to selection (R) with the GCA model was 0.19 Mg ha^{-1} for testcross grain yield, –6 g kg^{-1} for moisture, and 0.38 kg hL^{-1} for test weight. These R values with the GCA model were 68 to 76% of the corresponding R values with phenotypic selection (PS). The R values with the SB model were only 15 to 28% of the R values with PS. Increasing the size of the training population with random crosses from the same heterotic group was less important than including crosses with A and B as one of the parents. Prediction accuracy was most highly correlated with $h^2r^2\sqrt{N_{GCA}}$ and $h^2r^2\sqrt{N_{\times}}$. Our results indicated that the GCA model is routinely effective for genomewide selection within A/B crosses, before phenotyping the progeny in the cross.

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Abbreviations: A/B, biparental cross between parents A and B; GCA, general combining ability; h^2, heritability on an entry-mean basis; LD, linkage disequilibrium; $N_{\times}$, number of crosses pooled into the training population; N_{GCA}, number of individuals in the training population for the GCA model; N_M, number of markers; PS, phenotypic selection; R, response to selection; r_{MG}, correlation between marker-predicted genotypic value and true genotypic value; r_{MP}, correlation between marker-predicted genotypic value and phenotypic value; RR-BLUP, ridge regression-best linear unbiased prediction; $S_{A\star}$, genetic similarity between parent A and the ⋆ inbred from the ⋆/B cross; $S_{B\star}$, genetic similarity between parent B and the ⋆ inbred from the A/⋆ cross; SB, same genetic background; SNP, single nucleotide polymorphism.

Maize (*Zea mays* L.) breeding typically involves crossing two inbreds (parent A and parent B), developing selfed or doubled haploid progeny from the A/B cross, and evaluating the progeny based on their yield and agronomic performance when crossed to a tester. Parents A and B are typically from the same heterotic group, whereas the tester is an inbred from an opposite heterotic group. Each A/B testcross population is developed and analyzed separately from other biparental testcross populations. Traditionally, testcross selection within a biparental cross has been based solely on phenotypic information (Hallauer, 1990).

Advances in single nucleotide polymorphism (SNP) genotyping have drastically lowered the cost of obtaining high

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quality marker information. With the advent of cheap and quick genotyping, genomewide selection (or genomic selection) has been introduced (Meuwissen et al., 2001) and studied (Bernardo and Yu, 2007; Heffner et al., 2009; Lorenz et al., 2011; Heslot et al., 2012) as a method for predicting performance for complex traits. In genomewide selection, marker effects are estimated from phenotypic and marker data in a training population. The marker effects are then used to predict the performance of a test population that has been genotyped but not phenotyped.

The training population must be representative of the test population to obtain a high prediction accuracy. In theory, the best training population for an A/B population is a subset of the A/B population that has been phenotyped and genotyped (i.e., the population itself). In this article, the use of a subset of A/B as a training population for A/B itself is referred to as the A/B model. Because of the need to phenotype a subset of A/B as the training population, the A/B model increases the time and cost before genomewide selection can be performed within a biparental cross.

To eliminate the need to phenotype the A/B population itself, pooling multiple biparental crosses into a training population has been proposed (Schulz-Streeck et al., 2012; Zhao et al., 2012; Riedelsheimer et al., 2013). These multiple biparental crosses need to be of the same genetic background as A/B, and need to have been previously genotyped and phenotyped. In a few studies, pooling multiple crosses into a training population was found to be superior to the A/B model (Schulz-Streeck et al., 2012; Zhao et al., 2012). The increase in prediction accuracy was likely due to the increase in the number of individuals in the training population when multiple biparental crosses were pooled (Schulz-Streeck et al., 2012).

The accuracy of genomewide prediction may be increased if identity by descent between the markers in the A/B test population and in the biparental crosses pooled into a training population is guaranteed. Suppose that ★ is any inbred that is in the same heterotic group as A and B, that the same tester is used for all biparental crosses, and that the SNP markers analyzed are those that are polymorphic between A and B. If all available A/★ crosses are pooled into a training population, a SNP allele for which an effect is estimated in the training population (marker allele carried by parent A in the pooled A/★ biparental crosses) will be identical by descent to the corresponding SNP allele unique to A in the A/B test population. Likewise, if all available ★/B crosses are pooled into a training population, a SNP allele for which an effect is estimated in the training population (marker allele carried by parent B in the pooled ★/B biparental crosses) will be identical by descent to the corresponding SNP allele unique to B in the A/B test population.

To predict the performance within an A/B test population, pooling all available A/★ and ★/B biparental crosses into a training population for A/B is, therefore, likely to be superior to pooling multiple ★/★ crosses into a training population; the latter having been proposed and studied previously (Schulz-Streeck et al., 2012; Zhao et al., 2012). In this article, we refer to pooling the A/★ and ★/B biparental crosses as the GCA model because the model captures GCA effects of marker alleles. In the plant breeding literature, GCA pertains to the mean performance of an inbred when crossed with a series of other inbreds. Similarly, the GCA model in this study estimates the trait mean of a SNP allele in combination with SNP alleles from other inbreds. We refer to pooling multiple ★/★ crosses as the same background (SB) model.

In this study, we utilized a subset from 970 biparental maize populations to test the usefulness of the GCA model compared with the A/B and SB models. We also compared these models to PS and to a combined SB + GCA model. The data were for actual breeding populations from Monsanto from 2001 to 2008 and were therefore representative of the pedigree backgrounds, range of genetic diversity, population sizes, and extent of field testing that may be encountered in a commercial maize breeding program. Our objectives in this study were to (i) determine if the GCA model is useful for genomewide selection in an A/B cross, and (ii) assess the influence of training population size (N_{GCA}), number of crosses pooled into the training population ($N_{\times}$), linkage disequilibrium (r^2), and heritability (h^2), on the prediction accuracy with the GCA model.

MATERIALS AND METHODS

Test Populations

Phenotypic and marker data for 970 biparental testcross populations were provided to us by Monsanto. A total of 485 crosses were between inbreds from one heterotic group (Group 1) and 485 crosses were between inbreds from an opposite heterotic group (Group 2). Individuals in each of the 970 populations were testcrossed to an inbred from the opposite heterotic group. From the 970 biparental crosses, we chose 30 A/B testcross populations as the test populations for the A/B, GCA, SB, and SB + GCA models as well as for PS (Table 1). All pedigrees in the dataset were coded by Monsanto to protect confidentiality.

Two of the 30 A/B test populations were BC_1 populations, whereas the remaining 28 were F_2 populations. The 30 A/B test populations had 139 to 186 individuals (Table 1). Testcrosses of these individuals were evaluated for grain yield (Mg ha^{-1}), moisture (g kg^{-1}), and test weight (kg hL^{-1}) at 4 to 12 environments (year-location combinations) in the United States from 2001 to 2008. Phenotypic data were available as the mean of each individual within each location. Phenotypic data on some of the individuals were missing from some locations, making the phenotypic data unbalanced. All phenotypic data were at the testcross level, and the same tester was used for an A/B test population and for the training population used to predict the performance of the A/B cross. The use of the same tester eliminated confounding effects due to different testers in the performance of each set of A/B, A/★, ★/B, and ★/★ crosses

Table 1. Test and training populations for the A/B biparental cross (* is any inbred that is in the same heterotic group as A and B), general combining ability (GCA), and same background (SB) models in maize.

