An estimated 15 to 20% of maize grain yield is lost each year due to drought and such losses may further increase as droughts become more frequent and severe because of climate change (FAOSTAT, 2010). Phenotyping for drought tolerance is laborious and resource intensive, requiring multiple locations and years of field testing to accurately characterize the traits involved (Bruce et al., 2002; Collins et al., 2008). Direct selection for grain yield under drought is often inefficient because the heritability on an entry-mean basis ($h^2$) for grain yield is much lower under stress (Edmeades et al., 1999). In addition, the correlation between grain yield under abiotic stress conditions and nonstress conditions decreases as the level of stress increases (Bänziger and Lafitte, 1997; Ribaut et al., 2007).

One way to increase the efficiency of selection for drought tolerance is to select for secondary traits that are easy to measure, have high $h^2$, and are highly correlated with grain yield under drought (Edmeades et al., 1993; Bänziger et al., 2000). Indirect selection through a secondary trait may be more efficient than direct selection if $h^2$ is higher for the secondary trait than for the primary trait and if the genetic correlation between the primary
and secondary trait is sufficiently high. Grain yield under drought has been strongly correlated with a high harvest index, more ears per plant, and a short anthesis–silking interval (ASI) and moderately correlated with delayed leaf senescence, high leaf chlorophyll content, and plant height (Edmeades et al., 1999).

A second way to improve the efficiency of selection for abiotic stress is to select for molecular markers (Lande and Thompson, 1990) associated with grain yield under stress (Cattivelli et al., 2008; Messmer et al., 2009). Despite the initial promise of marker-assisted selection for quantitative traits, information on quantitative trait loci (QTL) has not directly led to drought tolerant cultivars (Tuberosa et al., 2002; Collins et al., 2008). As an alternative to selection based on markers with significant effects, genomewide selection uses a large number of random markers to predict performance (Meuwissen et al., 2001). Simulation and empirical results in maize have shown 14 to 50% larger gains with genomewide selection than with QTL-based selection (Bernardo and Yu, 2007; Massman et al., 2012).

A comparison of predicted gains from indirect selection through secondary traits versus genomewide selection will provide information useful for designing breeding programs to improve drought tolerance in maize. The intermated B73 × Mo17 (IBM) population is a valuable public resource for genetic studies in maize (Lee et al., 2002). A total of 238 intermated B73 × Mo17 recombinant inbreds, along with B73 and Mo17, were testcrossed to a proprietary Monsanto inbred tester (LH295) that combined well with both B73 and Mo17. Marker data for the IBM inbreds are publicly available from MaizeGDB (Lawrence et al., 2008). Data for 998 markers, which included simple sequence repeats and restriction fragment length polymorphisms, were used in this study.

**Drought Stress and Control Experiments**

Drought stress screening was conducted at the University of Minnesota Anoka Sand Plain Research Farm (45°35′ N, 93°10′ W) at Becker, MN, in 2009 and 2010. The soil at Becker (Hubbard loamy sand) has a low water-holding capacity. Drought experiments as well as adjacent control experiments were laid out in an augmented randomized complete block design (Federer, 1961), in eight sets of incomplete blocks consisting of 30 testcrosses and five hybrid checks replicated eight times. The testcrosses and check hybrids were planted in two 4.8-m rows spaced 0.76 m apart and at a plant population density of 77,000 plants ha⁻¹.

Drought stress was managed so that it was severe enough to delay silking and cause ear abortion and ultimately reduce grain yield by a target of 50% (Bänziger et al., 2000). In 2009, both the control and drought experiments at Becker initially received the recommended amounts of irrigation water. However, irrigation in the drought experiment was discontinued 6 wk after planting when most of the plants were at the V15 stage. In 2010, irrigation water was not applied in the drought experiment because of the amount of precipitation received (Table 1).

