Comparison of Full-sib Hybrids and Testcross Progeny Tests for Genomic Prediction and Line x Tester Analysis of Hybrids of two Multiparental Maize Populations

By

Brett L. Burdo

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This dissertation is approved by the following members of the Final Oral Committee:
Shawn M. Kaeppler, Professor, Agronomy
Natalia De Leon, Professor, Agronomy
James M. Johnson, Manager of Breeding Technologies, Agreliant Genetics LLC
Lucia Gutierrez, Assistant Professor, Agronomy
Jeffrey B. Endelman, Assistant Professor, Horticulture

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Chapter 1

Literature Review

Maize breeding has a long and rich history within the United States. C.G. Hopkins started the longest running selection experiment in maize in 1896, the Illinois long term selection experiment for oil and protein content (Hallauer et. al., 2010). The experiment, still ongoing, was also the first application of the progeny test in maize, later known as the *ear-to-row* procedure. In comparison to the earlier procedure of mass selection, the ear-to-row procedure allowed greater replication of the parent under selection and was more effective for selection of genetic effects.

The description of heterosis by George H. Shull (1908) was accomplished through application of this ear-to-row procedure. At the time, inbreeding was a widely observed but poorly understood phenomena, commonly attributed to the injurious effects of inbreeding itself. His experiment involved identifying classes of maize plants from a relatively homogenous population with distinct kernel-row numbers and self-pollinating or cross-pollinating an ear from each class. The selfed and crossed ears were planted in parallel rows. The mode of the kernel row number for the overall population was 14, and the mode of the cross-pollinated plants from each row class regressed towards this number. The mode for the self-pollinated rows of the class of 12 kernel-rows was 10, indicating that instead of selecting on variations of a single type, self-pollination was isolating a type from a heterogeneous population and removing its “hybrid character”. Shull immediately understood the importance of his findings. He suggested that instead of maize breeders focusing on identifying the value of a maize line in its pure state as was common at the time, they focus on the lines value in hybrid combination.

It is hard to overstate the impact of Shull's results for maize breeding. Selection of open-pollinated varieties had been largely ineffectual for increasing maize yield (Crow, 1998). Selection for pure-line performance in hybrid combinations, first as double-crosses (b=63.1 kg/ha per year) and later as single crosses (b=110.4 kg/ha per year), increased rate of improvement for maize yield substantially (Troyer, 1999). At the early stages of maize hybrid breeding, *n* inbred lines were evaluated for their hybrid potential in $n(n-1)/2$ combinations, but as the number of lines increased, evaluating this number of lines became prohibitive (Lopez-Perez, 1979). Davis (1927) first suggested the use of the topcross test, where untested inbreds are evaluated based on their performance when crossed to a common variety. The experiments of (Jenkins and Brunson, 1932) demonstrated the practical utility of this test and led to its widespread adoption. They demonstrated that the yield of inbred lines in a topcross test were correlated with the mean yield of those lines in a diallel series, and suggested that 50% of lines could be discarded based on this test with no risk of losing high performing single crosses. Sprague and Tatum (1942) formalized these and other observations into their concepts of General and Specific Combining Ability. General Combining Ability (GCA) is the average performance of a line in hybrid combination, while Specific Combining Ability (SCA) is the deviation of each hybrid from the expectation of the mean of their parental lines. Through a series of single cross experiments, they demonstrated that SCA was of greater relative magnitude in crosses of selected material, while GCA was greater in crosses between selected lines. Their conclusions were that initial tests can be performed based on top-cross tests when GCA variance is preponderant, followed by single cross tests to identify the most productive hybrid combinations. This strategy is the predominant procedure for maize breeding.

Concurrently with the development of these maize breeding procedures, there were experiments ongoing to interpret the results of these progeny tests in terms of competing theories for the explanation of heterosis. The competing theories were dominance, or the complementation of recessive alleles, and over-dominance where the heterozygote results in larger effects than either homozygote. The dominance hypothesis had strong evidence from decades of mendelian investigations of qualitative traits, while observations of over-dominant loci was rather uncommon. An oft repeated argument against the dominance hypothesis is that if the alleles were simply complementing each other, an inbred line with the performance of a hybrid should theoretically be able to be made. (Jones, 1917) refuted this argument, with reference to the confounding effect of linkage disequilibrium in the manifestation of overdominance, known as pseudo-overdominance. If two tightly linked, classically dominant genes are in linkage-phase repulsion, the measured dominance deviation can be well beyond the effect sizes expected by a single dominant gene.

Different breeding strategies are necessary for both the degree and each mode of action posited to explain heterosis. We currently assume a single reference population in Hardy-Weinberg and linkage Equilibrium (HW-LE) from which all inbred lines are derived, be they testers or the population being tested. Traits within a population that show no or little dominance should show similar breeding values as inbreds, topcrosses, diallel crosses, or factorial experiments. In the context of pure additivity, an inbred test should be the most efficient and reliable estimate of a lines' worth, while a topcross test should provide suitable results, but with σ^2_A reduced by approximately one half. If residual and environmental interactions are not similarly reduced, the reliability of the topcross test will be smaller, but this difference will depend on the traits susceptibility to environmental influence. In practice, some traits such as flowering time and plant height tend to be predicted reasonably well by the mean of their parents (Flint-Garcia et al., 2009). With dominance, a lines' value would be established based on the allelic complementation for deleterious recessives, plus a term for the beneficial alleles that are not necessarily the opposite allelic state of the line it has been crossed to. Compared to pure additivity, an overall increase in the amount of SCA is expected as the lines' value is now dependent on the degree of dominant alleles in the tester that will mask the deleterious effects of recessive alleles in the population being tested (Smith 1986). In this case, topcross tests may be of less value than diallel or factorial crosses, dependent on the level of dominance, and inbred tests should not be considered reliable. With pure over-dominance, the expectation is that line values will be established based solely on their complementation of the allelic status of an opposing inbred line. Any randomly selected inbred line from a single population will have a different set of homozygous alleles which will need to be complemented for maximum heterosis. While this case is admittedly a thought experiment, the idea of a *breeding value* in such a population loses much of its meaning, as heritable genetic effects would be entirely dependent on how well the line complements the homozygous states of the testers it is crossed to. SCA would be the predominant fraction of variance. Assuming the infinitesimal model, where many genes contribute to a trait, a breeder's only option is to thus test lines in many combinations to identify those best hybrids, such as a diallel. While pseudo-overdominance is fundamentally different on a biological level from overdominance, if we can assume no recombination between the dominant genes in repulsion phase linkage, the same testing regime applies as for overdominance.

	Max Hybrid Genotypic value	Best single tester(s)	Best progeny test
Additivity	{AA}	{AA,aa}	Inbred/Topcross
Dominance	{AA,Aa}	{aa}	Factorial
Overdominance	{Aa}	{aa,AA}	Diallel

Table 1 Genotypes of the best performing hybrid, Best single tester, and best progeny test under Additivity, Dominance, or overdominance. This single-locus case assumes fully inbred lines. The best progeny test is defined assuming the more relavent case of multiple alleles segregating in a population in Hardy Weinberg and Linkage Equilibrium.

The problem of selecting for overdominant yield was well recognized by Fred Hull (1945) in his paper on Recurrent Selection for Specific Combining Ability in Corn. I assigned the best progeny test as the one that identifies the best hybrid in a single cycle of selection with no recombination (Table 1). Hull, a proponent of the overdominance hypothesis, suggested recurrent selection in a population would be most efficient when crossed to a common inbred tester, recombined and then crossed to this same inbred tester. While some of the logic may seem paradoxical from the perspective of modern maize breeding:

> "To the extent that excess vigor arises from heterozygotes the best combination must involve average lines. Present highly selected lines may too frequently be fixed AA at the same loci and in that sense be already too good"

The reasoning was sound if overdominance is presumed to be the primary driver of heterosis. Selection based on the mean performance of an inbred crossed to a large number of lines would reach a limit below a line that had the maximum complement of homozygous alleles to another with overdominance. Moreover, his idea of fixing the opposite homozygous alleles responsible for heterosis has ultimately stood the test of time. Comstock, Robinson and Harvey (1949) were influenced by Hull in their paper outlining Recurrent Reciprocal Selection (RRS). They were also aware of the problem of selection in the presence of allelic interactions:

> "In view of the role of specific combining ability in determining the performance of hybrids, it obviously would be desirable if procedures were available for guiding the development of lines in such a way that their combining ability in predetermined combinations would be enhanced."

Their suggestion in was that improvement of two divergent populations should happen concurrently, with the reciprocal population being used in some fashion as a tester. Almost all modern maize breeding can be considered a form of recurrent reciprocal selection. By improving each population based in its progeny test with the reciprocal population, over generations each population will be fixed for the alleles responsible for responsible for heterosis. The result would be that the statistically non-additive variance of biological dominance is made statistically additive, and response to selection should increase. The ultimate biological basis of heterosis was also of less concern when using reciprocal recurrent selection as it could harness overdominant gene action and would tend to fix opposite alleles in the opposing population if dominance were present. The limit of selection would be lower in the case of overdominance, however. While a positive dominant allele fixed in both populations would simply increase the population mean, an overdominant allele fixed in both populations would reduce it.

Several modifications of the initial RRS procedure were proposed in interceding years. Hallauer and Eberhart (1970) introduced Full-sib RRS (FS-RRS), where inter-population improvement is achieved by evaluating paired S_0 families between two populations. Full-sib in this context refers to the progeny test where lines are evaluated based on their performance as “Full-sibs” with another unevaluated line of the reciprocal population. Russell and Eberhart (1975) suggested another modification, where new lines are evaluated based on their testcross performance with inbreds from previous cycles of selection, now commonly referred to as modified Recurrent Reciprocal Selection (mRRS). Full-sib RRS evaluates half as many progeny as mRRS, but at the cost of not allowing the estimation of separate breeding values for the parents of each cross. Selection thus occurs based on the genotypic value of the hybrid, and no transmitting ability is assessed on either parental line. Hallauer and Eberhart saw the benefit in being able to evaluate single crosses immediately, as Full-sib RRS populations would be expected to have twice the genetic variance of the corresponding mRRS population.

Further modifications of the FS-RRS selection procedure have been proposed, such as Doubled Haploid FS-RRS, demonstrated through simulation to increase gain per year over classical FS-RRS (Gallais, 2009). A modification of FS-RRS, S_2 Full-Sib Reciprocal Recurrent Selection (FS-S(2)-RRS), was developed to use inbred phenotypes to overcome the issue of not being able to partition breeding values using FS-RRS. Ordas et al. (2012) incorporated the phenotypes of the S_2 parents of the FS families from classical FS-RRS into a selection index with the hybrid phenotypes and compared gains with this modification to classical FS-RRS from two cycles of selection under optimum conditions and Mediterranean Corn Borer infested conditions. FS-S(2)-RRS led to greater gains from selection under optimum conditions than FS-RRS. Under infestation, two cycles of FS-RRS produced a non-significant decrease in yield from the intial population, while FS-S(2)-RRS was able to maintain it. Viana et al. (2013) demonstrated through simulation that classical half-sib RRS was more efficient for population improvement than FS-RRS precisely because FS-RRS does not allow the partitioning of parental GCAs.

The introduction of BLUP methodologies that utilize the relationships between inbreds has been rapidly integrated into breeding programs worldwide (Bernardo, 1995, 1996a, 1996b, 1996c). Bernardo demonstrated that single crosses from an applied breeding program could be faithfully predicted using covariance matrices derived from pedigree or marker information, that modelling covariance due to dominance was useful when SCA was high, and that predictions suffered dramatically when no parents of the hybrid to be predicted were included in the training data.

The utility of marker-based covariance matrices over those of pedigree is dependent on the population under study. Amongst the factorials of single crosses in Bernardo's initial study using RFLPs, marker-based covariance only represented a slight improvement over pedigree-BLUP. Simulation studies have also shown that when considering factorials among doubled haploids derived from biparental families, significant superiority of markers relative to pedigree based prediction should not be expected (Viana et al. 2017). Marker-based estimates are much more accurate than pedigree in the context of lines crossed by a single tester (Albrecht et al. 2011). Pedigree-based methods in initial stages of selection in a modern breeding program that utilizes doubled haploids derived from bi-parental families can only rely on predicting mean differences across families, as all lines within the same family have the same expected relationship. The ability to estimate relationships between inbreds with molecular markers could greatly increase the practical value of FS-RRS. Where only a single genotypic effect was able to be estimated with classical FS-RRS, substituting genomic relationship matrices (GRMs) for the genotypic identity matrix allows the partitioning of GCA for each parental line, as well as a term for the dominance deviation. While the utility of pedigree-BLUP for evaluation of untested lines is greatest when family sizes are small, G-BLUP can estimate relatedness in cases where pedigree relationships have been abolished, which was often the case in reciprocal recurrent selection schemes during between cycle intermating.

Thesis work

In this thesis, I evaluate two selection strategies for the initial evaluation of maize inbred lines. The lines that were evaluated are doubled haploids (DH) extracted from six-line synthetic populations derived from parents representing the Stiff Stalk and Iodent heterotic groups. Lines were either testcrossed to an inbred founder of the opposite group, as would be common practice in the modified RRS programs commonly used by maize breeding programs today, or randomly paired as in FS-RRS. Each population was evaluated in separate randomized complete block design experiments in 2014 and 2015 at two locations with two reps at each location, for grain yield and six ancillary traits. In the first chapter, G-BLUP models either including or excluding dominance were compared for their efficiency in partitioning GCAs for the inbred lines in the randomly-paired population. I also compared cross-validation accuracies within each population. The second chapter focused on Line x Tester analyses of selected and unselected lines from each of the Stiff Stalk and Iodent DH populations.

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Chapter 2

Genomic prediction of maize hybrid performance using testcrosses versus random pairs of untested lines

Abstract

Hybrid maize breeding is currently primarily a two-step process. New inbred lines are identified based on testcross performance, usually using multiple testers. Once the new inbreds are advanced, new hybrid combinations are identified from the pool of available inbreds. Using this process, it is possible that a high-performing hybrid is missed because one or both potential parents do not advance through the first phase of screening. In this experiment, we compared traditional and genomic GCAs estimated from models based on the traditional testcross advancement process versus using information from new untested hybrids produced by randomly crossing pairs of untested inbred lines, deemed Full-Sib (FS) hybrids. We used two six-parent synthetic populations from the Iodent and the Stiff Stalk heterotic groups. Double haploid (DH) lines were extracted and testcrossed to a founder of the opposite pool or intercrossed as random pairs. Hybrids were evaluated for grain yield and 6 ancillary traits at two locations in 2014 and 2015, with two replications per location. 32% of markers in the FS hybrids deviate from Hardy-Weinberg equilibrium at .001 significance, the vast majority towards excess heterozygosity. Marker based variance component estimates within the FS hybrid population that account for deviations from Hardy-Weinberg equilibrium, suggest that the variance present in this population is predominantly additive. Coincidence of selection of the top 25 lines based on traditional GCAs for grain yield within the testcross and FS hybrids was 48% for the Stiff Stalk and 11% for the Iodent. Coincidence of selection using an additive model for genomic GCA estimation and testcross traditional GCA estimation was higher, at 56% for parental DH lines from either heterotic group. Partitioning dominance variation in the model increased coincidence of selection to 62% for the Stiff Stalk parents but did not increase coincidence beyond 56% for the Iodent. General Combining Ability (GCA)-based prediction accuracy of the FS hybrids based on the testcrosses was 0.73 and could not be improved with genomic prediction of the hybrid values. 10-fold cross validated prediction of the grain yield of hybrids of untested DH lines was 0.45 and 0.48 under an additive and additive + dominance G-

BLUP model trained on the FS hybrids, respectively, and 0.49 and 0.48 when trained on the testcrosses. Prediction of grain moisture, test weight, plant height and ear height were worse when training on the intercrossed population, but better for prediction of flowering traits. Incorporating marker information does allow for greatly improved GCA estimation from the randomly paired population, but this is mostly due to accurate partitioning of additive effects, rather than an enhanced capacity to capture non-additive effects.

Introduction

Prediction of maize hybrid performance has been a goal of breeders almost since the beginning of hybrid breeding. Early in the hybrid breeding era, correlation studies demonstrated that parental inbred yield is a relatively poor predictor of hybrid yield. Davis (1927) first demonstrated the topcross method of crossing unevaluated lines to an established variety as an efficient means of early generation testing. As compared to the earlier method of estimating an inbred's worth as its average performance in a series of single crosses with multiple testers, the topcross (testcross) method was about as accurate, with the considerable benefit of allowing untested material to be wind pollinated in an isolation, and the possibility of commercial hybrids to be identified early on in the testing process (Jenkins and Brunson, 1932). Sprague and Tatum (1942) formalized these and other observations into the concepts of General Combining Ability (GCA) and Specific Combining Ability (SCA). GCA is the average performance of a line in all of its hybrid combinations, while SCA is the deviation in hybrid performance from what would be expected based on the sum of the GCAs of its parental lines. They observed that GCA is the largest proportion of genetic variance in single crosses of unselected material, while SCA variance was larger in single crosses of lines that had undergone previous selection. Their suggestion of a two-stage breeding program, where initial testing based on testcrosses is followed by later stage testing of new inbreds as numerous single crosses with multiple testers, is the predominant method used in maize breeding to date.

The long history of the testcross method in maize breeding is a testament to its utility in early stage testing. A longstanding issue, though, is the choice of appropriate testers. Untested materials are often crossed to a single or few testers for initial selection, and therefore GCA and SCA effects are dependent on the tester used. It is critical that the tester is representative of the potential suite of parents that are anticipated to be available to create new hybrids. As the proportion of SCA to GCA increases, the effectiveness of the testcross method for selection decreases.

Comstock et al. (1949) suggested Recurrent Reciprocal Selection (RRS) as a method for improvement of both GCA and SCA in crosses between two populations. Hallauer and Eberhart (1970) introduced Full-sib RRS, where inter-population improvement is achieved by evaluating paired S_0 families between two populations. Russell and Eberhart (1975) suggested another modification, where new lines are evaluated based on their testcross performance with inbreds from previous cycles of selection. In terms of population improvement, both methods attempt to utilize non-additive genetic variation for the improvement of the inter-population cross as opposed to the lines themselves. Inter-population testcrosses provide GCA estimates, but don't allow for partitioning of SCA effects. Full-sib RRS requires half the number of hybrids for evaluation as testcrossing and allows early evaluation of single cross hybrids, but at the cost of not being able to partition the breeding values of either parent in addition to any estimation of SCA. Simulation studies have shown Full-sib RRS and selection on the genotypic value of the hybrid to be inferior to selection based on parental GCA in pedigree breeding of popcorn (Viana et al. 2013).