	Test population									GCA model				
						N_M†				Populations				
Group‡	A/B population	Tester	$S_{A/B}$§	N¶	Locations	A/B	GCA	SB	SB + GCA	A/*	*/B	$N_\times$#	N_{GCA}††	SB model N_{SB}‡‡
1	P1/P2	T1	0.79	152	7	79 (0.62)	79	79	79	23	15	38	5255	5178
1	P3/P4	T1	0.74	164	8	58 (0.43)	47	55	58	11	17	28	4530	4419
1	P4/P5	T1	0.66	177	6	82 (0.49)	78	70	78	17	8	25	3858	3772
1	P6/P7	T1	0.59	183	12	67 (0.44)	66	63	66	17	5	22	3295	3225
1	P3/P8	T1	0.74	181	7	69 (0.51)	62	63	65	11	5	16	2800	2787
1	P1/P9	T2	0.82	174	5	74 (0.63)	68	68	68	7	8	15	1874	1961
1	P5/P8	T1	0.61	148	6	74 (0.36)	64	64	68	9	4	13	1724	1796
1	P9/P10	T2	0.85	152	8	68 (0.58)	63	63	64	9	4	13	1724	1796
1	P9/P2/P9	T2	0.79	159	6	87 (0.60)	67	63	79	8	5	13	2022	1958
1	P11/P12	T1	0.62	182	8	91 (0.45)	53	60	77	2	9	11	1325	1421
1	P13/P14	T3	0.76	178	8	86 (0.64)	82	60	84	7	3	10	1688	1620
1	P2/P15	T3	0.68	160	5	89 (0.57)	68	75	81	5	4	9	1477	1496
1	P16/P13	T3	0.83	178	7	53 (0.59)	47	39	50	7	2	9	1541	1468
1	P17/P18	T1	0.70	185	7	87 (0.50)	54	51	67	2	4	6	793	758
1	P19/P20	T4	0.64	186	5	100 (0.52)	67	39	77	1	3	4	697	615
2	P21/P22	T5	0.82	173	8	69 (0.51)	69	69	69	14	22	36	5168	5647
2	P23/P24	T6	0.84	174	7	49 (0.56)	44	44	46	23	8	31	4199	5241
2	P25/P22	T5	0.77	169	8	72 (0.44)	69	67	69	22	4	26	3960	4109
2	P26/P27	T6	0.76	184	6	66 (0.60)	60	61	65	15	9	24	3550	3913
2	P23/P25	T5	0.73	168	7	68 (0.40)	65	63	66	4	18	22	3188	3615
2	P24/P26	T6	0.74	183	6	66 (0.47)	66	66	66	8	14	22	1928	3255
2	P28/P27	T6	0.74	180	8	49 (0.43)	48	43	49	9	4	13	1829	1984
2	P29/P27	T6	0.75	175	7	69 (0.56)	61	59	69	4	9	13	1309	1930
2	P29/P30	T6	0.72	183	5	98 (0.53)	77	54	63	4	6	10	1771	1363
2	P31/P32	T7	0.74	172	4	65 (0.46)	57	31	56	2	8	10	1596	1692
2	P33/P34	T8	0.81	170	8	63 (0.39)	57	53	58	3	6	9	1042	1495
2	P35/P36	T9	0.76	181	7	85 (0.60)	54	54	64	4	2	6	634	1036
2	P37/P38	T10	0.78	139	4	62 (0.37)	48	22	51	3	2	5	710	645
2	P39/P40/P39	T5	0.78	184	5	83 (0.44)	60	31	52	3	2	5	650	715
2	P41/P42	T11	0.70	183	5	74 (0.50)	58	48	59	2	2	4	650	625

†N_M, number of markers used to estimate the performance of the A/B test population, markers for the GCA, SB, and SB + GCA models were removed if the marker was not present in at least two training populations. Mean r^2 of adjacent SNP markers is listed in parentheses for the A/B population.

‡Heterotic group.

§Simple matching coefficient between parents A and B.

¶N, number of individuals in the A/B test population.

#$N_\times$, number of biparental crosses in the training population for the GCA and the SB model.

††N_{GCA}, number of individuals in the training population for the GCA model.

‡‡N_{SB}, number of individuals in the training population for the SB model.

for which comparisons were made. However, different testers were used across the 30 A/B test populations (Table 1).

Testcross genetic variance (V_G) and heritability on an entry-mean basis (h^2) were estimated for each trait in all 970 populations. Restricted maximum likelihood estimates of variance components were obtained with the lme4 package (Bates et al., 2011) in R statistical software (R Development Core Team, 2012; Holland et al., 2003). A likelihood ratio test was used to determine the significance of the estimates of V_G. The p-value from the likelihood ratio test was divided by 2.0 to approximate an F-test of the null hypothesis (Holland et al., 2003). A V_G estimate with a p-value < 0.05 was considered significant. Across the 30 A/B crosses, the percentage of missing data (i.e., individual-location combinations) had a mean of only 2% and a maximum of 5% for each trait. The h^2 was estimated on an ad hoc basis as $h^2 = V_G/(V_G + V_R/e)$, where V_R was the residual variance and e was the mean number of environments. Because the data were entry means within each location, the genotype × environment interaction variance and within-location error variance were confounded in V_R. The value of e was estimated as the harmonic mean, given the unbalanced nature of the data (Holland et al., 2003). The 30 A/B test populations were chosen based on having a minimum population size of 50 individuals, a minimum of four A/★ and ★/B crosses, and a significant V_G.

The parents of the A/B test populations were genotyped with 2911 SNP markers, whereas the individuals within each A/B cross were genotyped with 49 to 100 SNP markers that were polymorphic between A and B. The A/B populations

with lower numbers of markers tended to be those whose parents were more similar based on the 2911 SNP markers. The linkage disequilibrium (LD) was calculated as the mean r^2 values between adjacent SNP markers with R statistical software (R Development Core Team, 2012). As with the pedigree data, the names of the SNP markers were coded by Monsanto to protect confidentiality.

As described in further detail below, the different models for designing training populations were compared based on two criteria: (i) the R in each A/B test population, and (ii) the correlation between marker-predicted performance and observed performance (r_{MP}) in each A/B test population.

A/B Model

In the A/B model, the individuals in the test population and the individuals in the training population were from the same A/B cross. The value of r_{MP} was calculated through a delete-one procedure along with cross-validation across environments.

With N individuals in an A/B cross, the performance of the first individual was predicted by ridge regression-best linear unbiased prediction (RR-BLUP) analysis of the effects of N_M total markers among the remaining $N - 1$ individuals. Given the low incidence of missing data, arithmetic means of the individuals across locations were used in RR-BLUP (i.e., with no correction for missing data); this procedure facilitated the cross-validation across environments as described in the next paragraph. The R package rrBLUP version 4.0 in R (Piepho, 2009; Endelman, 2011; R Development Core Team, 2012) was used to estimate the marker effects. For each trait, the performance of the first individual was predicted as $y_p = \mu + \mathbf{xg}$, where y_p was the predicted performance of the individual; μ was the estimated mean of the $N - 1$ individuals used as the training population; $\mathbf{x}$ was a $1 \times N_M$ row vector of genotype indicators; and $\mathbf{g}$ was a $N_M \times 1$ vector of RR-BLUP marker effects, estimated from the remaining $N - 1$ individuals, for the SNP alleles from the first parent. The elements of $\mathbf{x}$ were 1 if the test individual was homozygous for the SNP allele from parent A, –1 if the test individual was homozygous for the SNP allele from parent B, and 0 if the test individual was heterozygous. The delete-one analysis was sequentially repeated, with the performance of the second individual being predicted from the remaining $N - 1$ individuals, the performance of the third individual being predicted from the remaining $N - 1$ individuals, and so on. In the end, the performance of each of the N individuals was predicted from the remaining $N - 1$ individuals.

The above cross-validation was conducted across environments to eliminate a bias, present in the A/B model but not in the other models, due to the test population and training population being evaluated in the same environments. In this procedure, RR-BLUP marker effects were estimated from the performance of the $N - 1$ individuals in half of the environments. These marker effects were then used to predict the performance of the test individual in the remaining half of the environments.

For example, there were 20 combinations of three out of six environments. The delete-one RR-BLUP marker effects were then obtained for each of these 20 combinations, and the marker effects for each combination were used to obtain y_p for each of the N individuals as described above. For each of the 20 combinations, r_{MP} was obtained as the correlation between y_p and the mean performance of each of the N individuals in the remaining half of the environments that were not used to calculate marker effects. The mean r_{MP} across all 20 combinations was obtained. The same procedure was used for larger numbers of environments. When the number of environments (e) was an odd number, (e – 1)/2 environments were used to estimate marker effects and the observed performance of each of the N individuals was based on the remaining environments.