In addition to the control experiments at Becker in 2009 and 2010, rainfall control experiments were conducted during both years at the University of Minnesota Southern Research and Outreach Center in Waseca, MN (44°4′ N, 95°32′ W), and at the Southwest Research and Outreach Center in Lamberton, MN (44°14′ N, 95°16′ W). The soil type was Webster

**Materials and Methods**

**Germplasm and Marker Data**

The IBM population was developed by crossing inbreds B73 and Mo17, selfing the F₁ to form the F₂ generation, intermating F₂ plants for five generations, and obtaining recombinant inbreds by at least six generations of selfing from the fifth intermated generation (Lee et al., 2002). A total of 238 intermated B73 × Mo17 recombinant inbreds, along with B73 and Mo17, were testcrossed to a proprietary Monsanto inbred tester (LH295) that combined well with both B73 and Mo17. Marker data for the IBM inbreds are publicly available from MaizeGDB (Lawrence et al., 2008). Data for 998 markers, which included simple sequence repeats and restriction fragment length polymorphisms, were used in this study.

<table>
<thead>
<tr>
<th>Table 1. Amount of water received (mm) in both precipitation and irrigation and mean grain yield of testcrosses of 238 intermated B73 × Mo17 maize inbreds at Becker, Waseca, and Lamberton, MN, in 2009 and 2010. Soil types were Hubbard loamy sand at Becker, Normania loam at Lamberton, and Webster clay loam (2009) and Webster-Nicollet clay loam (2010) at Waseca.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Month</strong></td>
</tr>
<tr>
<td><strong>Becker</strong></td>
</tr>
<tr>
<td>May</td>
</tr>
<tr>
<td>June</td>
</tr>
<tr>
<td>July</td>
</tr>
<tr>
<td>Aug.</td>
</tr>
<tr>
<td>Sept.</td>
</tr>
<tr>
<td>July plus Aug. total</td>
</tr>
<tr>
<td>Mean grain yield, Mg ha⁻¹</td>
</tr>
</tbody>
</table>

†Irrigation water was applied only in the drought and control experiments at Becker.

‡The 30-yr mean precipitation (May to Sept.) at the rainfed locations was 519 mm at Waseca and 435 mm at Lamberton.
clay loam at Waseca in 2009, Webster-Nicollet clay loam at Waseca in 2010, and Normania loam at Lamberton in both years. Plots were 6.7 m long at both locations. The experimental design at Waseca and Lamberton was the same as in the control experiments in Becker. The drought experiments were therefore conducted in two environments (Becker in 2009 and 2010) whereas the control experiments were conducted in six environments (Becker, Waseca, and Lamberton in 2009 and 2010). As indicated later in the Results and Discussion, mean productivity was comparable between the irrigated control experiments at Becker and the rainfed control experiments in Waseca and Lamberton.

Traits Measured
The same traits were measured in the drought and control experiments. Days to male flowering (anthesis) were recorded when approximately 50% of the plants in the plot were shedding pollen, and days to female flowering (silking) were recorded when approximately 50% of the plants in the plot had extruded silks. The ASI was calculated as the difference between days to silking and days to anthesis. At the first sign of anthesis in each experiment, chlorophyll content readings were taken using a hand-held MINOLTA 502 chlorophyll SPAD (soil plant analysis development) meter (Minolta Camera, 1989) and recorded in SPAD units. Readings were taken on the third leaf from the tassel and on the ear leaf during flowering. The measurements were taken on five alternating plants from each plot, midway between the stalk and leaf tip and between the midrib and the edge of the leaf. Leaf senescence was recorded 3 wk after anthesis. Leaf senescence was recorded on a whole–canopy basis as a visually scored percentage of dead leaf tissue; lesions characteristic of major corn diseases were not readily evident in any of the experiments.

Plant height was measured on six plants as the distance in centimeters from the soil surface to the tip of the tassel. Stalk lodging was recorded as the percentage of plants with stalks broken below the ear. At Becker, grain yield in both the control and drought plots was determined by hand harvesting the mid-3 m of the two rows. Grain moisture content was obtained by oven drying a 500-g grain sample from each plot and equating the loss in sample weight to the amount of kernel moisture. Grain yield was calculated from shelled grain weight per plot and adjusted to 155 g H₂O kg⁻¹. In the control experiments at Waseca and Lamberton, the plots were harvested by a combine and plot weights and moisture were recorded.

Trait Means, Variances, and Heritability on an Entry-Mean Basis
Data were analyzed with SAS version 9.2 PROC GLM (SAS Institute, 2009) to adjust for set (incomplete blocks) effects based on the performance of the check hybrids in the augmented randomized complete blocks (Scott and Milliken, 1993). Analysis of variance was conducted using SAS PROC GLM with testcrosses and environments having random effects. The drought experiments in 2009 and 2010 were combined and analyzed across years. In the control experiments, means and variances were estimated across locations and years for each trait. Restricted maximum likelihood (REML) estimates of testcross genetic (Vg) and phenotypic variances were obtained with SAS PROC MIXED and were used to compute h² for each trait. Approximate standard errors of the h² estimates were derived from the asymptotic distributional properties of REML variance estimates using the delta method (Holland et al., 2003).