Modern maize breeding has changed significantly since the widespread application of doubled haploid (DH) technology, and the introduction of genomic selection, spurring interest on advancing breeding methods and incorporation of marker information (Meuwissen *et al.*, 2001). Here, we will revisit the ideas presented by Hallauer and Eberhart (1970) designed to maximize utilization of SCA and compare them with the established method of testcrossing. This study uses hybrids of DH lines as the experimental unit as opposed to S_0 x S_0 full-sib families. Simulation studies have shown with off-season nurseries expected genetic gain of DH-FS-RRS is 38% greater than using traditional S_0 x S_0 families (Gallais, 2009). The incorporation of marker information additionally allows us to estimate parental GCAs within a FS-RRS population, which was not possible before. Markers also allow us to assess the relative amount of additive and dominance variation and determine the proportion of the dominance variation that can be captured in our prediction models. This study utilizes DHs derived from two six-parent synthetic populations from the Stiff Stalk and Iodent heterotic groups. We testcrossed these DH lines to a founder of the reciprocal population and produced hybrids from random pairs of unevaluated DH lines between populations, deemed Full-Sib (FS) hybrids. Our objectives were (I) compare GCA-based and genomic prediction of intercrossed hybrids and parental GCAs (II) compare prediction accuracy of untested DH lines, training on either testcrosses or FS hybrids (III) compare prediction accuracies of additive models with those including dominance (IV) estimate the genomic additive and dominance variance within the FS hybrids.

Materials and Methods

Quantitative Genetic Foundation of the Crossing Strategy for Hybrid Breeding

We assume the synthetic populations from which DH lines are extracted are randomly mated populations in Hardy-Weinberg and in Linkage Equilibrium (HW-LE). From this population, we assume lines are extracted without selection altering gene frequencies from the base synthetic. Considering the case of two loci, A_i (i = 1, …i) and B_j (j = 1, …j), segregating independently within a testcross population and ignoring epistasis and higher order interactions, the testcross value Y_{ij}^T of a line with genotype A_iB_j/A_iB_j can be expressed as:

$$Y_{ij}{}^{T} = \mu_T + \alpha_{Ai}^{T} + \alpha_{Bj}^{T} + \cdots$$

Where:

μ_T is testcross mean performance

α_{Ai}^{T} is the additive effect of allele i at locus A

α_{Bj}^{T} is the additive effect of allele j at locus B

When HW-LE holds, the two locus case represented above extends to an arbitrary number of loci. In the context of a single tester, these additive effects are completely confounded with dominance effects.

These allelic effects, summed over all alleles in the testcross population, can be represented on a line basis as

$$Y_i^{\;T} = \mu_T + \{GCA_{DHi} + SCA_{DHi\,x\,T}\}$$

Where the GCA effect of the DH line cannot be resolved from the SCA effect of the line by tester.

Now we will consider the case of the FS Stiff Stalk x Iodent hybrids, using the same nomenclature and assumptions for the hybrid population.

$$Y_{ij}^{SSxIO} = \mu_{SSxIO} + \alpha_{Ai} + \alpha_{Bj} + d_{Ai} + d_{Bj} + \ldots$$

And

$$Y_{ij}^{\;SSxIO} = \mu_{SSxIO} + \{GCA_{DHSSi} + GCA_{DHIOj} + SCA_{DHSSixDHIOj}\}$$

Pairing lines 1:1 does not allow the estimation of the GCA effect of either line or their SCA with traditional phenotypic estimation. Pedigree structure was eliminated by full intermating and only selection on the genotypic effect of the hybrid is possible. Incorporating genomic covariance however, does allow partitioning of additive effects of the parents, with the added potential to partition dominance in this population.

Germplasm

The populations used in this study are two six-parent synthetic populations, each with founders chosen from the SS and IO maize heterotic groups (Table 1). These populations were inter-mated for three generations before DHs were derived courtesy of AgReliant Genetics (AgReliant Genetics, LLC. Westfield, IN, USA). Hybrids used in this study included 123 Stiff Stalk DH lines crossed by inbred line PHG72, 166 Iodent DH lines crossed by inbred line PHB47, and 144 FS hybrids by pairing SS and IO DH lines. The complete set of lines used in this study were genotyped and evaluated for grain yield and six ancillary traits. Each IO DH in the randomly paired population was observed once, whereas 19 SS DHs were used in two crosses in the randomly paired population. A total of 95 SS and 109 IO lines were present in both the FS and testcross populations.

Stiff Stalk		Iodent	
Founder	Pedigree	Founder	Pedigree
B73	BSSS	PHN11	PH806 X PH207(2)
B84	BS13 (S2) C0	PH207	PHG3BD2 X PHG3RZ1
PHJ40	PHB09 X PHB36	PHG29	PH806 X PH207(2)
LH145	A632Ht x CM105	PHG35	PHG3BD2 X PH595
NKH8431	NK377 X NKB386 X NK347	PHG50	PH848 X PH207
PHB47	SD105 X B37(3)	PHG72	PH891 X PH207

Table 1. Synthetic population founders, and their immediate pedigrees. BSSS = Iowa Stiff Stalk Synthetic, BS13 = Iowa Stiff Stalk Synthetic Derivative.

Genotypic data

The genetic markers used in this study were generated using the Illumina Maize SNP50 single nucleotide polymorphism (SNP) chip (Ganal et al. 2011). DNA extraction and marker generation assays were done by the University of Wisconsin - Madison Biotechnology Center (Madison, Wisconsin, USA) according to the manufacturer’s protocols (Illumina Inc., San Diego, California, USA). Markers were evaluated across an initial set of 289 DH lines plus the founder parents, and those markers with greater than 10% missing data, greater than 5% heterozygous calls, or less than 2.5% minor allele frequency (MAF) were removed from the data set. DH lines with >10% missing data or >5% heterozygous calls were then removed. Remaining heterozygous SNPs were then called as missing values, and missing values were imputed with the mean of the population, calculated separately for the SS and IO lines. In total, 33,902 polymorphic markers remained; 29,823 within the SS DH population and 18,247 within the IO DH population.

Experimental Design

Each experimental population was evaluated in separate blocks in 2014 and 2015 in a randomized complete block design with two replications at the University of Wisconsin – Madison, West Madison and Arlington Agricultural Research Stations. The combination of year and location are considered trials. The fields used were planted with soybeans the previous year and prepared using conventional tillage. Pre-planting nitrogen was applied as granular urea at a rate of 110 lbs/acre assuming a credit of 40 lbs/A N from the previous soy crop. Lorsban, an insecticide, was applied at 8 oz/ 1000 ft. A mixture of Simazine (16oz/acre), Callisto (5oz/acre), and Dual II-Magnum (24oz/acre) were used for pre-emergence weed control. The soil type at both locations is Plano silt loam. Hybrids were trialed in two row plots with a spacing of 0.79 m between rows at a density of 78,200 plants ha^{-1}. Seven traits were measured in the hybrids. Grain yield (GY) was the primary trait and is reported as a whole plot measurement (Mg/ha normalized to 15.5% grain moisture). Plant height (PH) and ear height (EH) are the average of three representative plants per plot, with EH measured as the distance from the soil surface to the node subtending the ear and PH measured from the soil surface to the ligule of the terminal leaf (cm). Male and female flowering were measured as growing degree days from planting to 50% plot anthesis and silking (GDDAnt, GDDSilk, growing degree days), respectively. Growing degree days were calculated as

$GDD = \sum\left(\frac{Tmax+Tmin}{2} - 50°F\right)$, where Tmax and Tmin are the maximum and minimum daily temperatures in Fahrenheit. On those dates that the temperature exceeded 86° F or was lower than 50° F, Tmax and Tmin were set to those respective values. Grain moisture (GM) was measured at the plot level as percent of harvest weight (%), and grain test weight (TW) was measured at the plot level (kg/hL). Plots with realized stands of less than 38,100 plants/ha were treated as missing. Plots with GM less than 10% or greater than 35% were outside of the range of the moisture sensor and were discarded. After data cleaning, the mean number of replications per genotype was 7.8, equivalent to 2% missing data at the plot level.

Each testcross and the FS hybrid population were grown in separate locations of the same field and analyzed separately with a two-stage model, where spatial correction within locations occur at the first stage, and Genotype within trial effects are used as response variables in the second stage model and all downstream analyses. All phenotypic analyses and predictions were carried out in ASReml-R (Butler et al. 2009).

$$y_{ijklm} = Rep_{ik} + D^{Trial}\{G_{ij} + Row_{il} + Col_{im} + e_{ijklm}\} \tag{1}$$

Where y_{ijklm} is the plot entry, $D^{Trial} = \begin{pmatrix} \sigma^2_{T1} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & \sigma^2_{Ti} \end{pmatrix}$ is the diagonal variance structure to estimate independent variances for genotypes, rows, columns and errors within trials, G_{ij} is the random effect of the jth genotype within the ith Trial, Rep_{ik} is the fixed effects for the kth Rep within the ith Trial, and Row_{il} and Col_{im} are the and the lth and mth random effect for rows and columns within the ith trial. $e_{jklm(i)}$ is the residual, which was independent among trials and modelled within trials as a separable first order autoregressive process; $\mathrm{AR1}_{(\mathrm{Row})} \otimes \mathrm{AR1}_{(\mathrm{Col})}$. Considering genotype within trial effects as random within the first stage led to differential shrinkage of genotypic values within each trial, shrinking the contributions of less reliable sites in the second stage analysis. We compared these results with considering genotypes as fixed in the first stage, the methods provided highly correlated estimates of genotypic effects, all trait estimates were from 0.98 -0.999 correlated.

$$y_{ij} = u + T_i + G_j + e_{ij} \tag{2}$$

Where y_{ij} was the vector of Genotype with Trial effects, u was the overall mean, T_i was the fixed effect of trials and G_j modelled the genotypic effect, and e_{ij} was the error, confounded with the genotype x trial interaction. Phenotypic reliabilities for each trait were derived from equation 2 as $r_i^2 = 1 - \frac{\mathbf{PEV}_i}{\sigma_G^2}$ (Mrode 2005). While reliability is a line specific parameter, it is equivalent to the broad-sense heritability if the data is completely balanced. The BLUPs of the genotypic effect from Equation 2 represented the pseudo-true genotypic values for each population.

Marker effects Models

Genomic predictions were calculated with equation (2), but with one or several genomic covariance matrices replacing the assumed identity matrix for the genotypic effect. The additive $\mathbf{G_A}$ matrices were calculated according to VanRaden (2008) method 1. The dominance matrix, $\mathbf{G_D}$ was calculated according to (Su et al., 2012), which is orthogonal to the additive matrix as calculated by Van Raden under HW-LE.

For the estimation of additive and dominance variance within the randomly-paired population, we compared three methods for constructing additive and dominance relationship matrices, the methods in Su et al. (2012), the breeding parameterization of (Vitezica et. al., 2013), and the Natural and Orthogonal Interactions (NOIA) matrices (Vitezica et al. 2017). The breeding parameterization of Vitezica's **D** parameterizes the Dominance relationship matrix as in the classical context of dominance as deviation from breeding value, as opposed to the parameterization in Su et al. that parameterizes dominance as the deviation from the additive genotypic effect. Both parameterizations assume HWE, which is violated within our FS Stiff Stalk x Iodent population. NOIA matrices do not rely on the assumptions of Hardy-Weinberg equilibrium for partitioning of interaction variances, which are required for accurate partitioning of variance components with the other methods. We tested the proportion of loci not in HWE using the R package HWxtest (Engels 2016).

Prediction Scenarios

Four prediction scenarios were compared (Table 2)

Prediction Scenario		**Model**
Overall		Y=Zb+G+e
		Where
(V1)	(A)	$G= G_A$
	(A+D)	$G= G_A+G_d$
(V2)	(A)	$G= G_{AStiffStalk}+G_{AIodent}$
	(A+D)	$G= G_{AStiffStalk}+G_{AIodent}+G_{Dhybrids}$
(CV1)	(A)	$G= G_A$
	(A+D)	$G= G_A+G_d$
(CV2)	(A)	$G=G_A$
	(A+D)	$G= G_A+G_d$

Table 2. Prediction equations for G-BLUP models used in our study. (V1) Genomic covariance matrices were considered as the (A) additive or (A+D) Additive and Dominant covariance between all hybrids under study. (V2) Genomic covariance matrices were (A) the additive covariance between the Stiff Stalk parental lines and the Iodent parental lines, or (A+D) the additive covariance between the Stiff Stalk parental lines, the Iodent parental lines, and the dominance covariance among all hybrids. For (CV1) and (CV2), genomic covariance matrices were of the (A) additive or (A+D) additive and dominance covariance of the hybrid populations under study.

In the overall model Y is the vector of phenotypes, Zb is the vector of fixed effects, G are the genetic effects, replaced by one or several genomic relationship matrices such that any $G \sim N(0, \hat{g}\sigma^2)$, and $e \sim N(0,\mathbf{I}\ \sigma^2_e)$.

Validation 1 (V1)

As an operation analogous to phenotypic selection in pedigree breeding, we report the correlation of the paired single cross phenotypic BLUPs with the mid-parent of the testcross phenotypic BLUPs. To assess if exploiting genomic relatedness information is of utility in such a scenario, we also report the accuracy of genome based-hybrid prediction of all single crosses with all testcross data as the training set, considering either **(A)** additive genomic covariance among all crosses or **(A+D)** additive and dominance covariance among all crosses. Significance of differences in predictive ability were assessed by Williams t-test for dependent correlations with the R package cocor (Diedenhofen and Musch 2015)

Validation 2 (V2)

To assess whether genomic information would enable more accurate prediction of parental GCAs from the Stiff Stalk x Iodent paired crosses, we evaluated the correlation between parental testcross phenotypic GCA estimates and genome estimated GCAs. The genomic GCAs were predicted using additive covariance among the parents, with separate relationship matrices, $\mathbf{A}_{io}$ and $\mathbf{A}_{ss}$ for the Iodent and Stiff Stalk parents, respectively. Partitioning of an SCA effect was not possible for the phenotypic GCAs, as each Iodent line was observed once. The **(A)** model for **(V2)** only partitioned the genetic variance of the FS hybrids into $\mathbf{A}_{io}$ and $\mathbf{A}_{ss}$ components, while the **(A+D)** model partitioned $\mathbf{G}_{D}$ as well. Accuracy for the **(A+D)** model was considered as the correlation between the phenotypic GCA estimate and the genomic GCA, the dominance covariance was considered residual and not included in the predictions. Significance was again assessed by Williams test.

Cross Validation 1 (CV1)

Genomic prediction within each population was carried out using 10-fold cross validation. Each prediction fold was stored, and reported correlation calculated on the entire population. Each population was sampled to be as large as the smallest population, which was the Stiff Stalk x PHG72 (n=123). Sampling was repeated for 10 cycles. Only **(A)** could be meaningfully modelled within the testcross populations, while both the **(A)** and **(A+D)** models were fit to the FS hybrids.

Cross Validation 2 (CV2)

To compare prediction of untested DH crosses with populations of either paired single crosses or testcrosses, we sampled the paired single cross population such that no hybrid shared a parental DH with another single cross in the estimation set. We then calculated the 10-fold cross validation accuracy of the single cross population with the remaining parents evaluated as parental testcrosses or single crosses. Sampling of the lines was repeated for 10 cycles. Both the **(A)** and **(A+D)** models were compared for **(CV2)**. Significance was assessed by corrected repeated k-fold cv test (Bouckaert and Frank 2004).

Results

Genetic data

Allele frequencies at the genetic marker loci was consistent with six founder parents with peaks near 0.17, 0.33, and 0.50. (Figure 1). A small number of loci had unexpectedly low minor allele frequencies within the Iodent DH set, which we suspect was due to introgressions from the haploid inducer lines. The allele frequency within the Stiff Stalk population is close to uniform, while the Iodent population is skewed further left due to the large contribution of PH207 in the pedigrees of the Iodent lines. Intra-chromosomal LD decays slowly within the Iodent DH set, (r2<0.3) at 5 Mb, and more rapidly within the Stiff Stalk, (r2<0.3) at 1 Mb (Figure 1B), consistent with the close pedigree relationship of most parents in the Iodent synthetic.

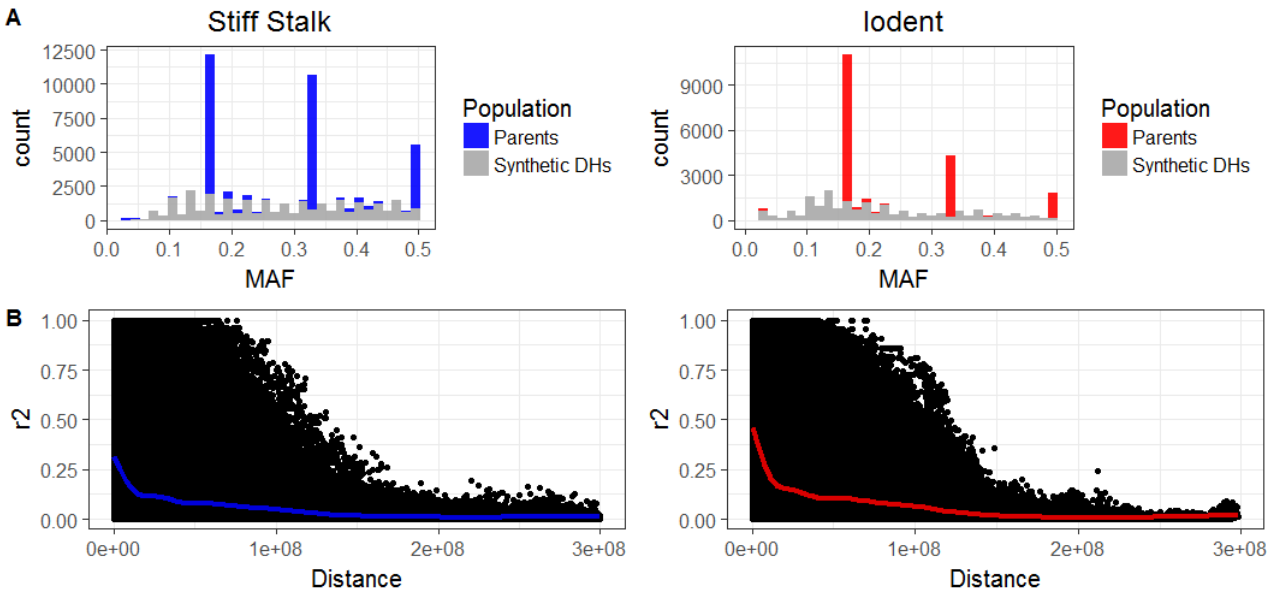

Figure 1. (A) Minor allele frequency distributions for the Stiff Stalk and Iodent synthetic doubled haploids (DHs), and their parents. (B) Local Linkage Disequilibrium (LD) for each population, calculated as the r^2 between all SNPs on the same chromosome.