The values of R for high grain yield, low moisture, and high test weight were obtained as follows. Again, suppose that an A/B population was evaluated in six environments. For each of the 20 combinations, the 10% of individuals with the best y_p values were identified for each trait. The mean observed performance of these individuals in the other half of the environments was obtained and was denoted as $y_{0.10}$. The R for each of the 20 combinations was then estimated as $y_{0.10} - \mu$. The final value of R was then obtained as the mean R across the 20 combinations. Simulations we have conducted (results not shown) have confirmed that this procedure is valid for estimating R, and that the estimated value does not correspond to the selection differential.

The variances of r_{MP} and R were obtained across the different repeats of the cross-validations across environments. These variances were then used to calculate LSD values ($p = 0.05$) for the mean r_{MP} and mean R.

General Combining Ability Model

The GCA model is based on the premise that effects of the two alleles at a SNP locus in an A/B cross can be sufficiently modeled as (i) the mean of effects (denoted by $m_{A\_}$) of a SNP marker in parent A when A is crossed with multiple inbreds, and (ii) the mean of effects (denoted by $m_{B\_}$) of a SNP marker in parent B when B is crossed with multiple inbreds. Suppose that $m_{A/B}$ is the testcross effect of the SNP allele from parent A within the A/B cross. Likewise, $m_{B/A}$ is the testcross effect of the SNP allele from parent B within the A/B cross. The marker effects are $m_{A/B} = m_{A\_}$ + residual and $m_{B/A} = m_{B\_}$ + residual. The GCA model ignores the residuals, which are specific to the A/B combination and which cannot be estimated unless A/B itself is evaluated.

In the GCA model, the number of A/★ and ★/B crosses that were pooled into a training population (N_x) for each A/B test population ranged from 4 to 38 (Table 1). The total size of the pooled training population (N_{GCA}) ranged from 634 to 5255 individuals, all with the same tester as the A/B population (Table 1). The number of polymorphic SNP markers used to genotype the A/★ and ★/B crosses ranged from 38 to 116 and had a mean of 74.

Because different sets of SNP markers were used in different populations, each A/★ and ★/B cross was analyzed separately to obtain RR-BLUP marker effects within each cross. For a given trait, the performance of all N individuals in the A/B test population was predicted as $\mathbf{y} = \mu\mathbf{1} + \mathbf{Xm}$, where $\mathbf{y}$ was an $N \times 1$ vector of predicted performance; μ was the estimated overall mean; $\mathbf{1}$ was an $N \times 1$ vector with elements equal to 1; $\mathbf{X}$ was an $N \times N_M$ matrix of genotype indicators with elements of 1, –1, and 0 (same as for $\mathbf{x}$); and $\mathbf{m}$ was an $N_M \times 1$ vector of RR-BLUP marker effects averaged across the A/★ and ★/B crosses. All markers in each A/★ and ★/B cross were used in RR-BLUP analysis within the cross. However, the N_M for obtaining $\mathbf{y}$ referred to the markers in the A/B test population. Markers in the A/B test population were removed if they were not present in

at least two A/★ or ★/B crosses. The separate RR-BLUP analyses for each A/★ and ★/B cross inherently accounted for population structure, with the fitted values of μ differing among the A/★ and ★/B crosses and thereby reflecting population structure.

We studied two versions of the GCA model that differed in how **m** was calculated. In the GCA model, marker effects were estimated as the unweighted mean across all A/★ and ★/B crosses in which a particular marker was polymorphic. Suppose the training population was obtained by pooling 10 A/★ crosses and 12 ★/B crosses and that all 22 crosses were polymorphic for SNP1, which was also polymorphic in A/B. Further suppose that parent A had the T allele and parent B had the C allele at the SNP1 locus. With biallelic SNPs, this means that the ★ parents in the 10 A/★ crosses carried the C allele, and the ★ parents in the 12 ★/B crosses carried the T allele. In the GCA model, the effect of the T marker allele at SNP1 was the unweighted mean of the estimated marker effects of the T allele in all 22 crosses. Likewise, the effect of the C marker allele of SNP1 was the unweighted mean of the estimated marker effects of the C allele in all 22 crosses.

Not all SNP markers in the A/B cross were polymorphic in all of the A/★ and ★/B crosses. With the previous example, suppose that SNP2 was not polymorphic in the last two ★/B crosses. In this situation, the mean marker effects at SNP1 were obtained from all 10 A/★ and 12 ★/B crosses, whereas the mean marker effects at SNP2 were obtained from all 10 A/★ crosses and the first 10 ★/B crosses.

In the GCA_{IBD} model, the effect of the T marker allele at SNP1 (found in parent A) was the unweighted mean of the estimated marker effects of the T allele in the 10 A/★ crosses only. Likewise, the effect of the C marker allele of SNP1 (found in parent B) was the unweighted mean of the estimated marker effects of the C allele in the 12 ★/B crosses only. The GCA_{IBD} model, therefore, guaranteed that estimates of mean marker effects were obtained only from those crosses where identity by descent (IBD) is guaranteed between a marker allele in the A/B cross and in the training population.

For the GCA model and GCA_{IBD} model, the values of r_{MP} and R were calculated in the same way as for the A/B model. Cross-validation across environments was done for the A/B test population according to the same procedure for splitting environments used in the A/B model. However, data from all environments were always used in estimating marker effects within the A/★ and ★/B populations, which were evaluated in sets of environments that were different from those used to evaluate the A/B cross.

Same Background Model

In the SB model, the number of randomly selected ★/★ crosses that were pooled into a training population for each A/B test population was equal to that for the GCA model. The total size of the pooled training population (N_{SB}) in the SB model was kept generally similar to that in the GCA model and ranged from 615 to 5647 individuals. The number of polymorphic SNP markers used to genotyped the ★/★ crosses ranged from 59 to 84 and had a mean of 73.

In the SB + GCA model, the training population for an A/B cross comprised all the A/★ and ★/B crosses from the GCA model and all the ★/★ crosses from the SB model. The procedures for calculating R and r_{MP} with the SB model and SB + GCA model were the same as those for the GCA model and GCA_{IBD} model.

Phenotypic Selection

In PS, the mean performance of an A/B individual in half of the environments was considered as the predictor of the performance of the same individual in the remaining half of the environments. Procedures for calculating the prediction accuracy of PS and R were the same as those used for r_{MP} and R in the GCA, SB, and SB + GCA models. For convenience, the prediction accuracy with PS was also denoted as r_{MP} in Tables 2 through 5, even though the prediction of performance with PS did not involve marker effects.

Genetic Similarity Thresholds

We investigated the effect in the GCA model of imposing a minimum similarity between the ★ parents and the A and B parents. Genetic similarity was calculated (i) between parent A and the ★ inbred from the ★/B cross ($S_{A★}$), and (ii) between parent B and the ★ inbred from the A/★ cross ($S_{B★}$). The genetic similarity was calculated as the simple matching coefficient (Sokal and Michener, 1958) across 2911 SNP markers that were used to screen all the parents.

The A/★ and ★/B crosses in the GCA model were then restricted to those in which the values of $S_{A★}$ and $S_{B★}$ both exceeded threshold values of 0.60, 0.70, or 0.80. Values of r_{MP} and R were calculated as described for the GCA model.

RESULTS AND DISCUSSION

Models for Predicting Performance within an A/B Cross

Based on the mean R and mean r_{MP} across the 30 A/B test populations (Table 2), the overall ranking of the six models we studied was as follows: PS > A/B > GCA > GCA_{IBD} > GCA + SB > SB. The overall ranking of the models was the same for the three traits we studied (grain yield, moisture, and test weight). However, the ranking of the six methods was not always the same across the 30 test populations (Tables 3–5).