Genetic correlations were estimated in two ways: first, from genetic variances and covariances using multivariate maximum likelihood estimation in SAS PROC MIXED (SAS Institute, 2009) as outlined by Holland (2006) and second, as the correlation between genomewide marker effects for each trait. In other words, with 998 markers used, the latter correlation referred to \( r(g_iX, g_iY) \), in which \( g_iX \) was the genomewide marker effect at the \( i \)th marker (\( i = 1 \) to 998) for trait \( X \) and \( g_iY \) was the genomewide marker effect at the \( i \)th marker for trait \( Y \).

Genomewide Marker Effects
Genomewide marker effects were estimated, by ridge regression-best linear unbiased prediction (RR-BLUP) (Meuwissen et al., 2001) in SAS PROC IML (SAS Institute, 2009). With a training set of \( N \) testcrosses and 998 markers used, the model was \( y = \mu + Xg + e \), in which \( y \) was an \( N \times 1 \) vector of mean phenotypic values for a given trait in the training set, \( \mu \) was an \( N \times 1 \) vector with all elements equal to 1, \( X \) was the overall mean for the trait, \( X \) was an \( N \times 998 \) matrix of marker genotype indicators, which had values of \( 1, 0, \) or \(-1\) for marker genotypes in a biparental cross, \( g \) was a \( 998 \times 1 \) vector of effects of the marker alleles from B73, and \( e \) was an \( N \times 1 \) vector of residuals. The corresponding mixed model equations were used to solve for \( g \) (Henderson, 1984). The variance of marker effects was \( V_g \) (Meuwissen et al., 2001), in which \( N_g = 998 \) was the total number of markers used. Cross validation similar to the procedures of Lee et al. (2008) and Lorenzana and Bernardo (2009) was used to evaluate the usefulness of the predictions. The 238 IBM testcrosses were randomly divided into five subsets. Four subsets were combined to form the training set and the remainder was the validation set. The correlation between predicted genotypic values and observed phenotypic values (\( r_{MP} \)) was estimated in the validation set with estimates of variances used in RR-BLUP being obtained from the training set.

Indirect Responses to Selection with Secondary Traits and Genomewide Markers
The efficiency of indirect selection (through secondary traits) to improve grain yield under drought was estimated as outlined by Falconer (1981). The efficiency of indirect selection was equal to \( | r_{gX} | h_X/h_Y \), in which \( r_{gX} \) was the absolute value of the estimated genetic correlation (estimated from genetic covariances) between trait \( X \) and trait \( Y \) and \( h_X \) and \( h_Y \) were the square roots of \( h^2 \) for traits \( X \) and trait \( Y \), respectively. The relative efficiency of genomewide selection over phenotypic selection was estimated as \( r_{MP}/h^2 \) (Dekkers, 2007). Approximate standard errors of relative efficiency were obtained in SAS PROC IML (SAS Institute, 2009) based on the asymptotic distributional properties of the variance and covariance estimates (Gilmour et al., 2006), and approximate 95% confidence intervals were obtained as twice the standard error.
**RESULTS AND DISCUSSION**

**Precipitation and Irrigation Water, Trait Means, and Heritability on an Entry-Mean Basis in Drought and Control Experiments**

During the critical months of July and August, the drought experiments at Becker received 45% (in 2009) and 54% (in 2010) of the amount of water received in the control experiments at the same location (Table 1). The amount of precipitation at the two rainfed locations (Waseca and Lamberton) differed between the 2 yr. In 2009, the total precipitation during the growing season (May–September) (Table 1) was 46% lower than the 30-yr historical mean at Waseca and 26% lower than the 30-yr historical mean at Lamberton. In 2010, the total precipitation during the growing season was 69% higher than the 30-yr mean at Waseca and 65% higher than 30-yr mean at Lamberton.