Phenotypic reliabilities and marker-based variance components

Reliabilities for all phenotypes are moderate to high, ranging from 0.66 for grain yield in the Iodent testcross population to 0.92 for test weight in the intercross population (Table 3). Reliabilities across populations generally follow patterns of variation consistent with the relationship of founder parents of the synthetic populations (Table 1) and crossing strategy. The IO synthetic is the most related including founder PH207 as one of the six parents and an additional four lines with PH207 as one of the progenitors of the six parents. The Stiff Stalk population is substantially more diverse, and the FS hybrids the most diverse. σ^2_G in the FS hybrids is greater than the sum of σ^2_G for both testcross populations across all traits measured.

Traits		Iodent x PHB47	Stiff Stalk x PHG72	Stiff Stalk x Iodent
GM	σ^2G	1.02	1.76	4.27
	σ^2e	0.71	1.11	1.85
	r^2	0.85	0.86	0.90
GY	σ^2G	0.16	0.59	0.82
	σ^2e	0.34	0.67	0.80
	r^2	0.66	0.77	0.80
TW	σ^2G	0.59	2.02	2.91
	σ^2e	0.66	1.13	0.94
	r^2	0.78	0.87	0.92
PH	σ^2G	15.16	46.12	71.53
	σ^2e	14.71	22.12	31.76
	r^2	0.80	0.88	0.90
EH	σ^2G	11.88	51.91	86.41
	σ^2e	16.81	25.72	35.81
	r^2	0.73	0.88	0.90
GDDAnt	σ^2G	138.13	219.72	491.33
	σ^2e	69.10	118.25	128.63
	r^2	0.80	0.78	0.88
GDDSilk	σ^2G	165.0	346.91	667.52
	σ^2e	114.57	197.29	162.94
	r^2	0.74	0.77	0.89

Table 3. Variance components and mean reliabilities for the phenotypes collected on the hybrid populations under study. GM = Grain Moisture, GY = Grain Yield, TW = Test Weight, PH = Plant Height, EH = Ear Height, GDDAnt = Growing Degree Days to Anthesis, GDDSilk= Growing Degree Days to Silking.

For the FS hybrid population, 10,778 or 32% of markers deviate from HWE at a significance level of 0.001 (Figure 2). An additional 9,982 markers are fixed in one population but segregate in the other. With the traditional genotypic relationship matrices, assuming HWE, the off-diagonal elements of the additive and dominance matrices have a Pearson correlation of 0.80, an extreme lack of orthogonality. The classical partioning of Vitezica (2013) reduces this correlation to 0.39, and the correlation of the off-diagonals of the NOIA matrices is much lower, at 0.25.

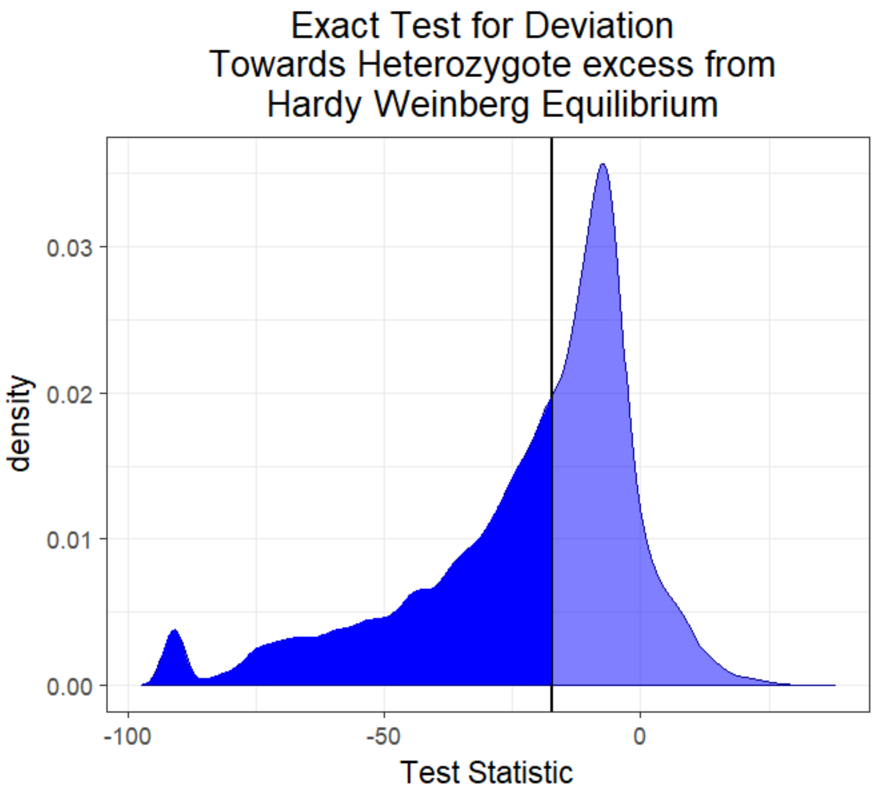

Figure 2. Test statistic distribution for Exact Test for deviation from Hardy-Weinberg Equilibrium within the Stiff Stalk x Iodent FS crosses. Highlighted region is density of marker test statistics that deviate towards heterozygote excess with a P-value >0.001.

The partitioning of additive and dominance covariance in the FS hybrid population is presented in Table 4. All models give almost equivalent estimates of error variance, but the ratio of dominance variance to additive variance is always higher when HWE is incorrectly assumed. In the case of grain yield, the dominance variance component is more than twice the additive with the genotypic parameterization of Su et al. (2012), dominance variance is one third of the additive with Vitezica's **D**, and one seventh with NOIA. The dominance genetic variance is always inflated when HWE is incorrectly assumed.

		Su et al., 2012		Vitezica et al., 2013		NOIA	
Trait	component	σ^2	SE	σ^2	SE	σ^2	SE
GY	σ^2_A	0.26	0.43	0.85	0.29	0.71	0.18
	σ^2_D	0.63	0.33	0.26	0.22	0.11	0.11
	σ^2_e	0.80	0.05	0.80	0.05	0.81	0.05
GM	σ^2_A	2.40	1.91	3.67	1.33	2.94	0.85
	σ^2_D	2.78	1.37	2.25	1.09	1.26	0.60
	σ^2_e	1.88	0.13	1.87	0.13	1.87	0.13
TW	σ^2_A	3.37	1.12	3.66	0.81	2.72	0.54
	σ^2_D	0.58	0.68	0.44	0.49	0.25	0.26
	σ^2_e	0.95	0.06	0.95	0.06	0.94	0.06
PH	σ^2_A	128.43	44.50	131.11	31.51	95.81	20.61
	σ^2_D	7.98	26.02	6.94	18.51	4.38	9.80
	σ^2_e	31.56	2.15	31.55	2.15	31.55	2.15
EH	σ^2_A	132.37	49.63	148.53	20.47	108.52	14.97
	σ^2_D	10.19	29.71	0.00	0.00	0.00	0.00
	σ^2_e	35.49	2.42	35.52	2.42	35.54	2.42
GDDAnt	σ^2_A	357.43	270.81	461.89	183.60	393.14	117.19
	σ^2_D	356.07	194.60	333.77	157.27	174.15	84.29
	σ^2_e	127.27	15.23	125.73	15.00	125.86	15.02
GDDSilk	σ^2_A	506.66	348.75	733.56	241.43	623.31	156.58
	σ^2_D	381.57	242.90	268.24	182.21	111.04	91.96
	σ^2_e	164.53	19.43	164.10	19.38	164.54	19.45

Table 4. Additive, dominance, and residual variance components estimated in the FS hybrid population with the genotypic parameterization of Su et al. 2012, Vitezica et al. 2013, or Natural and Orthogonal Interactions (NOIA) matrices. GM = Grain Moisture, GY = Grain Yield, TW = Test Weight, PH = Plant Height, EH = Ear Height, GDDAnt = Growing Degree Days to Anthesis, GDDSilk= Growing Degree Days to Silking.

Empirical and predicted hybrid performance

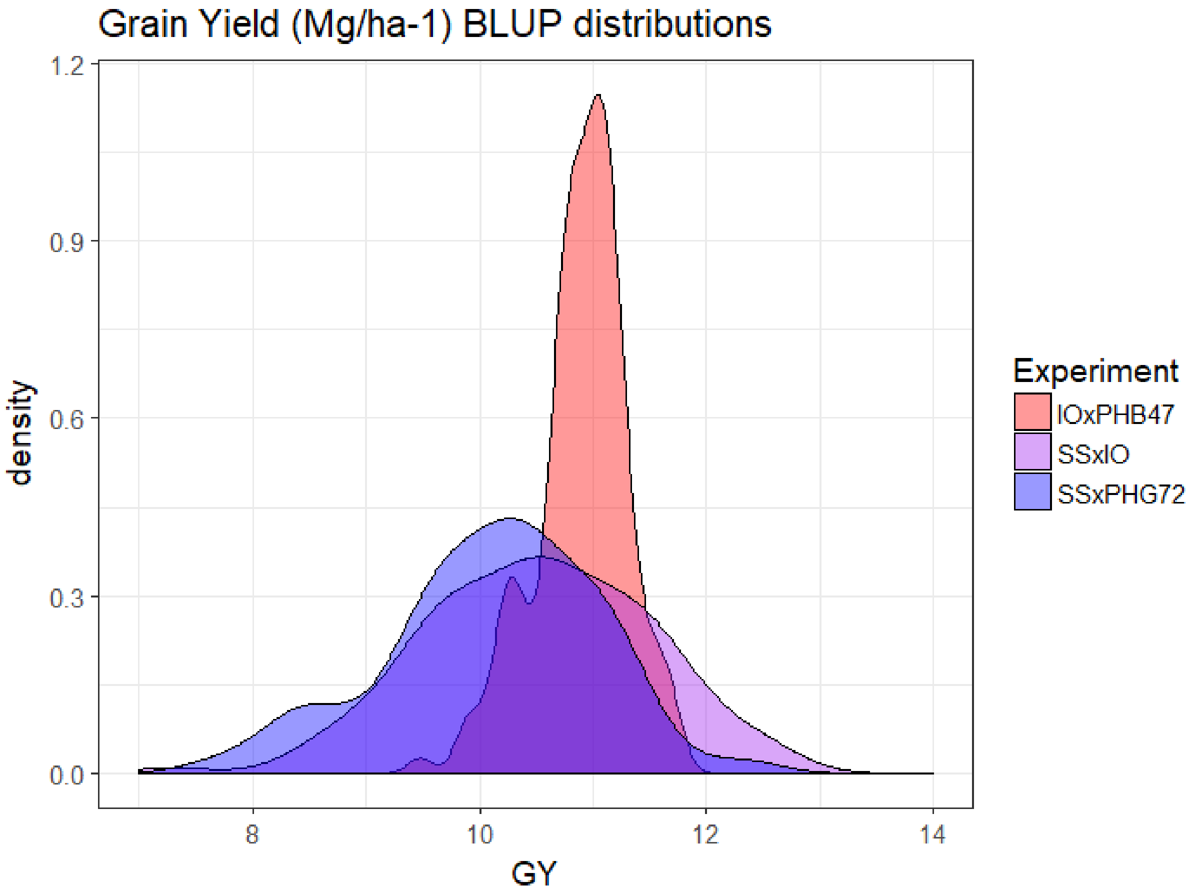

Figure 3. Distribution of Grain Yield (GY) genotypic BLUPs for the Iodent x PHB47 testcrosses (IOxPHB47), SS x PHG72 testcrosses (SSxPHG72), and SSxIO FS hybrids.

Context for our study included the concern that the current two-step inbred selection and hybrid identification process may exclude high-performing hybrids that would be produced from DH lines that did not reach the top of the inbred selection stage. DH lines were ranked based on their testcross performance and compared to the paired hybrids for grain yield. As a measure of comparing the similarity of selection between two models, we calculated the coincidence of selection, or percentage of lines that would be selected with either advancement procedure. Coincidences of selection for the top 25 based on phenotype alone were 48% for the Stiff Stalk lines and 16% for the Iodent parents, indicating that the top hybrids in the FS hybrids often did not come from inbreds that would have been in the top 25 of either testcross population. Considering genotypic values, out of the top 25 hybrids based on their phenotypic BLUPs of grain yield, 20 were from the FS hybrids, 2 were from the Stiff Stalk x PHG72 testcrosses, and 3 were from the Iodent x PHB47. Figure 3 illustrates this attractive property of FS-RRS, that for any population to be improved in a reciprocal fashion, random pairs of lines can always be expected to have at least the sum of the variance of the parental testcross families.

Incorporating genome-based covariance increased this to 56% coincidence between testcross and FS progeny tests for both the SS and IO DH sets. Partitioning dominance variation in the model increased coincidence of selection to 62% for the Stiff Stalk parents but did not increase coincidence beyond 56% for the Iodent. Phenotypic GCAs of the parents of the FS hybrids cannot partition SCA effects, or even the Stiff Stalk and Iodent GCA effects from each other, while the genomic GCAs of the parents can be partitioned with much greater accuracy.

Comparison of genomic prediction using testcross versus randomly paired populations

Prediction scenario V1, where FS hybrids are predicted with the mid-parent phenotypes of their parental testcross lines, generally follow the phenotypic accuracies (reliabilities) of the phenotypes (Table 5). The high mid-parent accuracies are consistent with a low proportion of SCA between the testcross and random intercross populations. Genomic information did not improve the already high mid-parent prediction accuracies, and hybrid prediction with additive and dominance covariance resulted in insignificantly lower accuracies than GCA-based prediction for four traits, including grain yield.

Scenario V2, where testcrosses were predicted with parental line breeding values estimated from the FS hybrids shows a much greater benefit from incorporation of genomic information, especially within the Iodent population. The EBV of the Iodent DHs would be expected to be worse than the Stiff Stalk, as the Iodent DH lines contribute less to the GCA variance. Additionally, partitioning out the dominance covariance with the (A+D) model further increased the accuracy of GEBV for GY and PH for both testcross populations, and flowering traits within the Iodent. Only the GM and GY breeding values of Iodent were significantly greater than phenotypic estimation, and this was regardless of utilizing the (A) or (A+D) model. This suggests there is dominance variance for some of the traits in the intercrossed set that our genomic prediction model can explain that is not estimated based on testcross information.

	Hybrid Prediction	Model	GM	GY	TW	PH	EH	GDDAnt	GDDSilk
V1	Phenotypic	Midparent	0.86	0.73	0.81	0.82	0.83	0.67	0.65
	Genomic	(A)	0.85	0.73	0.82	0.82	0.85	0.70	0.65
		(A+D)	0.84	0.71	0.82	0.80	0.80	0.70	0.65
V2	GCA								
	Stiff Stalk (n=95)	Phenotypic	0.71	0.63	0.67	0.70	0.74	0.64	0.56
		GEBV (A)	0.74	0.66	0.70	0.69	0.73	0.62	0.57
		GEBV (A+D)	0.74	0.70	0.71	0.71	0.73	0.62	0.57
	Iodent (n=109)	Phenotypic	0.53	0.40	0.54	0.55	0.43	0.23	0.26
		GEBV (A)	0.70**	0.53*	0.56	0.55	0.49	0.28	0.37
		GEBV (A+D)	0.66**	0.55*	0.55	0.55	0.50	0.32	0.373

Table 5. Prediction scenarios and accuracies of prediction. (V1) Prediction of FS hybrids with testcross data, based on midparent or genomic estimation. (V2). Correlation between testcross phenotypic values and GCA based or genome based prediction of parental GCAs in the intercrosses, (A) without accounting for dominance or (A+D) accounting for dominance. Significance was assessed via Williams T-test (*=.05,**=.01). GM = Grain Moisture, GY = Grain Yield, TW = Test Weight, PH = Plant Height, EH = Ear Height, GDDAnt = Growing Degree Days to Anthesis, GDDSilk= Growing Degree Days to Silking.

Estimated intra-population accuracies (CV1) were moderate across most traits, except for GDDAnt within the Stiff Stalk testcrosses, which was low at 0.222 (Table 6). While the prediction accuracy of the Iodent testcrosses were lower than the Stiff Stalk testcrosses for all traits but GDDAnt, the prediction accuracy was higher for GM, PH, EH, and GDDAnt. The estimation of dominance for the FS hybrids increased the GY accuracy from 0.537 to 0.565, but decreased accuracy of prediction for PH, EH, GM, GDDAnt and GDDSilk.

Prediction of novel FS hybrids (CV2) differs from (CV1) Stiff Stalk in training population size, but also by removing any parents that are shared between the training and validation set in the CV2.

Accordingly, the accuracies are always lower within the CV2 set of FS hybrid predictions. Comparing the accuracies of the training populations, we don't see significant differences between any of the models or populations. Still, we see a similar pattern between the (A) and (A+D) models, with the (A+D) model increasing accuracy for GY but leading to decreases in some of the ancillary traits, such as TW, EH, GDDAnt, and GDDSilk. When training on the testcrosses, modelling dominance for prediction led to decreased accuracy for all traits except PH. Comparing the two populations as training data for predicting new lines, the FS hybrids with the (A+D) model predicted GY as well as the testcross (A) model. The FS hybrids predicted flowering traits better than the testcrosses, but was worse for GM, TW, PH, and EH.