The predictions were expected to be most accurate when they were made from within the population itself. Predictions with PS and the A/B model were based on the performance of the A/B test population itself, and the superiority of PS and of the A/B model was, therefore, consistent with expectations. Phenotypic selection had the highest mean R for grain yield (0.25 Mg ha^{-1}), moisture (–7 g kg^{-1}), and test weight (0.56 kg hL^{-1}) (Table 2). Phenotypic selection also had the highest mean r_{MP} for all three traits (0.24 for grain yield, 0.44 for moisture, and 0.34 for test weight). Although the differences between the two methods were mostly nonsignificant ($p = 0.05$), the mean R and r_{MP} values were consistently lower with the A/B model than with PS. Across the three traits, mean R values with the A/B model were 72 to 86% of the R values with PS. As expected, the mean R and r_{MP} values within a trait were highly correlated across the six models we studied (correlations of 0.95 for grain yield, 0.98 for moisture, and 0.99 for test weight).

Table 2. Mean and range (in parentheses) of response to selection (R) and prediction accuracy (r_{MP}) across 30 test populations in maize. The R and r_{MP} values were for phenotypic selection (PS) and for the A/B, general combining ability (GCA), GCA-identity by descent (GCA_{IBD}), same background (SB), and SB + GCA models for genomewide selection.

Method	Grain yield (h^2 = 0.38)†		Moisture (h^2 = 0.66)		Test weight (h^2 = 0.53)	
	R	r_{MP}	R	r_{MP}	R	r_{MP}
	Mg ha^{-1}		g kg^{-1}		kg hL^{-1}	
PS	0.25a‡ (0.03, 0.58)	0.24a (0.05, 0.42)	–7a (–15, –2)	0.44a (0.21, 0.67)	0.56a (0.04, 1.06)	0.34a (0.07, 0.62)
A/B	0.18ab (–0.15, 0.57)	0.14b (–0.06, 0.39)	–6a (–16, 1)	0.38a (0.05, 0.67)	0.44ab (0.06, 0.85)	0.29ab (0.06, 0.60)
GCA	0.19ab (–0.05, 0.52)	0.14b (0.01, 0.40)	–6a (–13, 0)	0.32b (–0.02, 0.53)	0.38bc (–0.06, 0.87)	0.24bc (–0.05, 0.48)
GCA_{IBD}	0.15bc (–0.10, 0.54)	0.12b (–0.06, 0.31)	–4b (–9, 1)	0.26bc (–0.02, 0.51)	0.24d (–0.30, 0.74)	0.18cd (–0.07, 0.39)
SB	0.07c (–0.25, 0.50)	0.06c (–0.13, 0.30)	–1c (–4, 4)	0.11d (–0.07, 0.29)	0.11e (–0.31, 0.75)	0.07e (–0.07, 0.35)
SB + GCA	0.17b (–0.11, 0.52)	0.12b (–0.05, 0.44)	–4b (–8, 0)	0.25c (–0.02, 0.49)	0.29cd (–0.31, 0.91)	0.17d (–0.23, 0.36)
$LSD_{0.05}$	0.079	0.056	1.49	0.063	0.121	0.065

†Mean heritability (h^2) on an entry-mean basis.

‡Within a column, estimates with a common letter were not significantly different (p = 0.05).

Table 3. Response to selection (R) and prediction accuracy (r_{MP}) for grain yield with phenotypic selection (PS) and with the A/B, general combining ability (GCA), GCA-identity by descent (GCA_{IBD}), same background (SB), and SB + GCA models for genomewide selection in maize.

Test population	h^2†	R, Mg ha^{-1}						r_{MP}					
		PS	A/B	GCA	GCA_{IBD}	SB	SB + GCA	PS	A/B	GCA	GCA_{IBD}	SB	SB + GCA
P1/P2	0.62	0.53	0.48	0.52	0.54	0.50	0.52	0.42	0.27	0.30	0.29	0.15	0.14
P3/P4	0.31	0.29	0.10	0.15	0.20	0.22	0.21	0.19	0.05	0.09	0.14	0.11	0.13
P4/P5	0.43	0.33	0.18	0.26	0.20	0.29	0.36	0.28	0.22	0.25	0.20	0.10	0.14
P6/P7	0.50	0.27	0.30	0.11	0.12	0.04	0.11	0.28	0.26	0.10	0.04	0.03	0.09
P3/P8	0.43	0.17	0.11	0.27	–0.06	–0.25	0.08	0.21	0.09	0.16	–0.02	–0.02	0.16
P1/P9	0.40	0.10	0.28	0.36	0.31	0.15	0.41	0.26	0.34	0.40	0.31	0.24	0.44
P5/P8	0.34	0.41	0.45	0.40	0.36	0.02	–0.08	0.26	0.30	0.17	0.26	–0.04	–0.01
P9/P10	0.43	0.27	0.08	–0.04	0.03	0.12	0.34	0.25	0.23	0.01	0.00NS‡	0.30	0.23
P9/P2/P9	0.43	0.58	0.57	0.42	0.33	0.29	0.48	0.28	0.24	0.13	0.13	0.14	0.15
P11/P12	0.40	0.19	0.17	0.09	0.06	0.19	0.19	0.26	0.15	0.08	0.00NS	–0.06	0.17
P13/P14	0.52	0.39	0.39	–0.02	0.04	–0.06	–0.04	0.36	0.39	0.08	–0.02	0.12	0.12
P2/P15	0.31	0.20	0.24	0.04	–0.10	0.12	0.01NS	0.17	0.23	0.20	0.12	0.13	0.21
P16/P13	0.40	0.28	0.25	0.16	0.08	0.00NS	0.24	0.20	0.30	0.26	0.22	0.17	0.25
P17/P18	0.47	0.31	0.26	–0.03	0.03	0.13	0.20	0.29	0.20	0.18	0.08	0.08	0.10
P19/P20	0.22	0.09	0.24	0.35	0.09	0.00NS	0.21	0.16	0.15	0.16	0.10	0.04	0.19
P21/P22	0.47	0.33	0.28	0.37	0.19	0.28	0.34	0.31	0.16	0.08	0.19	0.04	0.09
P23/P24	0.20	0.09	0.04	0.38	0.12	0.13	0.30	0.07	0.02	0.02	0.05	0.00NS	0.06
P25/P22	0.43	0.26	0.16	0.32	0.06	0.17	0.19	0.28	0.16	0.22	0.21	0.10	0.19
P26/P27	0.24	0.13	0.17	0.07	0.09	0.03	0.12	0.12	0.15	0.22	0.18	0.12	0.27
P23/P25	0.57	0.33	0.16	0.23	0.42	0.04	0.15	0.38	0.22	0.14	0.23	0.07	0.09
P24/P26	0.47	0.35	0.06	0.05	0.05	–0.05	0.02	0.29	0.05	0.06	–0.06	0.02	0.04
P28/P27	0.35	0.20	–0.05	0.11	0.27	0.13	0.15	0.22	0.12	0.13	0.21	0.08	0.10
P29/P27	0.25	0.15	0.02	0.12	0.06	0.03	0.08	0.11	0.03	0.08	0.10	0.01	0.06
P29/P30	0.23	0.18	0.05	0.22	0.16	0.04	0.12	0.15	0.07	0.15	0.13	0.02	0.01NS
P31/P32	0.23	0.03	0.04	0.25	0.17	0.06	–0.01NS	0.05	–0.01NS	0.10	0.06	0.00NS	0.04
P33/P34	0.45	0.19	–0.11	–0.05	0.12	–0.08	–0.11	0.33	0.09	0.04	0.02	0.06	0.02
P35/P36	0.27	0.16	–0.15	0.00NS	0.02	–0.08	–0.01NS	0.17	–0.60	0.04	0.06	–0.09	–0.01NS
P37/P38	0.29	0.25	0.43	0.06	0.11	–0.17	0.50	0.27	0.24	0.07	0.03	0.01	0.08
P39/P40/P39	0.46	0.13	0.02	0.20	0.09	–0.02	0.03	0.18	0.06	0.11	0.09	–0.13	–0.05
P41/P42	0.24	0.30	0.04	0.28	0.29	–0.07	–0.01NS	0.27	0.12	0.18	0.15	0.00NS	0.01NS

†Heritability (h^2) on an entry-mean basis.

‡NS, not significantly different from zero (p = 0.05). All other estimates of R and r_{MP} were significant.