Total precipitation is not fully indicative of available soil water, and high mean yields were maintained in all four rainfed control experiments with mean grain yields of the IBM testcrosses ranging from 10.96 Mg ha\(^{-1}\) at Lamberton in 2009 to 14.49 Mg ha\(^{-1}\) at Waseca in 2010 (Table 1). The mean grain yields in the four rainfed control experiments were comparable to the mean grain yields of 11.93 to 12.79 Mg ha\(^{-1}\) in the control experiments at Becker in 2009 and 2010. In particular, the mean grain yield across the four rainfed control experiments (12.66 Mg ha\(^{-1}\)) was close to the mean grain yield across the two irrigated control experiments at Becker (12.36 Mg ha\(^{-1}\)). Furthermore, the mean grain yield in the lowest-yielding rainfed control experiment (Lamberton in 2009) was only 15% lower than the mean grain yield in the five other control experiments, and the 15% reduction was well below the 50% yield reduction that is typically targeted in managed-drought experiments (Bänziger et al., 2000). Performance in the control experiments at all six environments was therefore considered.

Across environments, the mean grain yield of the IBM testcrosses was 6.49 Mg ha\(^{-1}\) under drought and 12.56 Mg ha\(^{-1}\) in the control experiments, with the difference in mean yield being statistically significant \((P < 0.05)\) (Table 2). Drought stress therefore reduced grain yield by 48%. In the control experiments, the 238 IBM testcrosses showed significant differences \((P < 0.05)\) for grain yield, moisture, plant height, stalk lodging, and leaf chlorophyll content but not for ASI and leaf senescence. Such lack of significant differences for ASI and leaf senescence in the absence of stress has been previously reported (Bänziger et al., 2000; Lafitte et al., 2003). In contrast, there were significant differences under drought for all traits.

The \(h^2\) for grain yield was 0.60 in the control experiment and 0.37 under drought (Table 2). The decrease in \(h^2\) for grain yield under drought corresponded to the decrease in mean grain yields, a relationship that has been previously observed (Bolaños and Edmeades, 1996). Likewise, the \(h^2\) for plant height and stalk lodging was higher in the control experiments than in the drought experiments. The higher \(h^2\) and genetic variance for ASI and leaf senescence under drought stress underscores the need for managed stress environments in selecting for these secondary traits.

**Genetic Correlations among Traits**

In the drought experiments, the strongest genetic correlation (estimated from genetic covariances) was between grain yield and ASI \((-0.77)\) (upper diagonal in Table 3). This result was consistent with many previous findings that ASI is a reliable indicator of drought tolerance (Edmeades et al., 1993; Bolaños and Edmeades, 1993; Bänziger et al., 2000; Messmer et al., 2009). Grain yield under drought was also strongly correlated with plant height, leaf chlorophyll content, and leaf senescence under drought. Grain moisture and plant height had nonsignificant or weak genetic correlations with ASI, leaf chlorophyll content, and leaf senescence. The genetic correlation between grain yield in the control and drought experiments was 0.61, indicating that inbreds with superior testcross performance in nondrought conditions also tend to perform well under drought.
The trait correlations calculated from genomewide marker effects (lower diagonal in Table 3) agreed well with the genetic correlations estimated in the traditional manner from genetic covariances (upper diagonal in Table 3). The sign (positive or negative) of the correlations was the same for all trait pairs except for a few correlations involving plant height and grain moisture. When only the significant ($P = 0.05$) correlations are considered, the correlations based on genomewide marker effects had absolute values ranging from 0.22 to 0.79 whereas the correlations based on genetic covariances had absolute values ranging from 0.14 to 0.77. These results suggest that calculating genetic correlations from genomewide markers effects is a useful alternative to calculating genetic correlations from genetic variances and covariances, particularly for populations for which data on mean performance of inbreds for different traits as well as marker data—but not raw phenotypic data—are archived in databases.

### Efficiency of Indirect Selection through Secondary Traits versus Genomewide Selection

Direct phenotypic selection for grain yield under drought was considered to have a baseline relative efficiency of 1.00 (Table 4). Compared with direct selection for grain yield under drought, indirect selection based on grain yield in the control experiments had a relative efficiency of 0.78, indirect selection based on ASI had a relative efficiency of 1.04, and indirect selection based on leaf senescence had a relative efficiency of 0.98. The standard errors of these three relative efficiencies were large and none of these three relative efficiencies was significantly different from 1.00. The relative efficiency of genomewide selection for grain yield under drought was 1.24 and was significantly different from 1.00 ($P = 0.05$).