(CV1) Within population n=123	Model	GM	GY	TW	PH	EH	GDDAnt	GDDSilk
Iodent x PHB47	(A)	0.61 (0.06)	0.45 (0.05)	0.55 (0.05)	0.43 (0.08)	0.41 (0.07)	0.39 (0.06)	0.41 (0.05)
Stiff Stalk x PHG72		0.45 (0.03)	0.56 (0.02)	0.64 (0.02)	0.41 (0.03)	0.34 (0.03)	0.22 (0.02)	0.46 (0.02)
Stiff Stalk x Iodent		0.44 (0.05)	0.54 (0.04)	0.65 (0.03)	0.37 (0.04)	0.52 (0.02)	0.40 (0.07)	0.52 (0.04)
Stiff Stalk x Iodent	(A+D)	0.44 (0.03)	0.56 (0.02)	0.65 (0.03)	0.33 (0.04)	0.50 (0.03)	0.38 (0.09)	0.51 (0.05)
(CV2) Novel cross n=95		GM	GY	TW	PH	EH	GDDAnt	GDDSilk
Stiff Stalk x Iodent	(A)	0.29 (0.04)	0.45 (0.04)	0.48 (0.04)	0.22 (0.06)	0.31 (0.03)	0.37 (0.05)	0.41 (0.06)
	(A+D)	0.30 (0.05)	0.48 (0.04)	0.46 (0.03)	0.23 (0.03)	0.24 (0.04)	0.34 (0.05)	0.38 (0.05)
Testcrosses	(A)	0.41 (0.02)	0.49 (0.02)	0.56 (0.03)	0.35 (0.03)	0.35 (0.03)	0.34 (0.03)	0.36 (0.05)
	(A+D)	0.40 (0.02)	0.48 (0.02)	0.55 (0.03)	0.38 (0.01)	0.32 (0.03)	0.34 (0.03)	0.34 (0.04)

Table 6. (CV1) 10 fold cross validation accuracy (standard deviations in parenthesis) within the Iodent Testcrosses, Stiff Stalk Testcrosses, and the FS hybrids. (CV2). 10-fold cross validation accuracy (standard deviation in parenthesis) of predicting single crosses of novel doubled haploid lines, with training populations phenotyped as either testcrosses or FS hybrids.

Discussion

Partitioning parental GCA and hybrid SCA within a population of FS hybrids based on phenotypic incidence matrices, where male and female lines are observed in only one combination as was originally suggested for Full-sib RRS is not possible. In our case, while 19 Stiff Stalk lines were observed in more than one combination, each Iodent line was observed at most once, which precludes factoring a residual for estimation of SCA, as the Iodent and SCA factors are Identical. The small number of Stiff Stalk lines present in more than one combination in our experiment did allow for partitioning of the Stiff Stalk and Iodent GCA variance components. Using genomic relationship matrices, however, allows for estimation of GCA and SCA effects in the FS hybrids by substituting genomic covariance for the identical incidence matrices in traditional phenotypic selection.

When analyzing parental GCAs (V2), genomic prediction of parental GCAs was more successful than phenotypic prediction, especially within the Iodent lines. This can be explained by the smaller genetic variance within the Iodent lines testcrosses. Partitioning dominance deviations for estimation of parental GCAs was beneficial for most phenotypes, including grain yield. Coincidences of selection for GY between the parental testcross and FS GCAs increased with genomic information, from 42% to 62% in the Stiff Stalks and from 11% to 56% in the Iodents. Experiment (V1) Prediction of the genotypic values of the randomly-paired hybrids with the testcross phenotypes was high based on mid-parent values and could not be improved with genomic information. This result is well supported in the literature regarding prediction of maize and sunflower single crosses, when both parents are represented in the training data, genomic information holds no value over pedigree-based prediction (Reif et al., 2012; Viana et al., 2017; Westhues et al., 2017).

Modelling dominance led to non-significant increases in accuracy of prediction of grain yield whenever predicting within the FS hybrids (CV1 and CV2) but led to reductions when modelled for prediction of phenotypes that are generally considered additive, such as EH and flowering traits. These traits are generally assumed to be additive in their inheritance, so it would likely be safe to use a solely additive model when predicting them. Ultimately, the performance of each population for prediction of novel lines (CV2) is of most importance to a breeder, as this is where large savings on phenotyping effort can be made by not evaluating lines before evaluation in any crosses. Prediction within the FS hybrids with the A+D model predicted GY as well as the testcrosses, they predicted GM, TW, PH, and EH substantially worse. Prediction accuracies of the higher heritability ancillary traits being lower than grain yield seems counterintuitive at first, but it is in agreement with previous work on prediction within maize single crosses (Massman et al., 2013;Technow *et al.,* 2014). They found grain moisture to be predicted with lower relative accuracy than grain yield when training on T1 (one parent of the hybrid being predicted in the training set) and T0 (no parents of the hybrid being predicted in the training set) hybrids. Grain moisture was more accurately predicted than grain yield in the T2 set, where both parents of the hybrid to be predicted are represented in the training data. Our V1 set is analogous to their T2 nomenclature, where accuracies are generally related to the reliability of the traits, while the CV1 and CV2 sets would be considered T0.

Training on the testcross data predicted most ancillary traits of the FS hybrids better than other paired crosses (Table 6, CV2). These traits are generally additive in our populations, as evidenced by the high mid-parent prediction accuracies of the testcross phenotypes (Table 5, V1) so the confounding effect of their unobserved SCA with a particular tester is not a serious worry, and there are two testcrosses evaluated for each FS hybrid, so the additional replication could explain these benefits.

We think genomic prediction represents a significant increase in the practical utility of Full-Sib Reciprocal Recurrent Selection by allowing the estimation of GCA which was not possible before. Our other hypothesis, that the capture of the dominance variance in the FS hybrids that was unable to be partitioned in the testcrosses would greatly improve prediction, was ultimately not the case. Modelling dominance in the randomly-paired population increased accuracy from 0.45-0.48, and variance component estimation that takes into account the strong deviation from HWE in the randomly-paired population shows dominance explains little variance for grain yield (Table 4). From a practical selection standpoint, our data does not suggest that selection based on testcross performance is eliminating lines that would be superior hybrids if only they had been tested as FS hybrids. Dias et al. (2018) demonstrated a clear benefit from modelling dominance in a population consisting of both inter-heterotic and intra-heterotic group crosses, but no maize prediction study has provided evidence for a large benefit from modelling dominance in solely inter-heterotic group crosses (Viana et al., 2018). Kadam *et al.* (2016) demonstrated moderate to high prediction accuracies for grain yield (0.28-0.77, relative to heritability) amongst a random factorial of Stiff Stalk x Non-Stiff Stalk half-sib biparental families, similar to our Stiff-Stalk x Iodent intercrossed population. They suggested such populations could replace testcrossing for the initial evaluation of untested maize lines. While they did not explicitly compare to testcrossing, the fact that the ratio of SCA/GCA in their study was relatively low at 0.12, and modelling dominance did not distinctively increase prediction accuracy, suggests to us testcross populations would have likely provided similar prediction ability. Giraud *et al.* (2017) demonstrated mapping results in an incomplete factorial between two multi-parental populations representing the Dent and Flint European heterotic groups for silage traits and reported that while significant additive QTL could be identified, no significant dominance QTL were found in their inter-heterotic group crosses.

Our study fully supports the use of genomic information in breeding programs using Full-Sib Reciprocal Recurrent Selection. Our evidence does not suggest these FS hybrids replace testcrossing for evaluation of new lines. The idea that testcrossing between two heterotic groups leads to selection against lines that would prove to be superior if only they were only evaluated as single crosses isn’t supported by our study or much of the maize prediction literature. The A+D model is superior to the A model for prediction of GY within the random single crosses, suggesting this population does have dominance variance that can be modelled. This difference is small, however, does not improve upon predicting from the testcrosses, and needs to be taken in the context of the substantial logistical benefits testcrossing allows a breeder. Testcrossing does not require *per se* flowering information as our intercrossed population did. The cost of an isolation nursery of testcrosses increases less with each additional cross, compared to hand-pollination of a FS population of hybrids which increases linearly in cost. Testcrossing also allows testing with dominant native and transgenic trait combinations that will ultimately be a part of the elite hybrid but would require substantial effort to integrate into breeding germplasm for forward breeding. One open question is how genomic information could potentially capture non-additive genetic variation when considering crosses between more than two heterotic groups, as the Iodent and Stiff Stalk patterns are two of several in North American maize breeding, but that is the subject of future research.

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Chapter 3

Line x Tester analysis of Hybrids of Selected and Unselected Lines of Doubled Haploids Derived from Two Maize Synthetic Populations

Abstract

Two Line x Tester experiments were conducted on doubled haploid (DH) lines derived from two six-line synthetic varieties with founders representing the Iodent (IO) and Stiff Stalk (SS) heterotic groups of maize. Selection was based on performance for an index of Grain Yield (bu/acre) divided by % Grain Moisture at harvest, as either testcross or randomly paired hybrids based on two locations in 2015. Thirty selected and 25 were unselected lines were selected for advancement. The SS lines were crossed to PHP02, LH185, DK3IIH6, and the original tester, PHG72. The IO lines were crossed to LH74, LH185, PHJ89, PHJ40 and the original tester, PHB47. Evaluation occurred in 2016 and 2017 in two reps at two locations for the SI components and 6 ancillary traits. GCA variance for the tester lines was significant for the Selection Index (SI) for the IO lines, but not the SS. DH GCA was significant for the selected SS lines and the IO lines, and SCA was significant for both populations and both levels of selection. The ratio of SCA/GCA increased with selection in both populations for the SI and grain yield. We evaluated the correlation between tester genotypic values and breeding values estimated with the remaining testers. LH185 and PHJ89 predicted the remaining breeding values for the SI most closely for the IO crosses, and were also the best performing lines based on their GCA. LH185 was the best predictor of performance in the SS selected lines and had the highest SI GCA, while PHP02 predicted the unselected breeding values with greater accuracy. Selection led to a 6.1% increase in the SI in the IO and 6.9% increase in the SS but affected the component traits differentially. Grain moisture decreased 0.2% in the SS and 3.1% in the IO, while grain yield increased 6.4% in the SS and 3.1% in the IO. The genome estimated breeding values from the randomly paired population were more correlated with the DH GCAs than the testcross breeding values for the selected SS and both IO experiments, but were much less correlated for 3 out of 4 grain yield experiments and 21 out of 24 ancillary traits. For the trait with relatively high ratios of SCA to GCA, genome estimated breeding values from the randomly paired populations are as accurate as or more accurate than testcross estimated breeding values, for traits with lower SCA, it is the opposite.

Introduction

Inbred selection has long relied on use of male testers to identify lines with superior yield potential that combine well with other heterotic groups. Sprague and Tatum (1942) first described the concepts of General Combining Ability (GCA) and Specific Combining ability (SCA):

> “The term "general combining ability" is used to designate the average performance of a line in hybrid combinations.... The term "specific combining ability" is used to designate those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved.”

These concepts have been extremely useful in maize breeding, where the value of an inbred is defined based on performance when crossed to one or more inbreds from opposite heterotic groups. Sprague and Tatum observed that GCA was preponderant in unselected material, while SCA was relatively more important in selected material. The ratio of these two variances informs appropriate breeding strategies; higher estimates of GCA are more predictive of future performance of a line in new single cross combinations, while high SCA is specific to certain combinations and is therefore less predictive of the average value of an inbred.

The introduction of genomic selection in maize breeding has increased the rate of genetic gain largely by reducing phenotyping effort at the initial stages of selection (Osorio, 2013). Selection of new inbreds generally advances through a process of many lines with few testers and locations to testing of few selected lines with more partner inbreds at many locations. Therefore, the choice of the initial testers has the potential to strongly impact the inbred lines that are considered for intense evaluation in advanced stages of the breeding process. In the first chapter of this thesis, we reported on an experimental comparison of two progeny tests for untested doubled haploids (DH) derived from two six-line synthetic varieties of maize with founders representing the Stiff Stalk (SS) and Iodent (IO) heterotic groups. We either testcrossed to an inbred founder of the opposite heterotic group, or randomly paired lines between populations as in FS-RRS. Randomly pairing lines does not allow estimation of GCA or SCA in traditional phenotypic selection due to complete nesting, but genomic prediction can estimate each. While the initial experiment confirmed that genomic estimated breeding values (EBV) estimated from the randomly-paired population were more correlated to the testcross phenotypic EBV than traditional EBV from the randomly paired lines, a better test of the standard line advancement procedure is the use of these estimates for prediction of performance of lines as they advance through the breeding process based on crosses with multiple testers.

In this study we compared two Line x Tester experiments on the lines selected based on their mean performance in those initial stages of selection. Thirty lines ranked based on an intial testcross and twenty-five random lines from the SS and IO populations were testcrossed to five and four additional testers, respectively. Our objectives were (I) Estimate the GCA and SCA in each selected and unselected population (II) evaluate which single tester was most predictive of the GCA across the entire set of testers (III) estimate response to selection (IV) compare the prediction accuracy of the testcross GCAs and genomic GCAs of the randomly paired population from the first stage of selection to the GCAs across multiple testers.

Materials and Methods

The inbred lines used in this study were doubled-haploids (DHs) derived from two six-parent synthetic populations, each with founders representing the SS and IO maize heterotic groups. These populations were inter-mated for three generations, and DH lines were derived courtesy of AgReliant Genetics (AgReliant Genetics, LLC. Westfield, IN, USA). Thirty lines were ranked from each of the SS and IO population based on the GCA of their parental lines for an index of grain yield (bu/acre) divided by grain moisture (%) at harvest based on mean performance across testcross and randomly-paired populations from 2014 (see Chapter 1 for details). An additional twenty-five lines were randomly chosen from each population to cross to the new testers.

The Stiff Stalk lines were evaluated as crosses to four Iodent and Non-Stiff Stalk testers chosen, and the Iodent lines were evaluated as crosses to five Stiff Stalk and non-Stiff Stalk testers (Table 1). The additional testers were chosen to complement the initial testers, PHB47 for the Iodents and PHG72 for the Stiff Stalks. Specifically, use of non-Stiff Stalk testers with both populations was intended to broaden the diversity represented and the scope of inference. PHJ40 and LH74 (Stiff Stalks) and PHJ89 (Oh43-type non-Stiff Stalk) were crossed to Iodent DH lines. The additional Stiff Stalk testers were PHP02, an Iodent, while DK3IIH6 is of Oh43 X Iodent background. LH185, a line from the Mo17 family of the Non-Stiff Stalk heterotic group, was crossed to lines from both the Iodent and Stiff Stalk synthetic populations.

Testers crossed to Iodent			Testers crossed to Stiff Stalk		
Tester	Pedigree	Heterotic group	**Tester**	Pedigree	Heterotic group
LH74	A632 X B73	SS	**PHP02**	PHG44 X PHG29	IO
PHJ40	PHB09 X PHB36	SS	**LH185**	LH59 X LH123Ht	NSS
LH185	LH59 X LH123Ht	NSS	**DK3IIH6**	P3737	IO x Oh43
PHJ89	PHT77 X PHG47	NSS	**PHG72**	PH891 X PH207	IO
PHB47	SD105 X B37(3)	SS			

Table 1. Pedigree and heterotic groups for the testers. Heterotic groups: SS - Stiff Stalk, NSS - Non stiff stalk, IO - Iodent

Experimental design

Materials from the primary source populations (SS and IO) were grown separately in the same field, and data for each of those two experiments was analyzed separately. Within each experiment, each tester was separated in an incomplete block in 2016 and 2017 using a randomized complete block design with two replications at the University of Wisconsin – Madison, West Madison and Arlington Agricultural Research Stations. An environment was considered as the combination of year and location. The fields used were planted with soybeans the previous year and prepared using conventional tillage. Pre-planting nitrogen was applied as granular urea at a rate of 110 lbs/acre assuming a credit of 40 lbs/A N from the previous soy crop. Lorsban, an insecticide, was applied at 8 oz/ 1000 ft. A mixture of Simazine (16oz/acre), Callisto (5oz/acre), and Dual II-Magnum (24oz/acre) were used for pre-emergence weed control. The soil type at both locations is Plano silt loam. Hybrids were trialed in two row plots with a spacing of 0.79 m between rows at a density of 78,200 plants ha^{-1}. Eight traits were measured in the hybrids. Grain yield (GY) is reported as a whole plot measurement (Mg/ha normalized to 15.5% grain moisture). Grain moisture (GM) was measured at the plot level as percent of harvest weight (%). Plant height (PH) and ear height (EH) are the average of three representative plants per plot, with EH measured as the distance from the soil surface to the node subtending the ear and PH measured from the soil surface to the ligule of the terminal leaf (cm). Male and female flowering were measured as growing degree days from planting to 50% plot anthesis and silking (GDDAnt, GDDSilk, growing degree days), respectively. Growing degree days were calculated as $GDD = \sum\left(\frac{Tmax+Tmin}{2} - 50°F\right)$, where Tmax and Tmin are the maximum and minimum daily temperatures in Fahrenheit. On those dates that the temperature exceeded 86° F or was lower than 50° F, Tmax and Tmin were set to those respective values. Grain test weight (TW) was measured at the plot level (kg/hL). A selection index of $\left(\frac{GY\ (\frac{buschels}{acre})}{\%Moisture\ at\ harvest}\right)$ was the primary selection criterion and was reported as well. Plots with realized stands of less than 38,100 plants/ha were treated as missing. Stalk and Root lodging were measured two to four weeks before harvest (# plants lodged).

Variance components and combining ability estimation

The linear mixed model used for estimation of variance components and combining abilities, separate for the SS and IO populations as well as the selected and unselected lines was

(2) $$y_{ijkl} = \mu + T_i + DH_j + M_k + DHxM_{jk} + DHxT_{ij} + MxT_{ik} + DHxMxT_{ijk} + R_{l(i)} + e_{ijkl}$$

Where y_{ijklm} is the plot entry, μ is the overall mean, T_i is the fixed effect of the jth Env, DH_j and M_k are the random effects for the jth DH line and the kth Tester, and $R_{l(i)}$ is the fixed effect for the lth Rep within the ith Env, and $e_{jklm(i)}$ is the residual. Interactions are denoted with an x. The experiments were blocked by tester based on the assumption that controlling for the detrimental effect of the variance in plant height between testers was more important than controlling for within field variance. Significance of variance components were assessed by loglikihood ratio tests using ASRemlPlus (Brien 2016)

To evaluate which tester was most predictive of the performance of DH lines when crossed to other testers, we analyzed each tester x line combination individually, dropping terms for the testers and interactions as

(2) $$y_{ijkl} = \mu + T_i + DH_j + DHxT_{ij} + R_{l(i)} + e_{ijkl}$$

We then estimated accuracy as the correlation between the DH genotypic values estimated with equation 2 and DH GCAs, calculated across the remaining testers, with equation 1.