The values of the prediction accuracy with PS indicated that the correlation between the testing environments was low to moderate. Quantitative traits are strongly influenced by genotype × environment interaction, which leads to the genotypes reacting differently in different environments (Haldane, 1946; Cooper and

Table 4. Response to selection (R) and prediction accuracy (r_{MP}) for moisture with phenotypic selection (PS) and with the A/B, general combining ability (GCA), GCA-identity by descent (GCA_{IBD}), same background (SB), and SB + GCA models for genomewide selection in maize.

Test population	$h^{2\dagger}$	R, g kg^{-1}						r_{MP}					
		PS	A/B	GCA	GCA_{IBD}	SB	SB + GCA	PS	A/B	GCA	GCA_{IBD}	SB	SB + GCA
P1/P2	0.58	–6	–5	–5	–5	–2	–4	0.35	0.37	0.46	0.46	0.29	0.29
P3/P4	0.75	–11	–8	–7	–7	–3	–5	0.58	0.46	0.42	0.38	0.19	0.37
P4/P5	0.76	–6	–5	–4	–4	–3	–4	0.51	0.48	0.29	0.31	–0.01	0.38
P6/P7	0.85	–14	–12	–9	–8	–3	–6	0.67	0.37	0.46	0.40	0.11	0.42
P3/P8	0.73	–6	–6	–7	–6	–2	–5	0.46	0.41	0.38	0.36	0.11	0.36
P1/P9	0.55	–2	–3	–3	–4	–2	–4	0.26	0.26	0.30	0.25	0.17	0.34
P5/P8	0.77	–2	–3	–1	–1	1	–4	0.25	0.36	0.18	0.15	0.06	0.26
P9/P10	0.56	–15	–11	–13	–6	2	–2	0.61	0.47	0.28	0.16	0.06	0.17
P9/P2/P9	0.75	–4	–4	–3	–2	–1	–4	0.43	0.39	0.35	0.26	0.21	0.38
P11/P12	0.84	–10	–9	–5	–5	–2	–4	0.66	0.57	0.25	0.19	0.03	0.07
P13/P14	0.68	–2	–2	–2	–2	–2	–4	0.38	0.36	0.23	0.21	0.20	0.19
P2/P15	0.61	–3	–4	–4	–4	–3	–3	0.30	0.31	0.32	0.32	0.22	0.29
P16/P13	0.76	–8	–10	–8	–8	–1	–5	0.56	0.58	0.53	0.48	0.14	0.49
P17/P18	0.81	–14	–16	–6	–7	–4	–6	0.50	0.67	0.30	0.26	0.15	0.16
P19/P20	0.56	–6	–3	–3	1	1	–2	0.39	0.22	0.16	–0.01NS	0.00NS	0.11
P21/P22	0.43	–5	–7	–7	–5	–4	–7	0.29	0.38	0.36	0.35	0.24	0.29
P23/P24	0.62	–7	–5	–4	–4	–1	–2	0.40	0.34	0.29	0.23	0.21	0.30
P25/P22	0.64	–9	–6	–7	–5	–3	–4	0.46	0.36	0.28	0.25	0.12	0.19
P26/P27	0.74	–8	–6	–6	–4	–2	–4	0.53	0.48	0.42	0.32	0.17	0.19
P23/P25	0.62	–6	–5	–7	–5	–1	–4	0.48	0.35	0.41	0.39	0.17	0.33
P24/P26	0.71	–7	–6	–7	–1	0NS	–6	0.50	0.38	0.40	–0.02	0.04	0.31
P28/P27	0.81	–13	–11	–8	–9	–4	–8	0.62	0.56	0.43	0.51	0.13	0.29
P29/P27	0.75	–6	–5	–5	–4	–3	–4	0.52	0.49	0.49	0.38	0.20	0.41
P29/P30	0.63	–5	–4	–4	–4	1	–2	0.45	0.44	0.36	0.34	0.03	0.30
P31/P32	0.42	–6	–6	–5	–5	0NS	–3	0.40	0.26	0.24	0.20	0.01NS	0.21
P33/P34	0.51	–9	–4	–6	–5	–1	–5	0.35	0.12	0.20	0.15	0.04	0.14
P35/P36	0.59	–3	1	0NS	0NS	1	0NS	0.29	0.05	–0.02	0.05	–0.01	–0.02
P37/P38	0.38	–7	–6	–6	–3	4	–2	0.40	0.24	0.24	0.15	–0.07	0.22
P39/P40/P39	0.61	–2	–2	–2	0NS	1	–1	0.21	0.24	0.15	–0.01	0.04	0.03
P41/P42	0.73	–10	–9	–11	–8	–2	–3	0.53	0.55	0.40	0.33	0.09	0.09

†Heritability (h^2) on an entry-mean basis.

‡NS, not significantly different from zero ($p = 0.05$). All other estimates of R and r_{MP} were significant.

Delacy, 1994). While genotype by environment interaction variance could not be estimated with the data in this study, genotype × environment interaction in maize is usually strong (Ouyang et al., 1995) and it necessitates the testing of maize hybrids across multiple environments.

It is advantageous to predict the performance of individuals within an A/B cross before phenotyping the cross itself, which is required in PS and in the A/B model. In the GCA model, the training population was constructed by pooling previously phenotyped crosses with A and B as one of the parents. The mean R with the GCA model was 0.19 Mg ha^{-1} for grain yield, −6 g kg^{-1} for moisture, and 0.38 kg hL^{-1} for test weight (Table 2). The mean r_{MP} was 0.14 for grain yield, 0.32 for moisture, and 0.24 for test weight (Table 2). Across the three traits, mean R values with the GCA model were 68 to 76% of the R values with PS. Compared with the A/B model, the GCA model had statistically equal or slightly lower mean R and r_{MP}.

One important advantage of PS over genomewide selection was that responses to selection were always in the favorable direction with PS. In contrast, the five genomewide selection models had instances of responses in the unfavorable direction. For grain yield, all of the R values were all positive for PS, but three populations had a negative R with A/B model and four populations had a negative R with the GCA model (Table 3). The unfavorable gains may have been due to associations between SNPs and QTL that were not conserved among populations (Liu et al., 2011; Zhao et al., 2012).

The mean R and mean r_{MP} values were lower with the GCA_{IBD} model than with the GCA model for all three traits (Table 2). The small but consistent reductions in R and r_{MP} with the GCA_{IBD} model may have occurred because the marker effects was estimated from fewer crosses in the GCA_{IBD} model than in the GCA model. For example, in population P24/P26, eight A/⋆ and 14 ⋆/B

Table 5. Response to selection (R) and prediction accuracy (r_{MP}) for test weight with phenotypic selection (PS) and with the A/B, general combining ability (GCA), GCA-identity by descent (GCA_{IBD}), same background (SB), and SB + GCA models for genomewide selection in maize.