The higher $h^2$ of grain yield in nondrought (0.60) (Table 2) than in drought conditions (0.37) and the strong correlation (0.61) (Table 3) between the two traits were not enough to make indirect selection via grain yield in control experiments efficient. Previous studies on the efficiency of selection in nonstress environments to improve abiotic stress tolerance have led to conflicting results: some studies found that indirect selection was inefficient (Atlin, 2003; Lafitte et al., 2003; Venuprasad et al., 2007) whereas other studies found that indirect selection was efficient (Sinebo et al., 2002; Gallais et al., 2008). In breeding for drought tolerance in maize, concerns have been raised regarding selection for germplasm that performs well under drought but carries a yield penalty in well-watered conditions (Bolaños and Edmeades, 1993). In such a situation, performance under both drought and nondrought conditions may need to be considered jointly in breeding for drought tolerance.

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**Table 3. Genetic correlations estimated from genetic variances and covariances (upper diagonal) and correlations based on genomewide marker effects (lower diagonal) for drought-related traits in drought experiments of testcrosses of 238 intermated B73 × Mo17 maize inbreds. Correlations with grain yield in the control (nondrought) experiments are included.**

<table>
<thead>
<tr>
<th>Trait</th>
<th>Grain yield (control)</th>
<th>Grain yield</th>
<th>Moisture</th>
<th>Plant height</th>
<th>Chlorophyll</th>
<th>ASI†</th>
<th>Leaf senescence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grain yield (control)</td>
<td>0.66</td>
<td>0.61</td>
<td>0.31</td>
<td>0.56</td>
<td>0.14</td>
<td>−0.16 NS†</td>
<td>−0.23</td>
</tr>
<tr>
<td>Grain yield§</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moisture</td>
<td>0.23 NS</td>
<td>−0.26</td>
<td></td>
<td>−0.14</td>
<td>0.25</td>
<td>−0.21 NS</td>
<td>0.12 NS</td>
</tr>
<tr>
<td>Plant height</td>
<td>0.34</td>
<td>0.67</td>
<td>−0.07 NS</td>
<td>−0.05 NS</td>
<td>0.34</td>
<td>−0.32</td>
<td>−0.15</td>
</tr>
<tr>
<td>Chlorophyll</td>
<td>−0.06 NS</td>
<td>0.66</td>
<td>−0.28</td>
<td>−0.35</td>
<td>−0.02 NS</td>
<td>−0.28 NS</td>
<td>−0.60</td>
</tr>
<tr>
<td>ASI‡</td>
<td>−0.02 NS</td>
<td>−0.79</td>
<td>0.24</td>
<td>−0.35</td>
<td>−0.02 NS</td>
<td>0.32</td>
<td></td>
</tr>
<tr>
<td>Leaf senescence</td>
<td>−0.29</td>
<td>−0.73</td>
<td>0.02 NS</td>
<td>−0.22</td>
<td>−0.62</td>
<td>0.31</td>
<td></td>
</tr>
</tbody>
</table>

†ASI, anthesis-silking interval.
‡NS, not significantly different from zero at $P = 0.05$. All other correlation coefficients were significant.
§Other than grain yield (control), traits refer to performance in the drought experiments.
¶Standard error.
||

**Table 4. Relative efficiency of indirect selection through drought-related traits and of genomewide selection among testcrosses of 238 intermated B73 × Mo17 maize inbreds in control (nondrought) and drought experiments in Minnesota in 2009 and 2010.**

<table>
<thead>
<tr>
<th>Trait</th>
<th>Relative efficiency of indirect selection†</th>
<th>$r_{mp}$‡</th>
<th>Relative efficiency§</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grain yield (control)</td>
<td>0.78 ± 0.18†</td>
<td>0.48</td>
<td>0.80* ± 0.08</td>
</tr>
<tr>
<td>Grain yield§</td>
<td>1.00</td>
<td>0.46</td>
<td>1.24* ± 0.07</td>
</tr>
<tr>
<td>Moisture</td>
<td>0.48* ± 0.24</td>
<td>0.51</td>
<td>1.08 ± 0.04</td>
</tr>
<tr>
<td>Plant height</td>
<td>0.58 ± 0.28</td>
<td>0.44</td>
<td>1.42* ± 0.11</td>
</tr>
<tr>
<td>Chlorophyll</td>
<td>0.85 ± 0.14</td>
<td>0.47</td>
<td>0.84* ± 0.06</td>
</tr>
<tr>
<td>ASI†</td>
<td>1.04 ± 0.21</td>
<td>0.21</td>
<td>0.31* ± 0.18</td>
</tr>
<tr>
<td>Leaf senescence</td>
<td>0.98 ± 0.17</td>
<td>0.39</td>
<td>0.64* ± 0.05</td>
</tr>
</tbody>
</table>