Significance of selection was assessed by Wald test within ASreml-R (Butler et al. 2009)

Results

Independent variance component analysis of the selected and unselected lines from each population show greater reductions in variance for GM than GY for each population (Table 2). Testers interacted significantly with environments for every trait, while DH lines interacted significantly with environments for GY in all cases, but less for PH, EH, GDDAnt, and GDDSilk. For flowering traits, the selected Testers that were crossed to the Iodent material had much greater variance than the Stiff Stalk Testers.

		SI	GM	GY	TW	PH	EH	GDDAnt	GDDSilk
SS Unselected	Tester	0.06	0.79**	0.63*	1.78***	94.66***	31.06*	482.42***	161.62**
	DHxT	0.18*	0.18***	0.33**	0.4***	16.27***	12.89***	76.44***	40.8*
	DH	0.15	0.88***	0.71***	1.29***	74.35***	48.86***	448.82***	402.48***
	DHxTxEnv	0.27*	0.04	0.41*	0	0	0	0	17.14
	DHxEnv	0.32***	0.04	0.48***	0.19*	3.23	4.77*	6.41	5.43
	TxEnv	0.17***	0.31***	0.38***	0.26***	14.49***	16.09***	57.97***	31.86**
	Residual	1.34***	0.76***	2.05***	2.95***	68.75***	74.37***	560.42***	558.23***
SS Selected	Tester	0.07	0.69**	0.58	2.43***	103.15***	26.43*	527.2***	176.85***
	DHxT	0.33***	0.24***	0.37***	0.15	18.74***	13.89***	50.31**	91.61***
	DH	0.28***	0.49***	0.6***	1.25***	80.44***	72.63***	346.77***	291.17***
	DHxTxEnv	0.15	0.05	0.16	0	0.28	0	0	0
	DHxEnv	0.1	0.06*	0.21**	0.33***	1.9	5.83***	0	14.24
	TxEnv	0.19***	0.19***	0.46***	0.27***	12.25***	12.41***	35.5***	26.89**
	Residual	1.49***	0.75***	2.25***	3.15***	66.17***	62.26***	555***	643.91***
IO Unselected	Tester	0.39***	0.14	0.83**	2.4***	39.92***	3.84	1421.76***	1307.87***
	DHxT	0.13**	0.13***	0.15*	0.05	11.58***	7.5***	59.48***	33.99**
	DH	0.19***	0.46***	0.27***	0.38***	54.11***	46.7***	210.6***	188.01***
	DHxTxEnv	0.22***	0.08	0.31**	0	8.41**	7.4*	25.83	0.36
	DHxEnv	0.06	0.07**	0.11*	0.01	3.23*	0	8.56	0
	TxEnv	0.1***	0.16***	0.28***	0.17***	10.86***	4.92***	72.03***	51***
	Residual	0.98***	0.72***	1.77***	3.03***	46.45***	49.49***	426.27***	459.39***
IO Selected	Tester	0.28***	0.04	0.58**	2.64***	46.13***	2.84	1283.31***	1300.21***
	DHxT	0.31***	0.06**	0.54***	0.16*	11.65***	8.14***	80.42***	90.43***
	DH	0.15**	0.32***	0.33**	0.66***	69.46***	32.83***	282.53***	251.69***
	DHxTxEnv	0.05	0.04	0.08	0	0.52	1.43	7.67	2.51
	DHxEnv	0.17***	0.07***	0.28***	0.05	4.33**	0.06	32.83**	40.71***
	TxEnv	0.07***	0.28***	0.2***	0.1**	7.11***	4.51***	55.02***	53.33***
	Residual	1.07***	0.7***	1.81***	2.83***	59.55***	60.73***	388.71***	397.8***

Table 2. Variance components estimates For Testers (T), Doubled Haploids(DH), and interactions of those terms with eachother and Environments (Env). The traits under study were Selection Index (SI), Grain Moisture (GM), Grain Yield (GY), Test Weight (TW), Plant Height (PH), Ear Height (EH), Growing Degree Days to Anthesis (GDDAnt), and Growing Degree Days to Silking (GDDSilk). Significance was determined by loglikihood ratio tests between full and reduced models for each term (*=0.05,**=0.01,***=0.001).

The ratio of SCA/GCA variances increased with selection for both the Iodent and Stiff Stalk populations for the SI, as well as GY (Table 3). The increase is much greater for the IO population than the SS population. Even with selection, the ratio of SCA to GCA is still less than 1 for all traits, and the ratio is low for all other traits.

	SI	GM	GY	TW	PH	EH	GDDAnt	GDDSilk
SS Unselected	0.86	0.11	0.25	0.13	0.10	0.16	0.08	0.07
SS Selected	0.94	0.20	0.31	0.04	0.10	0.14	0.06	0.20
IO Unselected	0.22	0.22	0.14	0.02	0.12	0.15	0.04	0.02
IO Selected	0.72	0.17	0.59	0.05	0.10	0.23	0.05	0.06

Table 3. Ratio of SCA/GCA variances for the Selection Index (SI), Grain Moisture (GM), Grain Yield (GY), Test Weight (TW), Plant Height (PH), Ear Height (EH), Growing Degree Days to Anthesis (GDDAnt), and Growing Degree Days to Silking (GDDSilk).

The tester GCAs are reported in table 4. For Root Lodging (RL) and Stalk Lodging (SL), significant left skew in their distributions strongly violated normality assumptions. We report simple arithmetic means of lodging rates for each tester. LH185, a Mo17-type non-Stiff Stalk line, performs well when crossed to either the Stiff Stalk or Iodent lines, and the GCA estimates from the tester when crossed to either population are surprisingly similar. This was not expected, as estimated GCAs are deviations from a grand mean so the other testers considerably influence the size and direction of each GCA estimate, and in line x tester analysis a considerable amount of non-additive variance can be included in the estimated GCAs, which we assumed different across different heterotic patterns. Nevertheless, LH185 had similar estimates of GCA across both populations. It had the highest GCA for SI in the SS and second highest for IO. A substantial drawback, especially in northern regions of the United States such as Wisconsin, is that it flowers relatively late. LH185 has the highest GCA for flowering traits across both populations, and highest and second highest moisture GCA in the IO and SS, respectively. PHJ89 was the highest performing line when crossed to the IO lines. It was highest for SI and GY and did not have high GCA for GM, GDDAnt, or GDDSilk. Its only drawback was being the second highest for PH GCA as reduced plant height is generally desirable. In general, each new tester had better GCA for SI than our initial testers (PHB47 and PHG72), except for LH74 and PHJ40, crossed to the IO lines and 3IIH6, crossed to the SS. PHJ40 and LH74 are both low yielding, but PHJ40 had attractive maturity, with very low GCA for GDDAnt and GDDSilk. LH74 has no redeeming qualities, being both low yielding and having relatively late flowering. 3IIH6 was observed to be very susceptible to stalk lodging, as it stalk lodged at twice the rate of the other testers crossed to the SS lines.

	Tester	SI	GM	GY	TW	PH	EH	GDDAnt	GDDSilk	RL	SL
IO	LH185	0.21	0.19	0.52	-2.19	-5.54	-1.73	27.64	25.88	0.50	1.62
	LH74	-0.50	-0.04	-0.69	0.52	-3.39	-0.40	25.99	24.65	0.18	2.19
	PHB47	-0.21	-0.15	-0.43	0.24	8.22	1.18	16.63	16.97	3.05	3.06
	PHJ40	-0.26	-0.02	-0.36	2.17	-5.35	1.49	-56.04	-59.09	0.47	1.58
	PHJ89	0.76	0.02	0.98	-0.73	6.06	-0.54	-14.23	-8.40	0.49	0.62
SS	DK3IIH6	-0.21	-1.02	-0.87	-0.24	9.13	5.31	3.14	-0.42	8.09	10.58
	LH185	0.24	0.41	0.66	-1.70	2.40	-3.67	30.56	17.94	5.39	4.41
	PHG72	-0.04	-0.20	-0.18	2.02	-14.20	-4.43	-20.80	-5.67	1.22	5.43
	PHP02	0.01	0.81	0.40	-0.08	2.67	2.79	-12.90	-11.85	5.55	3.05

Table 4. GCA estimates of each tester crossed to the Selected lines of the Stiff Stalk (SS) and Iodent (IO) populations for the Selection Index (SI), Grain Moisture (GM), Grain Yield (GY), Test Weight (TW), Plant Height (PH), Ear Height (EH), Growing Degree Days to Anthesis (GDDAnt), Growing Degree Days to Silking (GDDSilk). Root Lodging (RL) and Stalk Lodging (SL) are reported as arithmetic means of number of plants lodged per plot.

If performance on a single tester is correlated with the performance of lines on different testers, breeders may be able to maximize the the number of lines being tested and reduce the number of testers being used without additional cost. A tester's predictive ability will be governed by both the unobserved DH x Tester interaction, its differential GxE, and the reliability of the estimation of its genotypic effect. For the Iodent population, the top two testers for predicting GCA of lines in the remaining population are also the two highest GCA lines for GY and SI, a very fortunate coincidence (Figure 1). PHJ40 was a very poor predictor of GY, probably related to its earliness compared to the other testers (GDDAnt GCA= -59). PHJ40 performs much better at predicting performance on other testers for the SI, which is formulated to remove some of the variance in yield attributable to maturity. Considering both traits, most of the testers showed the opposite pattern, with GY being predicted better than the SI. The largest difference is in the randomly selected 3IIH6 x SS testcrosses, which predict the other breeding values for GY at 0.67, but the SI at 0.41. This is mostly due to the reliability of the genotypic estimate, which is 0.36 for SI but 0.62 for GY. The correlation between yield and maturity, and between yield and moisture is well known to breeders (Mather and Kannenberg, 1989). By reducing the covariance between yield and maturity, which is one of the most heritable components of yield, the genetic variance in the SI is relatively reduced. In terms of predicting the selected SS lines, LH185 performs best for both SI and GY. For the random lines, PHP02 predicts the breeding values best for the SI, while PHG72, the first stage tester, ranks first for predicting GY of the breeding values of the other lines.

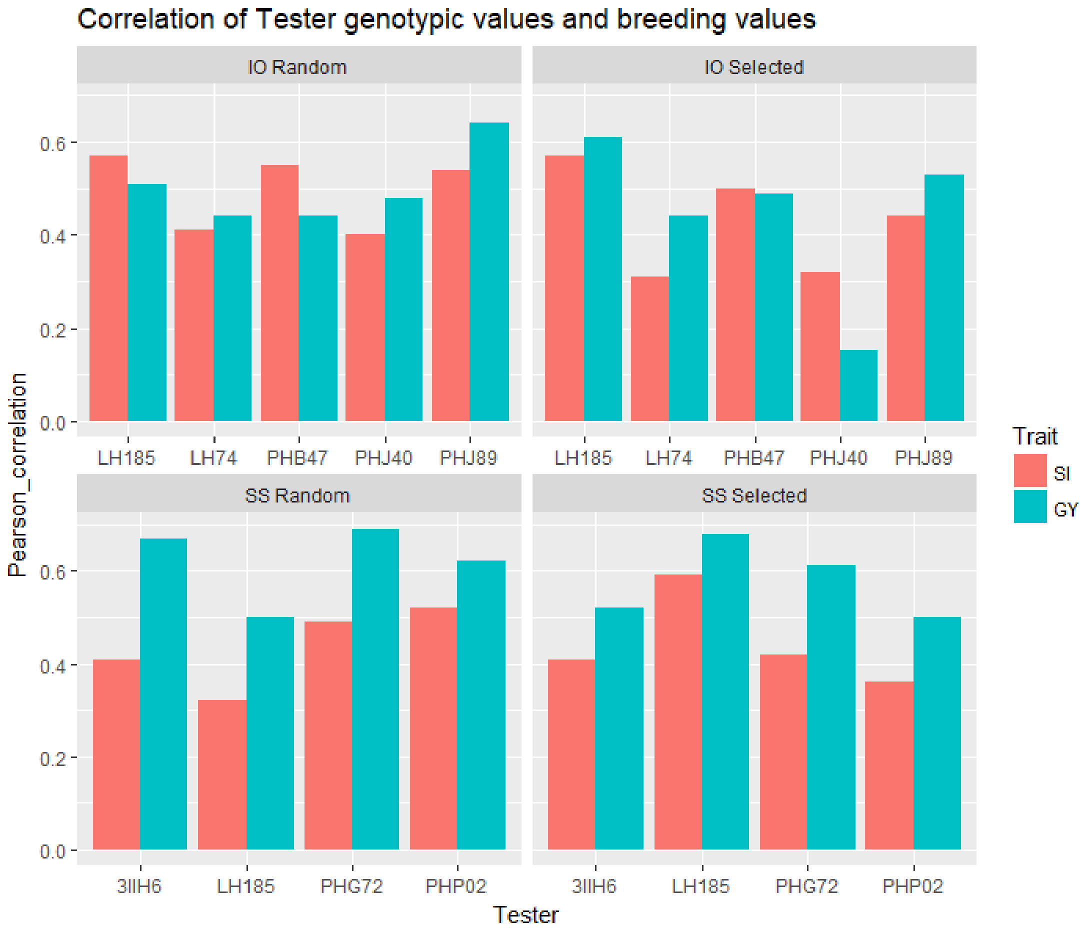

Figure 1. Correlation between DH values calculated per tester, and DH breeding values calculated with the remaining dataset for the Selection Index (SI) and Grain Yield (GY).

$$(3) \quad y_{ijkl} = \mu + Selection + T_i + \begin{pmatrix} DH_j^{Sel} & 0 \\ 0 & DH_j^{Ran} \end{pmatrix} + M_k + \begin{pmatrix} DHxM_{jk}^{Sel} & 0 \\ 0 & DHxM_{jk}^{Ran} \end{pmatrix} + \begin{pmatrix} DHxT_{ij}^{Sel} & 0 \\ 0 & DHxT_{ij}^{Ran} \end{pmatrix} + \begin{pmatrix} DHxMxT_{ijk}^{Sel} & 0 \\ 0 & DHxMxT_{ijk}^{Ran} \end{pmatrix} + MxT_{ik} + R_{l(i)} + e_{ijkl}$$

To test for a response to selection, we fit all 55 Selected and random lines in the same model (Model 3), which is equivalent to Model 1, but with a fixed term for selection and a diagonal variance structure for each term involving the selected DH lines. The significance was assessed via Wald test within ASReml-R (Butler et al. 2009). We also tested for the selection response separately for each environment and each tester. Selection led to significant increases in the SI for both IO and SS populations, 6.1% and 6.9% respectively, but effected the component traits of the index in different ways (Table 6). Selection reduced moisture by 2.9% within the IO and increased GY by 3.1%, though the increase in GY was not significant at $\alpha=0.05$. For the SS, selection increased GY by 6.4%, but led to non-significant decreases in GM. Considering ancillary traits, TW was the only trait with a significant correlated effect of selection, which decreased by %1.1. Time to flowering decreased slightly in the IO, but increased in the SS lines, which likely results from the SI selecting more effectively against maturity in the IO than the SS. Unfortunately, PH and EH increased with selection in both the SS and IO lines, though not significantly. Increases in PH and EH are nuisance correlations that increase the propensity for lodging, and taller plants gain a yield advantage when blocked in segregating populations through competition effects. In private companies, later stage testing of four-row plots is carried out to eliminate this advantage. Another cost-effective option would be to add PH and EH as terms to be selected against in the Selection Index. Comparing Selection response per environment for the SI and the components GY and GM, they varied in degree, and at times, direction. The IO lines had significantly lower moisture in every testing environment, and increased GY in each environment as well, though the only statistically significant change was the 5.5% increase in Arlington in 2017. Selection responses for the SI in the Iodent were highly significant in 2017, but not significant in 2016. The SS selections were not significant for GM in any environment and had a non-significant increase in GM in Arlington in 2016. While GY in 2017 at West Madison demonstrated a highly significant 10.2% increase, all other locations had non-significant increases in GY. Like the IO, the SS demonstrated significant increases for the SI in both environments in 2017, but non-significant increases in each environment of 2016.

	Trait	ΔG	% change	P-value
IO	SI	0.49	6.1***	5.3E-04
	GY	0.33	3.1	8.0E-02
	GM	-0.61	-2.9***	7.9E-04
	TW	-0.64	-1.1**	3.8E-03
	GDDAnt	-1.22	-0.1	7.9E-01
	GDDSilk	-2.75	-0.2	5.3E-01
	PH	3.90	1.6	8.4E-02
	EH	2.90	2.4	1.0E-01
SS	SI	0.56	6.9**	1.4E-03
	GY	0.64	6.4*	1.4E-02
	GM	-0.04	-0.2	8.6E-01
	TW	-0.21	-0.4	5.5E-01
	GDDAnt	3.26	0.3	5.7E-01
	GDDSilk	4.33	0.4	4.2E-01
	PH	4.24	1.6	9.0E-02
	EH	3.88	3.0	8.6E-02

Table 5. Mean difference and percent change between selected and unselected Stiff Stalk (SS) and Iodent (IO) lines for the Selection Index (SI), Grain Moisture (GM), Grain Yield (GY), Test Weight (TW), Plant Height (PH), Ear Height (EH), Growing Degree Days to Anthesis (GDDAnt), and Growing Degree Days to Silking (GDDSilk). Significance levels (*=0.05,**=0.01,***=0.001).

			Iodent			Stiff Stalk		
Trait	Year	Location	ΔG	% change	P-value	ΔG	% change	P-value
SI	2016	ARL	0.27	3.7	8.0E-02	0.39	5.2	6.8E-02
		WM	0.27	3.7	1.1E-01	0.27	3.6	2.3E-01
	2017	ARL	0.71	8.72***	2.5E-04	0.52	6.6*	4.3E-02
		WM	0.73	7.3***	9.1E-04	1.02	10.4***	3.3E-05
GM	2016	ARL	-0.44	-1.9**	5.9E-03	0.22	1.0	3.4E-01
		WM	-0.62	-2.9*	7.8E-06	-0.07	-0.3	7.9E-01
	2017	ARL	-0.65	-3.2*	2.0E-02	-0.33	-1.7	2.3E-01
		WM	-0.65	-3.2**	1.2E-03	-0.03	-0.2	9.2E-01
GY	2016	ARL	0.20	2.0	3.3E-01	0.60	6.1	5.2E-02
		WM	0.08	0.8	7.4E-01	0.27	2.9	3.6E-01
	2017	ARL	0.57	5.5*	4.4E-02	0.43	4.5	2.5E-01
		WM	0.49	3.9	6.6E-02	1.19	10.2***	4.9E-04

Table 6. Mean difference and percent change between selected and unselected Stiff Stalk (SS) and Iodent (IO) lines in each environment for the Selection Index (SI), Grain Moisture (GM) and Grain Yield (GY). Significance levels (*=0.05,**=0.01,***=0.001).