Test population	h^2†	R, kg hL^{-1}						r_{MP}					
		PS	A/B	GCA	GCA_{IBD}	SB	SB + GCA	PS	A/B	GCA	GCA_{IBD}	SB	SB + GCA
P1/P2	0.32	0.39	0.25	0.32	0.37	0.45	0.40	0.22	0.22	0.37	0.38	0.35	0.33
P3/P4	0.52	0.63	0.34	0.19	0.10	–0.02	0.12	0.32	0.25	0.12	0.10	–0.01NS‡	0.06
P4/P5	0.31	0.40	0.14	0.47	0.20	0.13	0.67	0.16	0.09	0.22	0.16	–0.07	0.12
P6/P7	0.83	1.06	0.75	0.50	0.74	0.04	0.38	0.62	0.11	0.33	0.30	0.03	0.28
P3/P8	0.67	0.72	0.63	0.11	0.09	0.07	0.11	0.44	0.45	0.31	0.29	0.10	0.21
P1/P9	0.47	0.46	0.16	0.26	0.23	0.29	0.31	0.24	0.16	0.24	0.14	0.07	0.18
P5/P8	0.47	0.58	0.37	0.63	0.42	–0.26	0.21	0.32	0.28	0.28	0.21	–0.02	0.26
P9/P10	0.52	0.73	0.39	0.69	0.14	–0.15	0.46	0.35	0.29	0.36	0.23	0.00NS	0.21
P9/P2/P9	0.46	0.39	0.47	0.24	0.41	–0.22	0.20	0.24	0.19	0.19	0.17	–0.01	0.17
P11/P12	0.52	0.42	0.29	0.23	0.13	0.20	0.21	0.28	0.26	0.12	0.11	0.08	0.16
P13/P14	0.62	0.25	0.32	0.27	0.22	0.20	0.20	0.32	0.27	0.20	0.22	0.02	0.13
P2/P15	0.35	0.27	0.09	0.14	0.25	0.05	0.13	0.10	0.06	0.16	0.18	0.12	0.15
P16/P13	0.71	0.67	0.78	0.71	0.38	0.08	0.50	0.48	0.60	0.43	0.35	–0.03	0.32
P17/P18	0.71	0.62	0.83	–0.06	–0.07	–0.31	–0.31	0.50	0.51	–0.05	0.03	–0.05	–0.07
P19/P20	0.66	0.79	0.50	0.19	0.11	0.01	0.20	0.38	0.18	0.04	0.09	0.05	0.07
P21/P22	0.54	0.68	0.46	0.87	0.27	–0.06	0.91	0.33	0.33	0.33	0.25	0.05	0.33
P23/P24	0.45	0.56	0.30	0.15	0.14	0.04	0.19	0.31	0.23	0.19	0.07	0.11	0.15
P25/P22	0.61	0.57	0.31	0.34	0.49	0.01NS	0.37	0.42	0.25	0.27	0.27	0.10	0.22
P26/P27	0.69	0.73	0.85	0.76	0.49	0.75	0.80	0.51	0.55	0.48	0.39	0.16	0.18
P23/P25	0.51	0.75	0.68	0.48	0.64	0.56	0.45	0.35	0.36	0.24	0.30	0.12	0.22
P24/P26	0.72	0.85	0.69	0.68	–0.21	0.45	0.07	0.52	0.49	0.42	–0.06	0.30	–0.23
P28/P27	0.46	0.43	0.17	0.17	0.12	0.01NS	0.02	0.27	0.18	0.13	–0.07	–0.01	0.02
P29/P27	0.60	0.55	0.51	0.49	0.28	0.28	0.44	0.41	0.43	0.41	0.28	0.23	0.34
P29/P30	0.28	0.04	0.06	0.33	0.19	–0.10	0.27	0.07	0.14	0.31	0.28	0.00NS	0.25
P31/P32	0.45	0.40	0.68	0.67	0.09	–0.29	0.46	0.27	0.32	0.28	0.13	–0.03	0.24
P33/P34	0.59	0.81	0.38	0.29	0.50	0.59	0.25	0.43	0.32	0.22	0.16	0.11	0.20
P35/P36	0.27	0.36	0.10	–0.02	–0.30	0.28	0.15	0.17	0.06	–0.02	0.01	0.07	0.05
P37/P38	0.38	0.41	0.73	0.73	0.39	0.00NS	0.12	0.49	0.55	0.39	0.28	0.17	0.36
P39/P40/P39	0.62	0.42	0.34	0.13	0.25	0.19	0.34	0.17	0.25	0.08	0.18	0.09	0.20
P41/P42	0.70	0.73	0.65	0.41	0.19	0.18	0.20	0.55	0.37	0.17	0.12	0.01NS	0.04

†Heritability (h^2) on an entry-mean basis.

‡NS, not significantly different from zero ($p = 0.05$). All other estimates of R and r_{MP} were significant.

crosses were pooled into the training population. Marker effects in the GCA model were, therefore, estimated from 22 crosses, whereas marker effects in the GCA_{IDB} model were estimated from eight crosses (marker effects for P24) and 14 crosses (marker effects for P26).

In the GCA model, increasing the level of genetic similarity between the ★ parent and the A/B cross did not improve the predictions. We found no significant difference ($p = 0.05$) in R and r_{MP} when the training populations only included A/★ and ★/B crosses for which the values of $S_{A★}$ and $S_{B★}$ both exceeded threshold values of 0.60, 0.70 or 0.80. The influence of genetic similarity was confounded with changes in the size of the training population, because higher thresholds for genetic similarity reduced the number of crosses that could be included in the training population. However, the R and r_{MP} were similar even as the population size greatly decreased due to removing populations below the genetic similarity threshold. This result suggested that the contributions of the A and B parents themselves (in the A/★ and ★/B crosses) may be providing most of the information for predictions in the GCA model. Previous studies have shown that r_{MP} decreased when the relationship between the training and test population was weak, especially when the training population was small (Habier et al., 2010; Asoro et al., 2011; Clark et al., 2012). However, the use of crosses that have A and B as one of the parents inherently leads to a strong relationship between the training and test population, to the extent that previous results that focus on weaker relatedness do not apply.

The SB model was ineffective even though (i) the crosses pooled into the training population were from the same heterotic group as the A/B cross, (ii) the number of crosses pooled into a training population was equal between the SB and GCA models, and (iii) the size of the training population was roughly the same between the SB and GCA models (Table 1). The mean r_{MP} across the

three traits was only 0.06 to 0.11 with the SB model, and the R with SB model was only 15 to 28% of the R with PS (Table 2). These results were inconsistent with several previous studies that showed combining multiple related populations (Schulz-Streeck et al., 2012; Zhao et al., 2012; Windhausen et al., 2012) or multiple populations from opposite heterotic groups (Technow et al., 2013) improved the prediction accuracy over the A/B model, but they were consistent with one previous study that showed that including populations with the same genetic background can cause a lower or even negative prediction accuracy (Riedelsheimer et al., 2013). This result may have been due to opposite linkage phases between the QTLs in the training and test populations (Lorenz et al., 2012; Riedelsheimer et al., 2013).

Increasing the size of the training population has been previously found to be an important factor in increasing the prediction accuracy (Heffner et al., 2011a). Compared with the GCA model, the SB + GCA model had double the number of crosses in the training population and roughly double the size of the training population. However, the GCA model was as effective or more effective than the SB + GCA model. While the differences were often nonsignificant, the mean R and r_{MP} values were consistently lower with the SB + GCA model than with the GCA model (Table 2). Increasing the size of the training population with random populations is, therefore, less important than including A/★ and ★/B crosses in the training population for the A/B cross. Similar results were found by Riedelsheimer et al. (2013).

Influence of Heritability, Linkage Disequilibrium, Size of the Training Population, and Number of Markers on the GCA Model

The h^2 values for grain yield, moisture, and test weight varied widely among the 30 test populations (Table 1). While the mean h^2 was 0.38 for grain yield, 0.66 for moisture, and 0.53 for test weight, the h^2 within a test population ranged from 0.20 to 0.62 for grain yield (Table 3), 0.38 to 0.85 for moisture (Table 4), and 0.27 to 0.83 for test weight (Table 5). With the GCA model, the correlation between h^2 and r_{MP} was positive for each trait but was significant only for moisture (Table 6).

The 30 A/B test populations differed widely in the number of individuals in the training population for the GCA model (N_{GCA}). However, the N_{GCA} was always large, ranging from 634 to 5255 (Table 1). With the GCA model, the correlations between N_{GCA} and r_{MP} were positive but significant only for moisture (Table 6). Our results agree with previous studies that indicated that an increase in N results in an increase in r_{MP} (Lorenzana and Bernardo, 2009; Asoro et al., 2011; Heffner et al., 2011a, 2011b; Guo et al., 2012; Lorenz et al., 2012).

Table 6. Correlation between prediction accuracy (r_{MP}) versus the number of individuals in the training population general combining ability (GCA) model (N_{GCA}), number of biparental crosses in the training population GCA model ($N_{\times}$), heritability on an entry-mean basis (h^2), linkage disequilibrium (r^2) between adjacent SNP markers, and number of markers (N_M).