†Significantly different from a relative efficiency of 1.00 at $P = 0.05$.
‡$r_{mp}$, correlation between predicted genotypic values and observed phenotypic values. All $r_{mp}$ values were significant at $P = 0.05$.
§Relative efficiency of genomewide selection versus phenotypic selection to improve the trait itself.
\*Standard error.
§Relative efficiency of indirect selection to improve grain yield under drought.
†ASI, anthesis-silking interval.
The secondary trait ASI led to the highest relative efficiency (albeit not significantly greater than 1.00) for improving grain yield under drought in this study and previous recurrent selection experiments for drought tolerance in maize have shown a strong reduction in ASI among drought tolerant plants, to the extent that ASI is generally considered by maize breeders as the secondary trait in maize that is most indicative of drought tolerance (Bolaños and Edmeades, 1993; Edmeades et al., 1993; Byrne et al., 1995; Bolaños and Edmeades, 1996; Ribaut et al., 1996). As shown in this study, variation in ASI may not be expressed in control experiments and managed drought conditions are needed to effectively select for reduced ASI.

A selection index could be constructed to combine information from several traits correlated with drought tolerance. For example, selection could be based on both grain yield under drought and ASI. Based on the estimates of genetic and phenotypic variances and covariances for these two traits, a Smith-Hazel index (Smith, 1936; Hazel, 1943) would have the form $I = 0.213 \cdot (\text{grain yield in Mg ha}^{-1}) - 0.150 \cdot \text{(ASI in d)}$, and this index has a predicted relative efficiency (Baker, 1986) of 1.13. On the other hand, results from selection with a Smith-Hazel index in plants have been erratic (Elgin et al., 1970) and plant breeders have generally preferred less formal indices (e.g., base index: Williams, 1962) for combining information for different traits (Bernardo, 2010).

Genomewide selection for drought tolerance would likewise require phenotyping in managed drought experiments, and the per-cycle response to genomewide selection for this trait was predicted to be about 24% higher than the per-cycle direct response (Table 4). In addition, subsequent cycles of marker-based selection would not require managed drought conditions. This feature indicates that much of the advantage of genomewide selection over indirect phenotypic selection for drought tolerance would be in gain per unit time and cost (Bernardo and Yu, 2007; Massman et al., 2012). The current cost of phenotyping a hybrid for drought tolerance at the Becker location is about US$20 per plot whereas the cost per sample of genotyping-by-sequencing is approaching US$20 (Elshire et al., 2011). Given that replication across environments of managed drought experiments is needed (Bruce et al., 2002; Collins et al., 2008), the per-sample cost of phenotyping for drought tolerance exceeds the cost of genotyping.

Furthermore, gains per unit time can be maximized by conducting up to three generations of genomewide selection in 1 yr in greenhouses or year-round nurseries (Bernardo and Yu, 2007; Eathington et al., 2007; Bernardo, 2008). One cycle of testcross phenotypic selection usually requires 2 yr in temperate regions, that is, 1 yr for field evaluations and multiple generations in the second year to recombine the selected individuals or selfed families and to self and testcross plants or selfed families for the next cycle of selection. Therefore, for grain yield under drought stress (relative efficiency of 1.24 with genomewide selection), the cumulative response from three cycles of genomewide selection (in 1 yr) is predicted to be about 3.7 times the gain from one cycle of testcross phenotypic selection (in 2 yr), assuming that per-cycle gains from genomewide selection are maintained across three cycles. On the other hand, results from empirical experiments in maize at the University of Minnesota have suggested diminishing or erratic gains from later cycles of genomewide selection (Massman et al., 2012). While our results in this study suggest that genomewide selection would be superior to indirect selection for ASI, empirical experiments are needed to validate genomewide selection strategies for drought tolerance in maize.

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