The responses for the SI over each tester varied considerably (Table 7). Neither of the initial testers showed the largest or most significant response for the SI or its component traits, but as selections were based on phenotypic BLUPs of the DHs using both testcross and randomly-paired populations this isn't necessarily expected. Within the IO, the Stiff Stalk testers LH74 and PHJ40 did show the most significant response, which would follow given the lines were originally selected on the Stiff Stalk tester PHB47. The responses in GM were most significant with the NSS testers LH185 and PHJ40, while the responses in GY were larger in the Stiff Stalk testers LH74 and the original tester, PHB47. Another plausible explanation for the line responses by tester of the IO do follow a general trend that the estimated responses are inversely related to the testers GCA (Table 4). LH74 has the lowest GCA for the SI and GY but produces the largest selection response for these traits. Similarly, the testers with the highest GCA for GY, LH185 and PHJ89, are much lower in their responses to selection. These results would support the idea of using a "poor" tester to maximize variance (Hallauer *et al.*, 2010). We do not know the degree to which heterotic pattern comes into play in this case. The selection response for the SI by tester for the SS lines is smallest for the initial tester and the other tester, PHP02, which is from the same heterotic group, Iodent. The original tester, PHG72, shows a non-significant increase in moisture, opposite of the direction of selection, but a significant increase in GY offsets this and the response is still a significant increase for the SI. DK3IIH6, a non-Stiff Stalk with a background of Oh43 and Iodent, showed the most significant responses for the lines for each trait, while LH185, a non-Stiff Stalk of the Lancaster heterotic pattern, showed the largest responses.

		Tester	% change	ΔG	P-value
Iodent	SI	LH185	4.45	0.38	1.17E-01
		LH74	10.54***	0.77	6.54E-07
		PHB47	6.64**	0.52	2.65E-03
		PHJ40	3.99***	0.32	1.32E-05
		PHJ89	5.14*	0.46	2.51E-02
	GM	LH185	-3.47**	-0.75	5.82E-03
		LH74	-3.45	-0.73	1.27E-01
		PHB47	-3.31*	-0.68	4.06E-02
		PHJ40	-1.08	-0.22	4.30E-01
		PHJ89	-2.95**	-0.62	3.75E-03
	GY	LH185	1.16**	0.13	9.92E-03
		LH74	6.79***	0.65	3.02E-04
		PHB47	3.34*	0.34	1.53E-02
		PHJ40	2.79***	0.29	1.29E-04
		PHJ89	2.09	0.25	3.54E-01
Stiff Stalk	SI	DK3IIH6	8.63***	0.66	0.00E+00
		LH185	10.6*	0.88	2.82E-02
		PHG72	5.46**	0.45	3.86E-03
		PHP02	3.12	0.26	2.42E-01
	GM	DK3IIH6	-0.26***	-0.05	1.65E-11
		LH185	-1.1***	-0.22	3.92E-06
		PHG72	0.93	0.18	2.66E-01
		PHP02	-0.37**	-0.08	1.53E-03
	GY	DK3IIH6	7.95***	0.71	2.33E-09
		LH185	9.19**	0.97	1.00E-03
		PHG72	6.45*	0.64	2.45E-02
		PHP02	2.53*	0.28	4.74E-02

Table 7. Selection responses by tester expressed as mean difference between random and selected and as percentage for the Selection Index (SI), Grain Yield (GY) and Grain Moisture (GM). Significance was assessed by Wald test. Significance levels (*=0.05,**=0.01,***=0.001).

In chapter 1, we evaluated two progeny tests, the established method of testcrossing, and randomly pairing lines between two populations, deemed FS hybrids, in the context of a genomic prediction enabled breeding program. Here we estimated the correlation between the GCAs of the selected and unselected lines from the Line x Tester experiments with the Breeding values of estimated from each line advancement strategy. Selection of these lines in 2015 was based on BLUPs of lines that were in both or either experiment, to assure a fair comparison we only used lines that were present in both the randomly paired and testcross populations. The Genomic Estimated Breeding Values (GEBVs) were estimated with the (A+D) model that partitioned separate GCA effects for the SS and IO lines as well as a dominance effect. The correlations for the Selection index were higher for the single cross GEBVs than the testcross EBVs in 3 out of 4 cases. For GY, the opposite pattern was seen, where the Testcross EBVs were more correlated with the Line x Tester GCAs in 3 of 4 cases. For the ancillary traits, Testcross EBVs predicted Line x Tester GCAs better in 21 out of 24 trait x population combinations. Differences between the accuracies of the line advancement procedures for the ancillary traits were generally larger within the Iodent population, which is consistent with the relative genetic variance of the populations. The genetic variance of the SS population is three to five times as large as the IO population for the ancillary traits in the testcross populations, so the amount of confounding due to variance of the reciprocal population can be assumed larger for the IO than the SS. However, the SI is more accurately predicted with single cross GEBVs in all cases besides the randomly selected Stiff Stalk lines. It is also the trait with the highest relative amount of SCA to GCA, which are the traits these populations were designed to capture. The lack of precise estimates of breeding values for more additive traits, even with genomic estimation, could be overcome through including the inbred phenotypes in an index, as has been proposed before (Moreno-González and Hallauer, 1982). Including inbred phenotypes substantially reduces the benefit of evaluating lines as random-pairs over testcrosses though, and the differences in accuracies between the advancement procedures are smaller for the SI than most of the other traits.

		Iodent		Stiff Stalk	
Selection	Trait	Single Cross GEBV	Testcross EBV	Single Cross GEBV	Testcross EBV
Random (IO n=14, SS n=21)	SI	0.47	0.43	0.22	0.3
	GY	0.45	0.32	0.51	0.68
	GM	0.34	0.86	0.63	0.86
	TW	0.28	0.7	0.8	0.78
	PH	0.38	0.57	0.8	0.84
	EH	0.65	0.66	0.81	0.86
	GDDAnt	0.13	0.61	0.74	0.79
	GDDSilk	0.33	0.65	0.69	0.85
Selected (IO n=17, SS n=18)	SI	0.67	0.6	0.24	0.2
	GY	0.61	0.66	0.56	0.59
	GM	0.51	0.77	0.61	0.71
	TW	0.77	0.76	0.73	0.91
	PH	0.74	0.78	0.69	0.95
	EH	0.84	0.74	0.88	0.95
	GDDAnt	0.46	0.83	0.43	0.81
	GDDSilk	0.44	0.89	0.5	0.74

Table 8. Correlation of Genome Estimated Breeding Values (GEBV) or Testcross Estimated Breeding values (EBV) from chapter 1 with the General Combining Abilities estimated in current Line x Tester experiment.

Conclusions

One of our experimental goals was to identify the best inbred testers for each population based on these Line x Tester experiments. For the IO population, the best lines in terms of their GCA, LH185 and PHJ89, also predicted the breeding values based on the remaining lines most accurately (Figure 1). This is somewhat suprising, given that the remaining testers are from the Stiff Stalk heterotic group, and LH185 and PHJ89 are Non-Stiff Stalk testers. It may be related to the Stiff Stalk testers' propensity for stalk lodging, which lodge at higher rates than PHJ89 and LH185. PHJ89 has the most attractive combination of maturity traits for northern Wisconsin as well as high accuracy in predicting the breeding values of the remaining lines, it is likely the best choice for a Non-Stiff Stalk tester of this Iodent material. Given how much of North American maize germplasm is of the Stiff Stalk heterotic pattern, continued use of a Stiff Stalk tester also seems warranted (Van Heerwaarden et al., 2012). PHB47, the original Stiff Stalk tester, is suitable for this. The suitable testers for the SS lines would be LH185 and PHG72, based on their predictive ability and germplasm representation.

The DH lines selected in these Line x Tester experiments were selected based on performance in the Stiff Stalk x Iodent heterotic pattern, though significant responses to selection are still generally seen across testers from different heterotic groups. The combining ability of the selected populations should prove useful as they advance to single cross evaluation. The varied responses to selection across testers from different heterotic groups reaffirms the importance of testing lines in combination with a diverse set of germplasm to maximize genetic gain.

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Supplementary Information

Supplementary Table 1. General Combining Abilities for the Doubled Haploid lines (DH) from the Stiff Stalk (SS) and Iodent (IO) populations for the Selection Index (SI), Grain Moisture (GM), Grain Yield (GY), Test Weight (TW), Plant Height (PH), Ear Height (EH), Growing Degree Days to Anthesis (GDDAnt), and Growing Degree Days to Silking (GDDSilk).

Exp	DH	SI	GM	GY	TW	PH	EH	GDDAnt	GDDSilk
IO Random	W10005_0129	0.52	0.55	0.95	0.60	24.00	17.74	33.10	26.08
	W10005_0147	0.48	-0.73	0.33	-0.30	-0.54	-1.46	-7.23	-5.29
	W10005_0429	0.45	0.58	0.84	-0.35	5.78	0.45	18.66	12.49
	W10005_0399	0.42	-0.85	0.15	-0.76	-4.07	-3.26	-26.34	-23.59
	W10005_0186	0.35	-0.79	0.15	0.52	-2.94	-4.60	-19.97	-20.44
	W10005_0006	0.30	0.63	0.66	0.34	9.02	8.43	-15.71	-13.24
	W10005_0292	0.27	-0.10	0.33	-0.05	-1.61	-2.22	-6.42	-3.47
	W10005_0076	0.26	-0.44	0.14	-1.27	-0.12	-4.94	1.49	0.32
	W10005_0131	0.26	-0.47	0.11	0.19	1.33	-4.12	-0.73	-6.11
	W10005_0454	0.16	-1.03	-0.21	-0.75	2.93	5.31	3.45	8.27
	W10005_0216	0.16	0.17	0.28	-0.50	1.72	4.44	6.37	4.33
	W10005_0305	0.14	-0.11	0.13	-0.30	-6.07	-5.31	-14.56	-11.06
	W10005_0185	-0.06	-0.31	-0.17	0.13	-0.61	-2.73	-12.49	-8.77
	W10005_0229	-0.11	0.14	-0.06	0.45	-5.37	-7.24	-1.27	1.55
	W10005_0023	-0.11	0.29	-0.01	0.30	-4.65	5.05	-4.65	-11.42
	W10005_0192	-0.12	0.23	-0.07	-0.32	0.91	-3.29	16.75	12.90
	W10005_0234	-0.13	-0.37	-0.30	-0.65	6.12	5.72	1.06	-5.76
	W10005_0117	-0.18	-1.07	-0.64	0.52	-3.79	4.30	-4.71	-4.84
	W10005_0063	-0.23	0.12	-0.25	0.24	-11.35	-0.56	-0.97	-4.03
	W10005_0013	-0.28	0.59	-0.10	0.80	4.68	6.89	13.55	3.94
	W10005_0257	-0.31	0.34	-0.24	0.88	-7.07	-6.87	-3.64	-6.74
	W10005_0092	-0.32	0.42	-0.22	0.42	0.81	8.32	14.85	22.26
	W10005_0214	-0.41	0.62	-0.30	0.14	1.57	-0.92	15.61	24.82
	W10005_0594	-0.65	-0.04	-0.81	0.29	-10.52	-11.42	-11.58	-4.59
	W10005_0453	-0.85	1.64	-0.68	-0.53	-0.15	-7.69	5.38	12.40
IO Selected	W10005_0015	0.52	0.66	1.01	0.04	13.77	6.92	-6.74	-1.49
	W10005_0139	0.43	-0.79	0.28	-0.66	12.45	4.88	12.96	11.18
	W10005_0199	0.38	-0.06	0.51	0.33	3.51	6.56	22.62	21.93
	W10005_0029	0.34	-0.40	0.31	-0.41	4.44	0.10	-11.75	-10.96
	W10005_0389	0.34	0.54	0.71	-0.74	15.29	9.17	21.55	6.18
	W10005_0329	0.24	-0.28	0.25	1.24	3.70	5.87	-14.37	-18.98
	W10005_0444	0.23	0.22	0.42	0.06	-1.39	1.03	3.84	3.72
	W10005_0294	0.22	-0.72	0.04	0.48	-7.44	-3.75	-17.10	-11.41
	W10005_0028	0.22	1.09	0.75	-1.29	8.01	4.40	19.50	13.53
	W10005_0331	0.15	0.06	0.25	-0.18	-0.07	-1.87	-13.00	-6.65

	W10005_0352	0.15	0.05	0.24	-1.24	4.54	0.87	7.83	17.34
	W10005_0336	0.13	-0.36	0.05	-1.72	12.57	1.91	15.75	12.89
	W10005_0137	0.10	-0.11	0.12	-0.22	1.68	0.46	16.93	17.21
	W10005_0150	0.01	-0.13	-0.06	0.42	1.41	5.62	0.81	0.90
	W10005_0153	-0.01	0.13	0.03	0.45	-1.80	2.57	1.85	4.50
	W10005_0469	-0.07	0.09	-0.05	0.34	-8.22	-3.96	-2.39	-1.30
	W10005_0065	-0.07	-0.15	-0.13	-0.94	1.95	-3.70	5.90	6.14
	W10005_0225	-0.10	0.16	-0.08	-0.14	5.52	0.30	-4.92	3.81
	W10005_0405	-0.13	0.54	-0.01	0.85	3.38	8.03	23.44	26.01
	W10005_0005	-0.16	0.04	-0.23	0.05	-8.79	-7.39	-21.59	-24.23
	W10005_0437	-0.16	-0.05	-0.27	0.85	-6.81	-4.67	-24.85	-21.70
	W10005_0339	-0.18	-0.49	-0.41	0.41	2.14	2.96	-1.06	-1.91
	W10005_0156	-0.18	-0.95	-0.61	-0.36	-4.76	2.62	29.49	24.54
	W10005_0426	-0.18	0.99	0.11	-0.41	-1.35	-1.68	8.48	-8.12
	W10005_0202	-0.28	-0.29	-0.51	0.73	-7.90	-0.42	-0.77	1.18
	W10005_0445	-0.29	-1.03	-0.78	0.32	-15.41	-5.77	-22.45	-25.42
	W10005_0024	-0.34	0.81	-0.18	0.85	2.06	-0.99	5.14	5.47
	W10005_0124	-0.34	-0.07	-0.47	0.72	-12.95	-13.49	-19.24	-13.28
	W10005_0218	-0.49	0.12	-0.66	-0.74	-7.70	-8.06	-12.63	-6.00
	W10005_0245	-0.50	0.39	-0.61	0.93	-11.82	-8.51	-23.22	-25.06

Exp	DH	SI	GM	GY	TW	PH	EH	GDDAnt	GDDSilk
SS Random	W10004_0008	0.56	0.83	1.43	0.82	3.34	10.12	9.18	-2.06
	W10004_0007	0.42	0.56	1.08	0.72	-2.44	1.98	29.94	21.31
	W10004_0169	0.38	-0.84	0.38	-1.45	-8.71	-6.95	-13.34	-13.93
	W10004_0206	0.21	0.50	0.64	0.37	-3.55	-3.15	-8.38	-7.13
	W10004_0208	0.18	1.42	0.92	0.77	12.07	8.17	-2.45	-4.55
	W10004_0143	0.17	-0.13	0.30	0.86	0.56	1.09	-20.23	-10.11
	W10004_0131	0.16	0.94	0.73	-0.43	-4.94	-9.00	7.74	4.67
	W10004_0217	0.12	0.10	0.29	-0.99	-10.66	-10.19	-18.93	-19.07
	W10004_0098	0.11	-1.50	-0.38	1.28	14.38	13.09	5.64	4.64
	W10004_0178	0.10	0.77	0.53	0.16	2.60	-4.01	7.94	6.34
	W10004_0223	0.10	0.47	0.43	0.94	6.45	3.44	35.70	25.70
	W10004_0049	0.08	-1.26	-0.26	-2.49	-5.95	0.68	0.45	12.63
	W10004_0220	0.02	-0.20	-0.03	-0.85	-4.93	-6.07	-16.24	-1.84
	W10004_0053	0.00	1.72	0.70	-1.87	3.57	4.64	49.26	44.10
	W10004_0120	-0.08	-1.89	-0.87	0.12	8.28	-0.68	-44.51	-50.29
	W10004_0185	-0.16	0.11	-0.25	-0.98	-11.85	-11.02	-21.69	-11.25
	W10004_0133	-0.16	1.10	0.14	0.70	-3.81	3.22	5.14	4.25
	W10004_0275	-0.16	-0.30	-0.50	-0.41	4.43	5.63	-11.73	-15.68
	W10004_0152	-0.19	-0.61	-0.59	0.51	11.04	3.58	14.59	27.24
	W10004_0063	-0.21	-0.86	-0.73	-0.35	10.51	1.40	11.58	15.75
	W10004_0181	-0.21	-0.38	-0.61	1.08	-1.64	1.19	-6.39	-5.24
	W10004_0087	-0.25	-0.26	-0.57	0.91	-18.27	-10.97	-18.86	-19.99