Factor	Grain yield	Moisture	Test weight
N_{GCA}	0.18	0.43*	0.33
$N_{\times}$	0.13	0.42*	0.38*
h^2	0.16	0.39*	0.14
r^2	0.29	0.35	0.15
$h^2\sqrt{N_{GCA}}$	0.26	0.57*	0.43*
$h^2r^2\sqrt{N_{GCA}}$	0.36*	0.58*	0.48*
$h^2\sqrt{N_{\times}}$	0.22	0.55*	0.46*
$h^2r^2\sqrt{N_{\times}}$	0.31	0.57*	0.52*
N_M	0.35	0.01	0.18

*Significant (p = 0.05) based on a Fisher z-transformation. All other correlation coefficients were nonsignificant.

The expected prediction accuracy (r_{MG}) is a function of $\sqrt{N_{GCA}h^2}$ instead of N_{GCA} and h^2 individually (Daetwyler et al., 2010). Because r_{MP} is equal to $r_{MP}h$, r_{MP} is a function of $h^2\sqrt{N_{GCA}}$. Our empirical results were consistent with this theoretical result from Daetwyler et al. (2010), with the correlation between r_{MP} and $h^2\sqrt{N_{GCA}}$ for the GCA model being significant for moisture and test weight but not for grain yield (Table 6). These results generally agree with previous research that found that within the same trait, the product of Nh^2 is more important than N and h^2 evaluated individually (Combs and Bernardo, 2013b).

We have previously found that the Daetwyler et al. (2010) equation for prediction accuracy can be modified by incorporating information on LD (r^2) between adjacent markers (Lian et al., 2013). The correlation between r_{MP} and $h^2r^2\sqrt{N_{GCA}}$ was 0.36 for grain yield, 0.58 for moisture, and 0.48 for test weight (Table 6). The higher correlations of r_{MP} with $h^2r^2\sqrt{N_{GCA}}$ than with $h^2\sqrt{N_{GCA}}$ indicated that, when the genome is unsaturated with markers, mean r^2 values contribute to the expected prediction accuracy (Lian et al., 2013).

In addition to the large variability in the number of individuals in the training population, there was also a large variability in the number of crosses that comprised the training population for the GCA model ($N_{\times}$). The correlation between $N_{\times}$ and r_{MP} was significant for moisture and test weight, but not for grain yield (Table 6). The training populations with the most A/★ and ★/B crosses tended to have the largest R values. For example, in the P21/P22 population, 38 A/★ and ★/B crosses were used in the training population, and R was high at 0.37 Mg ha^{-1} for grain yield (Table 3), –7 g kg^{-1} for moisture (Table 4), and 0.87 kg hL^{-1} for test weight (Table 5).

As with $h^2\sqrt{N_{GCA}}$, the correlations between r_{MP} and $h^2\sqrt{N_{\times}}$ were higher than the correlations with $N_{\times}$ and h^2 evaluated individually (Table 6). These correlations were

increased further by incorporating LD. The correlations between r_{MP} and $h^2r^2\sqrt{N_\times}$ were 0.31 for grain yield, 0.57 for moisture, and 0.52 for test weight. Further studies are needed to evaluate the effect of increasing $N_\times$ while keeping N_{GCA} constant, or of increasing N_{GCA} while keeping N_X constant. On the other hand, knowledge of the independent effects of N_{GCA} and $N_\times$ would be of little practical value because, in practice, N_{GCA} and $N_\times$ would tend to be highly correlated.

The correlation between the number of markers (N_M) and r_{MP} was not significant for any of the traits (Table 6). Previous studies have indicated that r_{MP} increases as the N_M increases, but r_{MP} plateaus once the genome is covered with markers (Lorenzana and Bernardo, 2009; Asoro et al., 2011; Heffner et al., 2011a; 2011b; Guo et al., 2012; Combs and Bernardo, 2013b). Large chromosomal segments are passed intact from parents to progeny in a biparental cross, to the extent that markers spaced 10 to 15 cM are largely sufficient (R. Bernardo, unpublished data, 2013) for genomewide selection within a biparental cross. Finding many polymorphic markers can also be difficult in crosses between related elite inbreds, such as those in this study. The mean r^2 between adjacent markers across the 30 populations was 0.51 with a range of 0.36 to 0.64 (Table 1), and the mean r^2 among all 970 populations (0.46) was likewise high. The high r^2 values indicated that although marker coverage is low there was substantial LD for genomewide selection. A previous study in maize found that genomewide selection was still effective when the r^2 was as low as 0.26 to 0.35 (Massman et al., 2013). Nevertheless, increasing the number of markers may help increase the R and r_{MP} for the GCA, A/B, SB, and SB + GCA models.

Overall, $h^2r^2\sqrt{N_{GCA}}$ and $h^2r^2\sqrt{N_\times}$ were the two criteria with the highest correlations with r_{MP} and for which the correlations were significant across all three traits, except for $h^2r^2\sqrt{N_\times}$ for grain yield (Table 6). These two criteria should therefore be the ones used for designing genomewide selection programs with the GCA model. When prediction accuracy is expressed as r_{MG} instead of r_{MP}, the corresponding criteria would be $r^2\sqrt{h^2N_{GCA}}$ and $r^2\sqrt{h^2N_\times}$.

Implications in Inbred Development

Our results show that selection within an A/B cross is most effective when selection decisions—made from either field data (PS) or marker-based predictions (A/B model)—are based on the performance of the A/B cross itself. But PS and the A/B model are highly time consuming and expensive because the A/B population itself needs to be phenotyped. Time and cost are particularly limiting in inbred development that does not involve recurrent selection; in the latter, the time and cost in phenotyping can be justified by the increase in the gain per unit time when multiple cycles of genomewide selection are performed in a year-round nursery or greenhouse (Massman et al., 2012; Combs and Bernardo, 2013a).

The GCA model led to the highest R and r_{MP} among the models that eliminate the need to phenotype the A/B test population itself. The GCA model relies on information from previously phenotyped and genotyped crosses with inbreds A and B as one of the parents and is conducive in advanced breeding programs that use elite inbreds as the parents of new breeding crosses. In the context of inbred development, genomewide selection with the GCA model seems most useful during the stages of the breeding program when gains from PS are zero or are low. In particular, the evaluation of individual F_2 plants per se has a low genetic correlation with the testcross performance of the F_2 plant or of an inbred derived from the F_2 plant when heterosis is substantial and when heritability is low (Smith, 1986; Bernardo, 1991; Mihaljevic et al., 2004). Current gains for hybrid grain yield from any mass selection for grain yield among individual F_2 plants are, therefore, probably zero or close to zero. Our results indicated that, on average, genomewide selection with the GCA model among F_2 plants in an A/B cross would lead to single-trait gains of 0.19 Mg ha^{-1} (or 3 bushels per acre) for grain yield, −6 g kg^{-1} (or −0.6%) for moisture, and 0.38 kg hL^{-1} (or 0.30 lb per bushel) for test weight (Table 2). These gains were 68 to 76% of the corresponding gains with PS based on testcross performance in replicated experiments and could be achieved at a fraction of the cost of PS.

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References

Asoro, F.G., M.A. Newell, W.D. Beavis, M.P. Scott, and J.-L. Jannink. 2011. Accuracy and training population design for genomic selection on quantitative traits in elite North American oats. Plant Gen. 4:132–144. doi:10.3835/plantgenome2011.02.0007

Bates, D., M. Maechler, and B. Bolker. 2011. Welcome to lme4—Mixed-effects models project. R Foundation for Statistical Computing, Vienna, Austria. http://lme4.r-forge.r-project.org/ (accessed 2 Dec. 2013).