	W10004_0066	-0.37	-0.47	-0.97	0.73	4.47	5.39	11.53	0.04
	W10004_0111	-0.39	0.32	-0.87	-1.08	2.49	1.08	6.12	12.67
	W10004_0013	-0.43	-0.15	-0.95	0.92	-7.46	-2.63	-12.06	-18.19
SS Selected	W10004_0258	0.66	-0.98	0.38	-0.64	5.95	4.94	-2.76	-6.81
	W10004_0192	0.53	0.25	0.94	-0.08	12.90	8.84	27.18	31.89
	W10004_0090	0.36	-1.33	-0.16	-1.13	-18.23	-16.48	-39.81	-42.67
	W10004_0105	0.31	0.43	0.70	1.12	9.72	9.36	26.65	8.94
	W10004_0148	0.31	-0.32	0.26	1.40	7.48	6.50	13.86	9.03
	W10004_0202	0.30	0.14	0.48	-0.40	-5.57	-4.36	-18.32	-14.20
	W10004_0038	0.28	-0.61	0.09	-1.20	-5.45	4.78	-7.59	-5.57
	W10004_0225	0.26	1.11	0.93	-0.49	-7.26	-0.18	-22.05	-24.62
	W10004_0212	0.23	0.34	0.54	0.18	7.67	1.88	-6.72	-0.02
	W10004_0140	0.22	-0.83	-0.12	0.08	9.28	12.11	10.53	16.19
	W10004_0041	0.21	0.41	0.48	-0.29	-5.53	-4.40	-10.93	-5.15
	W10004_0045	0.19	0.86	0.70	0.37	10.80	16.72	25.42	9.65
	W10004_0306	0.15	0.14	0.33	0.85	-6.79	-5.19	5.28	4.13
	W10004_0313	0.14	-0.79	-0.17	-0.57	-13.78	-7.37	-20.87	-13.76
	W10004_0026	0.11	0.33	0.34	1.68	0.82	-1.91	-0.43	-6.04
	W10004_0232	0.08	0.30	0.27	-1.26	0.90	-2.55	4.78	8.68
	W10004_0101	0.07	-0.51	-0.13	-1.02	-9.84	-7.91	-13.82	-5.33
	W10004_0121	0.01	0.08	0.07	0.79	0.10	1.94	14.75	15.43
	W10004_0123	0.01	-0.32	-0.11	0.63	8.13	7.21	7.50	-3.31
	W10004_0080	-0.02	1.36	0.62	-0.76	2.96	5.54	25.93	17.07
	W10004_0119	-0.04	0.18	0.02	0.21	-2.91	-3.15	-7.73	-9.02
	W10004_0069	-0.14	-0.26	-0.29	-0.46	-6.80	-7.67	-11.39	-2.37
	W10004_0094	-0.17	0.59	0.00	1.89	8.37	-5.23	3.03	1.76
	W10004_0031	-0.17	0.30	-0.11	1.71	11.43	13.45	26.72	17.83
	W10004_0115	-0.29	-1.11	-0.97	-2.00	4.40	-10.24	-5.77	-2.41
	W10004_0145	-0.38	0.42	-0.37	-0.11	-0.85	-2.70	5.20	-1.16
	W10004_0142	-0.43	0.39	-0.45	0.95	1.39	-4.10	1.76	-0.88
	W10004_0064	-0.47	-0.46	-0.83	-1.17	-8.56	-6.63	-28.67	-31.60
	W10004_0144	-1.06	-0.06	-1.57	0.94	-15.97	-12.24	-20.19	11.37
	W10004_0095	-1.28	-0.03	-1.88	-1.22	5.26	9.05	18.45	22.95

Supplementary Table 2. Specific combining abilities calculated separately for the Selected and Random Stiff Stalk (SS) and Iodent (IO) populations for the Selection Index (SI), Grain Moisture (GM), Grain Yield (GY), Test Weight (TW), Plant Height (PH), Ear Height (EH), Growing Degree Days to Anthesis (GDDAnt), and Growing Degree Days to Silking (GDDSilk).

Tester	DH	SI	GM	GY	TW	PH	EH	GDDAnt	GDDSilk
Random IO x LH185	W10005_0129	0.25	-0.27	0.19	-0.02	0.70	1.33	1.01	-1.93
	W10005_0454	0.23	-0.20	0.14	-0.05	-0.95	-1.42	-4.87	1.22
	W10005_0131	0.22	-0.33	0.10	-0.06	-1.34	-1.50	-5.26	1.69
	W10005_0192	0.19	0.15	0.22	-0.02	-1.34	-0.19	0.43	2.87
	W10005_0594	0.17	0.20	0.23	-0.14	6.05	0.93	6.82	1.84
	W10005_0006	0.17	0.00	0.21	0.02	0.33	-0.91	-9.03	-7.71
	W10005_0292	0.16	0.25	0.25	-0.05	-0.56	0.20	-4.92	-2.29
	W10005_0117	0.15	-0.21	0.03	0.07	-0.32	1.54	6.81	3.26
	W10005_0399	0.15	-0.59	-0.06	0.10	-4.40	-2.11	-10.91	-8.00
	W10005_0185	0.14	0.20	0.20	0.04	-2.78	-0.46	-9.81	-3.75
	W10005_0216	0.08	-0.19	0.02	-0.05	0.03	1.52	-1.92	-0.54
	W10005_0076	0.07	0.28	0.13	-0.06	0.89	1.42	7.74	3.60
	W10005_0063	0.05	-0.04	0.06	0.10	1.10	0.51	6.27	2.73
	W10005_0429	0.04	0.16	0.12	0.04	1.91	1.13	-1.19	0.72
	W10005_0257	-0.01	0.42	0.12	0.04	1.24	0.34	-0.74	-0.98
	W10005_0147	-0.03	0.17	-0.02	-0.04	0.03	-0.87	2.72	2.17
	W10005_0214	-0.11	-0.11	-0.12	0.07	0.74	-0.62	2.44	1.81
	W10005_0023	-0.12	0.44	-0.01	0.04	-1.10	-2.44	9.47	6.20
	W10005_0186	-0.16	-0.03	-0.16	-0.02	-0.41	0.38	1.44	-0.52
	W10005_0013	-0.17	-0.07	-0.19	0.00	0.97	1.24	-1.20	-1.61
	W10005_0234	-0.18	0.10	-0.18	0.01	1.96	0.39	4.16	1.51
	W10005_0453	-0.21	0.12	-0.16	0.10	-0.14	-0.78	-2.40	-2.50
	W10005_0229	-0.24	0.50	-0.11	-0.03	-0.64	-0.59	-2.40	0.63
	W10005_0092	-0.26	-0.40	-0.36	-0.12	-1.73	-2.32	3.15	-1.23
	W10005_0305	-0.46	-0.08	-0.52	-0.01	-1.71	-1.42	3.36	1.46
Random IO x LH74	W10005_0147	0.52	-0.24	0.47	0.03	0.80	0.34	-1.67	-0.09
	W10005_0186	0.45	-0.37	0.31	-0.05	-0.35	-0.25	2.48	2.15
	W10005_0429	0.22	0.07	0.27	0.00	2.19	0.83	10.38	4.13
	W10005_0129	0.18	-0.08	0.18	0.06	2.96	1.13	2.30	2.66
	W10005_0234	0.17	-0.14	0.13	-0.03	1.36	1.81	2.92	-0.47
	W10005_0399	0.14	0.05	0.14	-0.01	2.55	-0.06	-0.05	-0.12
	W10005_0214	0.11	0.08	0.14	-0.01	0.23	-0.19	-2.90	-3.05
	W10005_0229	0.08	-0.13	0.07	-0.01	-2.97	-1.89	-10.41	-7.01
	W10005_0013	0.08	0.09	0.12	0.03	0.64	0.96	2.13	2.57
	W10005_0305	0.08	0.14	0.15	0.03	-4.65	-3.83	-9.66	-1.87
	W10005_0023	0.08	-0.19	0.04	-0.04	-2.54	0.52	-10.58	-4.63

	W10005_0131	0.06	-0.21	-0.02	0.03	1.33	-0.18	-1.85	-3.98
	W10005_0117	0.06	-0.03	0.05	-0.08	0.04	-0.02	2.49	0.91
	W10005_0594	0.01	0.09	0.04	0.09	-2.36	-1.07	-10.06	-5.94
	W10005_0076	0.01	-0.06	0.00	0.09	-2.42	-1.60	-0.29	1.34
	W10005_0192	-0.03	-0.01	-0.01	0.07	3.26	1.25	-2.12	-0.09
	W10005_0257	-0.04	-0.37	-0.15	0.01	-4.67	-2.37	-4.57	-3.61
	W10005_0292	-0.10	-0.08	-0.11	-0.03	-3.98	-2.65	-2.83	-1.31
	W10005_0063	-0.21	0.04	-0.20	0.05	-0.97	-0.69	-2.08	-2.53
	W10005_0006	-0.22	0.51	-0.10	-0.06	0.54	1.42	7.72	2.89
	W10005_0453	-0.25	0.41	-0.17	-0.09	-1.04	-0.96	-2.16	-0.13
	W10005_0092	-0.25	0.23	-0.20	-0.02	-2.59	2.97	8.57	9.60
	W10005_0185	-0.32	-0.06	-0.31	-0.07	10.50	5.89	10.90	4.22
	W10005_0216	-0.52	0.13	-0.49	-0.01	0.06	-0.99	7.35	1.33
	W10005_0454	-0.55	0.14	-0.51	0.02	1.18	1.10	5.24	3.67
Random IO x PHB47	W10005_0216	0.30	0.21	0.39	0.02	-5.42	-3.57	0.46	-0.29
	W10005_0214	0.23	0.05	0.28	-0.07	-2.36	0.72	4.38	2.50
	W10005_0229	0.22	-0.31	0.13	0.07	3.19	2.97	3.22	-0.89
	W10005_0013	0.17	0.28	0.31	-0.02	0.96	2.59	1.49	-1.94
	W10005_0454	0.16	-0.05	0.14	0.00	0.24	0.15	-0.91	-2.42
	W10005_0192	0.10	-0.10	0.09	0.02	2.49	0.76	4.46	0.84
	W10005_0076	0.09	-0.09	0.06	0.00	1.01	-1.26	-3.78	-1.45
	W10005_0131	0.08	-0.09	0.05	0.08	-2.41	-0.75	3.79	2.57
	W10005_0399	0.07	-0.04	0.05	-0.02	0.91	2.45	2.98	1.30
	W10005_0305	0.03	-0.11	0.00	0.03	1.85	1.49	2.78	0.49
	W10005_0117	0.03	-0.17	-0.02	-0.08	0.87	-0.29	0.28	1.28
	W10005_0594	0.00	-0.33	-0.08	0.00	0.72	0.36	-1.12	0.70
	W10005_0129	0.00	-0.09	0.00	-0.07	-0.19	-1.14	2.62	1.67
	W10005_0147	-0.01	-0.30	-0.11	0.03	2.38	2.69	-4.78	-1.90
	W10005_0292	-0.02	0.14	0.00	0.08	-2.43	-2.07	-2.29	-0.30
	W10005_0023	-0.03	-0.23	-0.10	0.05	2.50	1.66	0.43	-0.48
	W10005_0006	-0.07	-0.22	-0.14	-0.01	-1.41	-1.98	-4.09	1.84
	W10005_0234	-0.13	-0.12	-0.18	0.05	-0.30	-0.19	-9.27	-5.39
	W10005_0257	-0.13	-0.07	-0.15	0.12	0.12	-0.63	-0.51	-2.22
	W10005_0185	-0.14	-0.02	-0.15	-0.01	-2.78	-3.53	-1.54	-1.60
	W10005_0092	-0.15	0.45	-0.01	0.01	2.24	-0.07	-2.46	-1.81
	W10005_0186	-0.17	0.14	-0.13	-0.06	0.56	-1.28	-3.47	0.55
	W10005_0453	-0.21	0.36	-0.11	-0.12	-0.88	-2.41	4.06	5.77
	W10005_0063	-0.22	0.19	-0.20	-0.06	-0.14	1.15	2.13	3.55
	W10005_0429	-0.29	0.30	-0.19	-0.06	-0.20	1.97	1.72	-1.91
Random IO x PHJ40	W10005_0092	0.32	-0.06	0.34	0.11	2.82	1.52	0.57	-0.86
	W10005_0063	0.32	-0.14	0.30	-0.11	-3.25	-1.37	-2.80	-2.59
	W10005_0292	0.22	-0.06	0.21	0.00	1.52	1.64	5.47	1.10
	W10005_0006	0.21	-0.04	0.24	0.11	0.18	0.32	0.27	0.06

	W10005_0454	0.21	0.07	0.20	-0.06	-0.35	-0.89	-2.69	-2.22
	W10005_0429	0.18	-0.32	0.09	0.00	-1.33	-0.96	-5.05	-1.88
	W10005_0186	0.14	-0.14	0.06	0.04	1.33	0.47	-3.42	-6.92
	W10005_0214	0.12	-0.27	0.07	0.01	0.15	-0.64	-5.19	-1.04
	W10005_0453	0.10	-0.44	0.07	0.04	2.03	2.91	2.01	-0.91
	W10005_0305	0.06	0.26	0.13	-0.19	0.49	0.92	0.81	0.83
	W10005_0257	0.03	-0.05	0.03	0.00	1.84	2.48	-1.98	0.13
	W10005_0216	0.02	0.13	0.06	-0.06	1.99	1.64	-4.53	-0.75
	W10005_0185	-0.04	-0.04	-0.07	0.06	-1.19	-1.33	1.04	2.58
	W10005_0076	-0.05	-0.12	-0.09	-0.03	-0.87	1.14	-0.33	-0.82
	W10005_0234	-0.07	0.12	-0.04	0.04	-0.54	-0.48	2.76	4.02
	W10005_0192	-0.15	0.13	-0.09	-0.07	-0.75	-2.17	0.46	0.19
	W10005_0147	-0.15	0.21	-0.11	-0.06	-1.48	-2.25	3.57	1.42
	W10005_0399	-0.17	0.42	-0.06	-0.06	0.03	0.53	10.11	7.36
	W10005_0131	-0.17	0.15	-0.14	0.01	0.98	2.35	-0.58	-2.31
	W10005_0023	-0.18	-0.12	-0.22	-0.09	-2.22	-1.37	-4.06	-2.73
	W10005_0013	-0.22	-0.44	-0.35	0.11	-0.57	-0.38	-0.11	0.02
	W10005_0594	-0.22	0.02	-0.21	0.14	-1.49	-0.08	1.56	2.74
	W10005_0117	-0.28	0.28	-0.23	0.06	1.10	0.00	-2.16	1.26
	W10005_0229	-0.28	0.18	-0.23	0.06	-1.78	-0.16	1.75	-0.23
Random IO x PHJ89	W10005_0305	0.38	-0.25	0.31	0.09	2.72	2.00	-1.40	-2.90
	W10005_0185	0.32	-0.16	0.23	0.01	-3.87	-1.00	-4.12	-3.03
	W10005_0216	0.23	-0.23	0.17	0.03	3.72	2.12	0.43	1.04
	W10005_0023	0.18	0.18	0.27	0.08	2.36	2.43	3.42	-0.42
	W10005_0229	0.15	-0.19	0.11	-0.03	1.06	-1.49	7.49	7.78
	W10005_0429	0.15	-0.05	0.17	-0.02	-1.33	-2.90	-0.59	1.21
	W10005_0092	0.12	-0.10	0.11	0.08	-0.56	-0.76	-5.62	-1.67
	W10005_0234	0.12	-0.06	0.09	-0.16	-1.16	-0.61	-0.27	-0.71
	W10005_0006	0.11	-0.08	0.15	-0.02	2.29	2.51	0.70	0.53
	W10005_0399	0.09	-0.07	0.02	-0.10	0.05	-1.34	-9.57	-4.80
	W10005_0454	0.06	-0.25	-0.08	-0.02	0.51	1.90	4.21	1.25
	W10005_0076	0.04	-0.13	-0.02	-0.17	1.36	-0.49	-2.92	-2.60
	W10005_0131	0.00	0.36	0.07	-0.04	1.72	-0.59	3.69	0.92
	W10005_0147	-0.01	-0.04	-0.04	0.00	-1.85	-0.16	-1.89	-2.56
	W10005_0186	-0.03	0.18	0.00	0.15	-1.77	-0.06	-2.67	1.05
	W10005_0257	-0.05	0.17	0.03	-0.05	-0.05	-0.92	6.77	5.47
	W10005_0013	-0.06	0.31	0.07	-0.01	-0.99	-3.30	1.52	1.66
	W10005_0292	-0.07	-0.27	-0.17	0.00	5.11	2.52	2.76	2.17
	W10005_0117	-0.08	-0.17	-0.17	0.10	-2.49	-0.53	-8.74	-7.58
	W10005_0129	-0.08	0.59	0.15	0.10	1.67	1.53	3.42	2.32
	W10005_0063	-0.10	-0.01	-0.10	0.04	0.83	0.31	-3.80	-1.89
	W10005_0192	-0.19	-0.11	-0.24	-0.04	-3.47	-0.18	1.49	-1.47
	W10005_0594	-0.40	0.01	-0.41	-0.05	-5.17	-1.96	-0.46	-0.17