Bernardo, R. 1991. Correlation between testcross performance of lines at early and late selfing generations. Theor. Appl. Genet. 82:17–21. doi:10.1007/BF00231272

Bernardo, R., and J. Yu. 2007. Prospects for genomewide selection for quantitative traits in maize. Crop Sci. 47:1082–1090. doi:10.2135/cropsci2006.11.0690

Clark, S.A., J.M. Hickey, H.D. Daetwyler, and J.H. van der Werf. 2012. The importance of information on relatives for the prediction of genomic breeding values and the implications for the makeup of reference data sets in livestock breeding schemes. Genet. Sel. Evol. 44:4. doi:10.1186/1297-9686-44-4

Combs, E., and R. Bernardo. 2013a. Genomewide selection to introgress semidwarf maize germplasm into U.S. Corn Belt inbreds. Crop Sci. 53:1427–1436. doi:10.2135/cropsci2012.11.0666

Combs, E., and R. Bernardo. 2013b. Accuracy of genomewide selection for different traits with constant population size, heritability, and number of markers. Plant Gen. 6:1–7. doi:10.3835/plantgenome2012.11.0030

Cooper, M., and I.H. Delacy. 1994. Relationships among analytical methods used to study genotypic variation and genotype-by-environment interaction in plant breeding multi-environment experiments. Theor. Appl. Genet. 88:561–572. doi:10.1007/BF01240919

Daetwyler, H.D., R. Pong-Wong, B. Villanueva, and J.A. Woolliams. 2010. The impact of genetic architecture on genome-wide evaluation methods. Genetics 185:1021–1031. doi:10.1534/genetics.110.116855

Endelman, J.B. 2011. Ridge regression and other kernels for genomic selection with R package rrBLUP. Plant Gen. 4:250–255. doi:10.3835/plantgenome2011.08.0024

Guo, Z., D.M. Tucker, J. Lu, V. Kishore, and G. Gay. 2012. Evaluation of genome-wide selection efficiency in maize nested association mapping populations. Theor. Appl. Genet. 124:261–275. doi:10.1007/s00122-011-1702-9

Habier, D., J. Tetens, F.-R. Seefried, P. Lichtner, and G. Thaller. 2010. The impact of genetic relationship information on genomic breeding values in German Holstein cattle. Genet. Sel. Evol. 42:5. doi:10.1186/1297-9686-42-5

Haldane, J. 1946. The interaction of nature and nurture. Ann. Eugen. 13:197–205. doi:10.1111/j.1469-1809.1946.tb02358.x

Hallauer, A.R. 1990. Methods used in developing maize inbreds. Maydica 35:1–16.

Heffner, E.L., J.-L. Jannink, H. Iwata, E. Souza, and M.E. Sorrells. 2011a. Genomic selection accuracy for grain quality traits in biparental wheat populations. Crop Sci. 51:2597–2606. doi:10.2135/cropsci2011.05.0253

Heffner, E.L., J.-L. Jannink, and M.E. Sorrells. 2011b. Genomic selection accuracy using multifamily prediction models in a wheat breeding program. Plant Gen. 4:65–75. doi:10.3835/plantgenome.2010.12.0029

Heffner, E.L., M.E. Sorrells, and J.-L. Jannink. 2009. Genomic selection for crop improvement. Crop Sci. 49:1–12. doi:10.2135/cropsci2008.08.0512

Heslot, N., H.-P. Yang, M.E. Sorrells, and J.-L. Jannink. 2012. Genomic selection in plant breeding: A comparison of models. Crop Sci. 52:146–160. doi:10.2135/cropsci2011.06.0297.

Holland, J.B., W.E. Nyquist, and C.T. Cervantes-Martínez. 2003. Estimating and interpreting heritability for plant breeding: An update. In: J. Janick, editor, Plant Breed Reviews. John Wiley & Sons, New York. Vol. 22. p. 9–112.

Lian, L., A. Jacobson, S. Zhong, and R. Bernardo. 2013. Genome-wide prediction accuracy within 1000 biparental maize populations. Poster 272. 55th Annu. Maize Genet. Conf. 14–17 Mar. 2013, Pheasant Run, IL. www.maizegdb.org/maize_meeting/abstracts/2013Program.pdf.

Liu, W., M. Gowda, J. Steinhoff, H.P. Maurer, T. Würschum, C.F.H. Longin, F. Cossic, and J.C. Reif. 2011. Association mapping in an elite maize breeding population. Theor. Appl. Genet. 123:847–858. doi:10.1007/s00122-011-1631-7

Lorenz, A.J., S. Chao, F.G. Asoro, E.L. Heffner, T. Hayashi, H. Iwata, K.P. Smith, M.E. Sorrells, and J.-L. Jannink. 2011. Genomic selection in plant breeding: Knowledge and prospects. Adv. Agron. 110:77–123. doi:10.1016/B978-0-12-385531-2.00002-5

Lorenz, A.J., K.P. Smith, and J.-L. Jannink. 2012. Potential and optimization of genomic selection for fusarium head blight resistance in six-row barley. Crop Sci. 52:1609–1621. doi:10.2135/cropsci2011.09.0503

Lorenzana, R.E., and R. Bernardo. 2009. Accuracy of genotypic value predictions for marker-based selection in biparental plant populations. Theor. Appl. Genet. 120:151–161. doi:10.1007/s00122-009-1166-3

Massman, J.M., A. Gordillo, R.E. Lorenzana, and R. Bernardo. 2013. Genomewide predictions from maize single-cross data. Theor. Appl. Genet. 126:13–22. doi:10.1007/s00122-012-1955-y

Massman, J.M., H.-J.G. Jung, and R. Bernardo. 2012. Genomewide selection versus marker-assisted recurrent selection to improve grain yield and stover-quality traits for cellulosic ethanol in maize. Crop Sci. 53:58–66. doi:10.2135/cropsci2012.02.0112.

Meuwissen, T.H., B.J. Hayes, and M.E. Goddard. 2001. Prediction of total genetic value using genome-wide dense marker maps. Genetics 157:1819–1829.

Mihaljevic, R., C.C. Scho, H.F. Utz, and A.E. Melchinger. 2004. Correlations and QTL correspondence between line per se and testcross performance for agronomic traits in four populations of European maize. Crop Sci. 45:114–122. doi:10.2135/cropsci2004.0114

Ouyang, Z., R.P. Mowers, A. Jensen, S. Wang, and S. Zheng. 1995. Custer analysis for genotype × environment interaction with unbalanced data. Crop Sci. 35:1300–1305. doi:10.2135/cropsci1995.0011183X003500050008x

Piepho, H.P. 2009. Ridge regression and extensions for genomewide selection in maize. Crop Sci. doi:10.2135/cropsci2008.10.0595

R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Riedelsheimer, C., J.B. Endelman, M. Stange, M.E. Sorrells, J.-L. Jannink, and A.E. Melchinger. 2013. Genomic predictability of interconnected biparental maize populations. Genetics 194:493–503. doi:10.1534/genetics.113.150227

Schulz-Streeck, T., J.O. Ogutu, Z. Karaman, C. Knaak, and H.P. Piepho. 2012. Genomic selection using multiple populations. Crop Sci. 52:2453–2461. doi:10.2135/cropsci2012.03.0160

Smith, O.S. 1986. Covariance between line per se and testcross performance. Crop Sci. 26:540–543. doi:10.2135/cropsci1986.0011183X002600030023x

Sokal, R.R., and C.D. Michener. 1958. A statistical method for evaluating systematic relationships. Univ. Kansas Sci. Bull. 38:1409–1438.

Technow, F., A. Bürger, and A.E. Melchinger. 2013. Genomic prediction of northern corn leaf blight resistance in maize with combined or separated training sets for heterotic groups. Gene Genet. Genom. 3:197–203. doi:10.1534/g3.112.004630.

Windhausen, V.S., G.N. Atlin, J.M. Hickey, J. Crossa, J.-L. Jannink, M.E. Sorrells, B. Raman, J.E. Cairns, A. Tarekegne, K. Semagn, Y. Beyene, P. Grudloyma, F. Technow, C. Riedelsheimer, and A.E. Melchinger. 2012. Effectiveness of genomic prediction of maize hybrid performance in different breeding populations and environments. Gene Genet. Genom. 2:1427–1436. doi:10.1534/g3.112.003699.

Zhao, Y., M. Gowda, W. Liu, T. Würschum, H.P. Maurer, F.H. Longin, N. Ranc, and J.C. Reif. 2012. Accuracy of genomic selection in European maize elite breeding populations. Theor. Appl. Genet. 124:769–776. doi:10.1007/s00122-011-1745-y