	W10005_0214	-0.62	0.42	-0.53	0.01	1.58	0.58	5.69	4.27
Tester	DH	SI	GM	GY	TW	PH	EH	GDDAnt	GDDSilk
Selected IO x LH185	W10005_0336	0.95	0.00	1.21	0.02	2.99	2.27	5.26	-0.15
	W10005_0329	0.55	0.06	0.75	0.27	-0.63	-1.00	-8.22	-6.32
	W10005_0150	0.48	-0.03	0.61	-0.12	1.66	1.97	8.10	6.45
	W10005_0024	0.47	0.02	0.76	-0.12	2.45	1.67	6.01	11.75
	W10005_0199	0.38	-0.14	0.30	0.10	3.27	-0.30	7.48	5.21
	W10005_0029	0.35	0.13	0.56	-0.05	0.99	0.39	3.94	6.84
	W10005_0444	0.33	0.03	0.51	-0.10	3.00	0.29	-3.26	-2.10
	W10005_0352	0.32	0.16	0.63	-0.04	-0.01	-0.58	1.13	2.89
	W10005_0294	0.27	-0.17	0.08	0.02	-2.87	-3.09	-4.19	-6.64
	W10005_0015	0.20	0.32	0.62	0.06	-0.77	1.32	0.39	-2.43
	W10005_0389	0.15	0.02	0.20	0.01	1.55	1.87	5.20	2.47
	W10005_0137	0.14	-0.34	-0.18	-0.33	1.12	0.47	5.47	5.15
	W10005_0225	0.11	0.44	0.63	0.05	-1.39	-0.58	5.74	3.72
	W10005_0426	0.11	-0.05	0.20	0.04	0.58	1.77	-4.51	-6.71
	W10005_0028	0.06	0.13	0.22	-0.06	0.25	-0.04	4.12	-1.14
	W10005_0331	0.05	-0.01	0.05	-0.07	-1.47	-1.40	-8.78	-2.15
	W10005_0005	0.03	0.18	0.18	0.03	-2.51	-0.67	4.62	3.66
	W10005_0139	-0.02	-0.30	-0.44	0.10	-1.22	-0.60	-4.08	-4.19
	W10005_0469	-0.10	0.12	-0.01	0.14	-2.77	-2.98	-1.78	-3.36
	W10005_0437	-0.11	-0.07	-0.23	-0.10	-4.01	-3.67	-8.24	-12.13
	W10005_0065	-0.12	-0.08	-0.25	-0.84	3.38	0.94	0.16	-2.28
	W10005_0202	-0.19	-0.03	-0.33	0.19	-2.21	-1.71	-3.58	0.85
	W10005_0218	-0.25	-0.11	-0.42	0.21	-1.82	-0.80	-2.87	1.27
	W10005_0245	-0.26	-0.06	-0.33	-0.13	-0.43	-0.15	-2.24	-1.49
	W10005_0124	-0.46	0.08	-0.57	0.15	-1.66	-1.27	-9.44	-7.72
	W10005_0339	-0.51	0.07	-0.62	0.10	2.78	-0.25	-6.69	1.26
	W10005_0445	-0.57	0.01	-0.77	0.19	-1.50	-1.54	-14.01	-18.51
	W10005_0153	-0.59	-0.03	-0.79	0.33	-0.73	0.04	3.34	2.87
	W10005_0405	-0.76	0.10	-0.90	-0.12	-2.46	0.44	18.29	17.13
	W10005_0156	-0.79	-0.14	-1.17	-0.06	3.05	2.23	4.37	7.63
Selected IO x LH74	W10005_0015	0.86	-0.15	0.95	0.08	0.40	-0.67	-8.80	-9.86
	W10005_0124	0.66	-0.04	0.96	0.13	0.57	-1.04	-6.12	-4.61
	W10005_0065	0.59	0.13	0.90	0.29	-4.44	-2.57	-2.47	3.22
	W10005_0137	0.48	0.11	0.70	0.10	-2.44	-2.64	-6.81	-7.50
	W10005_0199	0.44	-0.17	0.39	0.11	1.16	2.25	-4.01	-3.87
	W10005_0225	0.33	-0.29	0.15	0.11	3.33	2.47	-1.46	-6.98
	W10005_0426	0.31	-0.08	0.43	0.20	1.63	1.57	9.03	0.99
	W10005_0156	0.21	0.08	0.27	-0.16	1.07	0.24	10.00	5.82
	W10005_0339	0.15	-0.07	0.15	-0.35	0.24	-0.25	9.88	-3.48
	W10005_0389	0.15	0.10	0.29	-0.34	0.98	-1.92	14.40	12.67
	W10005_0028	0.13	0.11	0.34	-0.38	3.19	3.13	5.72	3.71

	W10005_0005	0.10	-0.20	-0.04	-0.32	-0.87	-1.44	-15.50	-17.91
	W10005_0153	0.00	0.18	0.15	-0.12	-0.87	-1.00	-7.55	-7.96
	W10005_0029	-0.01	0.00	-0.06	0.12	3.11	1.30	2.16	1.45
	W10005_0405	-0.05	0.16	0.14	0.17	1.24	2.77	5.60	9.05
	W10005_0331	-0.05	-0.06	-0.14	-0.05	1.47	1.25	1.96	3.50
	W10005_0218	-0.08	-0.13	-0.14	0.05	-0.68	-2.00	-3.52	-1.93
	W10005_0352	-0.09	0.04	-0.11	0.18	-4.39	-2.78	2.38	4.97
	W10005_0336	-0.16	-0.12	-0.32	-0.05	3.93	-1.32	-2.54	4.28
	W10005_0294	-0.20	0.18	-0.16	0.14	-3.46	-2.65	-13.61	-9.90
	W10005_0245	-0.29	-0.17	-0.48	-0.09	-1.53	-0.03	-1.72	-0.29
	W10005_0139	-0.37	-0.10	-0.63	0.16	0.96	0.25	4.55	9.13
	W10005_0444	-0.42	0.23	-0.34	0.05	1.15	0.41	2.22	2.15
	W10005_0445	-0.44	-0.08	-0.70	-0.30	0.94	0.16	6.93	4.97
	W10005_0024	-0.48	0.18	-0.38	0.15	3.19	3.86	1.81	-0.54
	W10005_0150	-0.58	0.16	-0.67	0.03	-2.09	0.51	-11.23	-10.14
	W10005_0329	-0.60	0.11	-0.67	0.00	0.29	1.44	0.14	-2.23
	W10005_0469	-1.15	-0.15	-1.60	0.13	-8.95	-2.44	10.19	23.00
Selected IO x PHB47	W10005_0405	0.59	-0.03	0.82	0.06	-0.01	-0.14	-3.29	-2.26
	W10005_0139	0.51	0.23	0.78	-0.01	0.72	1.03	1.72	-4.91
	W10005_0389	0.44	-0.05	0.52	0.22	-0.39	-0.19	-1.02	-2.29
	W10005_0137	0.34	0.07	0.48	0.21	-1.38	0.08	-1.54	-0.42
	W10005_0445	0.31	0.06	0.39	0.33	0.70	0.31	3.30	7.71
	W10005_0156	0.24	0.10	0.29	-0.11	-4.22	-2.04	-9.45	-9.59
	W10005_0469	0.24	-0.15	0.16	-0.29	2.84	0.98	-3.93	-12.75
	W10005_0329	0.14	-0.07	0.08	0.03	1.94	0.54	3.80	3.68
	W10005_0005	0.11	0.02	0.16	0.36	1.04	1.34	-2.70	-1.16
	W10005_0352	0.10	-0.02	0.10	-0.48	2.82	1.87	4.30	1.34
	W10005_0218	0.10	-0.01	0.18	-0.21	2.02	1.68	4.81	6.97
	W10005_0202	0.07	-0.14	-0.02	-0.38	1.05	1.42	-1.36	-4.56
	W10005_0029	0.02	-0.04	-0.06	-0.24	1.27	-0.70	-1.39	0.80
	W10005_0225	-0.04	-0.16	-0.16	0.07	2.34	0.40	-4.06	3.14
	W10005_0336	-0.05	0.11	-0.02	-0.35	-1.12	-0.73	11.21	14.50
	W10005_0028	-0.06	0.21	0.26	0.12	-1.07	-3.46	-11.08	-4.68
	W10005_0437	-0.06	0.09	0.01	0.00	-0.55	-2.14	-10.24	-7.47
	W10005_0426	-0.08	0.16	0.11	-0.08	-1.37	0.68	4.23	-4.19
	W10005_0199	-0.11	-0.01	-0.17	-0.06	-1.47	1.24	8.25	8.34
	W10005_0153	-0.11	-0.23	-0.34	0.05	2.33	1.26	-1.00	-0.11
	W10005_0331	-0.11	0.04	-0.12	0.19	-0.14	-0.40	0.12	3.00
	W10005_0294	-0.13	-0.13	-0.36	0.07	0.94	1.89	6.90	3.64
	W10005_0024	-0.14	-0.04	-0.11	0.16	-0.08	0.32	-5.62	-6.84
	W10005_0124	-0.14	0.05	-0.07	-0.03	0.27	-0.19	4.23	3.60
	W10005_0339	-0.28	-0.22	-0.59	-0.10	0.50	-0.42	-2.12	2.83
	W10005_0150	-0.33	-0.06	-0.46	-0.03	-0.30	0.50	5.23	3.79

	W10005_0245	-0.36	0.15	-0.26	0.32	-1.53	-1.16	-4.60	-10.08
	W10005_0015	-0.37	-0.12	-0.59	0.05	1.68	0.00	0.62	1.83
	W10005_0444	-0.39	0.01	-0.50	0.08	-3.48	0.40	3.26	6.14
	W10005_0065	-0.69	-0.06	-0.92	0.07	-3.31	-1.00	2.46	1.20
Selected IO x PHJ40	W10005_0218	0.72	0.04	1.05	0.10	1.34	-0.23	1.90	-1.64
	W10005_0139	0.47	-0.09	0.38	-0.34	0.81	-0.14	0.50	3.77
	W10005_0331	0.26	0.05	0.41	-0.14	0.56	-1.46	7.59	-2.22
	W10005_0294	0.26	-0.05	0.22	-0.16	0.92	1.36	-0.67	1.18
	W10005_0005	0.23	-0.06	0.26	-0.07	-1.17	1.13	2.72	1.35
	W10005_0469	0.22	0.11	0.42	-0.11	3.43	2.02	-5.26	-6.31
	W10005_0444	0.18	-0.11	0.12	0.19	-1.15	-0.61	-4.78	-3.40
	W10005_0225	0.15	0.08	0.29	-0.10	2.29	0.81	2.67	5.93
	W10005_0336	0.14	0.01	0.11	-0.07	-2.87	0.68	-4.24	-5.40
	W10005_0199	0.14	0.06	0.21	-0.06	0.02	1.26	-1.60	-1.74
	W10005_0029	0.09	0.09	0.12	-0.16	0.43	0.39	8.98	6.29
	W10005_0405	0.08	0.08	0.22	-0.10	1.33	-1.40	-4.80	-3.08
	W10005_0150	0.04	0.11	0.11	0.27	-1.61	-1.67	-2.03	-1.56
	W10005_0339	0.03	0.11	0.11	0.47	1.34	3.15	0.85	2.08
	W10005_0153	0.02	0.03	0.07	-0.11	-3.68	-2.23	-1.44	-3.93
	W10005_0137	0.01	0.09	0.12	-0.05	-1.47	-1.04	-1.53	2.29
	W10005_0028	-0.21	-0.11	-0.30	0.10	-0.68	0.76	1.26	0.33
	W10005_0329	-0.24	-0.03	-0.38	0.16	-1.00	-0.32	-0.11	-2.01
	W10005_0015	-0.26	0.02	-0.30	0.04	-1.03	-2.15	-0.72	-0.40
	W10005_0352	-0.28	0.07	-0.27	0.32	1.45	0.38	0.74	-2.33
	W10005_0426	-0.31	-0.18	-0.49	-0.14	0.09	0.97	-7.18	2.06
	W10005_0065	-0.32	-0.01	-0.44	0.15	0.19	-1.61	1.20	1.25
	W10005_0024	-0.46	-0.13	-0.68	-0.21	-3.35	-1.08	-2.04	-4.71
	W10005_0124	-0.55	-0.04	-0.73	-0.07	2.14	1.41	10.53	12.58
	W10005_0389	-0.70	-0.14	-0.99	0.25	0.32	3.91	-6.07	-4.48
Selected IO x PHJ89	W10005_0444	0.77	-0.11	0.90	-0.21	0.25	-0.23	3.65	-1.45
	W10005_0389	0.67	0.18	1.13	-0.32	0.10	-1.40	-6.38	-6.15
	W10005_0469	0.65	0.09	0.94	0.21	4.07	1.45	0.10	-1.03
	W10005_0153	0.64	0.08	0.95	-0.04	2.65	2.57	7.17	10.75
	W10005_0329	0.64	-0.12	0.62	-0.13	0.02	0.80	0.31	0.06
	W10005_0015	0.64	0.06	0.96	-0.22	2.03	3.22	6.58	10.34
	W10005_0028	0.54	-0.13	0.70	-0.09	-0.36	0.70	5.54	6.65
	W10005_0150	0.40	-0.21	0.30	-0.05	2.57	0.08	0.15	1.79
	W10005_0065	0.39	0.00	0.49	0.11	4.51	3.32	0.31	-1.19
	W10005_0139	0.31	0.10	0.39	-0.07	0.82	0.66	0.99	0.22
	W10005_0294	0.26	0.04	0.28	0.05	3.22	1.56	6.71	7.61
	W10005_0029	0.25	-0.25	-0.05	0.23	-5.06	-1.36	-17.04	-19.31
	W10005_0352	0.25	-0.24	0.04	-0.29	0.90	1.32	-6.32	-0.64
	W10005_0339	0.25	0.00	0.29	-0.03	-4.50	-1.50	-2.22	-3.37

	W10005_0331	0.17	-0.01	0.20	0.03	-0.43	1.55	-4.59	-4.52
	W10005_0445	0.10	-0.20	-0.20	-0.13	-2.73	-0.37	-2.61	-3.30
	W10005_0156	-0.03	-0.23	-0.38	0.25	-0.71	0.23	3.49	4.95
	W10005_0199	-0.06	0.26	0.11	-0.01	-2.39	-2.82	-3.69	-0.05
	W10005_0024	-0.09	0.13	0.11	0.24	-1.87	-5.01	1.29	2.31
	W10005_0245	-0.12	0.16	0.07	0.13	1.50	-0.77	1.96	2.86
	W10005_0405	-0.12	-0.20	-0.28	0.20	0.47	0.33	-9.12	-11.50
	W10005_0437	-0.17	-0.03	-0.23	0.31	3.42	4.65	11.41	11.80
	W10005_0124	-0.21	-0.06	-0.34	0.00	-3.50	-2.26	-4.68	-8.63
	W10005_0426	-0.41	0.36	-0.07	-0.11	-1.16	-5.40	0.83	4.93
	W10005_0202	-0.46	0.11	-0.47	0.37	-0.16	0.19	4.72	4.14
	W10005_0336	-0.60	-0.07	-0.90	0.02	-0.83	-0.43	-5.20	-8.60
	W10005_0137	-0.76	0.05	-0.92	0.02	4.45	3.24	9.23	6.67
	W10005_0225	-0.76	-0.04	-1.04	-0.17	-5.64	-3.02	-4.29	-4.45
	W10005_0005	-0.80	0.08	-0.94	0.00	2.03	-2.19	4.71	5.34
	W10005_0218	-1.50	0.24	-1.75	-0.33	-2.15	-0.66	-3.91	-6.83

Tester	DH	SI	GM	GY	TW	PH	EH	GDDAnt	GDDSilk
Random SS x DK3IIH6	W10004_0008	0.64	-0.02	0.73	-0.05	0.29	-0.57	-0.65	-2.06
	W10004_0217	0.38	0.27	0.64	0.72	-2.52	-3.28	-2.68	-1.42
	W10004_0208	0.29	0.11	0.43	0.21	1.22	2.53	-6.99	-3.52
	W10004_0087	0.29	-0.53	0.28	0.03	3.88	5.05	2.50	0.08
	W10004_0152	0.21	0.27	0.46	0.40	-0.24	-2.40	-7.91	-2.21
	W10004_0206	0.16	0.17	0.25	0.36	1.65	-0.45	5.00	5.20
	W10004_0131	0.05	0.02	0.07	0.18	-1.47	-1.40	-4.13	-2.80
	W10004_0066	0.04	-0.14	0.10	0.48	1.77	1.68	-2.95	-1.00
	W10004_0053	0.02	0.31	0.19	-0.36	-6.88	-6.41	-9.60	-6.67
	W10004_0275	-0.04	-0.40	-0.10	-0.07	-0.60	0.54	-0.70	-0.29
	W10004_0178	-0.04	0.01	-0.05	0.08	1.68	1.30	1.95	0.11
	W10004_0007	-0.08	-0.48	-0.35	0.47	-4.61	-3.43	-0.77	2.71
	W10004_0133	-0.13	-0.37	-0.23	-0.18	3.04	3.39	-5.90	-4.43
	W10004_0223	-0.14	-0.58	-0.35	-0.32	3.26	4.50	6.46	-0.12
	W10004_0120	-0.16	-0.22	-0.24	-0.57	4.38	1.59	3.80	4.80
	W10004_0169	-0.18	-0.07	-0.36	-0.09	-1.21	-0.37	-1.83	2.07
	W10004_0185	-0.21	0.31	-0.11	-0.16	-4.32	-2.79	-2.48	-2.44
	W10004_0063	-0.25	0.07	-0.24	-0.07	3.62	3.51	4.94	-2.15
	W10004_0013	-0.31	0.06	-0.35	-0.18	-1.35	-0.45	3.28	1.47
	W10004_0181	-0.33	0.41	-0.28	-0.34	-0.30	0.12	2.26	0.62
	W10004_0220	-0.35	0.37	-0.32	-0.36	-1.62	-0.75	8.93	4.31
	W10004_0098	-0.59	0.22	-0.66	-0.20	2.05	0.41	8.36	8.44
Random SS x LH185	W10004_0275	0.49	0.34	0.87	-0.78	-0.28	-1.17	-3.70	-0.72
	W10004_0007	0.39	0.14	0.55	0.05	2.73	3.59	7.63	-1.05
	W10004_0169	0.30	-0.19	0.23	-0.12	4.00	1.88	7.61	-1.85
	W10004_0181	0.21	-0.19	0.24	0.07	-0.86	1.96	-0.03	0.13

	W10004_0013	0.20	0.11	0.35	0.52	1.68	1.01	-9.71	-6.07
	W10004_0185	0.18	-0.25	0.19	-0.29	1.73	0.07	0.75	3.49
	W10004_0178	0.14	-0.05	0.18	-0.54	3.42	1.09	-1.97	-0.16
	W10004_0223	0.11	0.45	0.31	0.24	2.44	-1.75	-1.06	1.54
	W10004_0206	0.11	0.46	0.34	0.47	2.10	-1.95	-1.50	2.05
	W10004_0008	0.09	-0.44	-0.11	1.08	-4.28	1.35	4.69	-0.92
	W10004_0131	0.09	0.51	0.31	-0.20	3.02	0.20	-1.68	0.08
	W10004_0220	0.07	0.40	0.21	0.14	-2.31	-0.09	-6.15	-0.04
	W10004_0133	0.05	0.15	0.16	0.50	-1.28	0.19	0.10	1.99
	W10004_0208	0.02	0.25	0.15	0.08	-1.97	-3.97	-1.83	-1.78
	W10004_0087	0.02	-0.29	-0.07	-0.34	-3.98	-3.95	-4.55	-0.96
	W10004_0063	-0.01	-0.32	-0.14	-0.56	-0.73	0.16	-0.13	3.69
	W10004_0120	-0.02	-0.63	-0.30	0.05	-3.96	-3.66	-10.81	-7.04
	W10004_0049	-0.11	-0.26	-0.28	-0.54	-3.97	-1.55	-6.54	-2.17
	W10004_0217	-0.14	-0.30	-0.34	-0.95	-1.52	-1.27	9.84	2.15
	W10004_0053	-0.20	0.11	-0.23	-0.19	4.34	5.28	15.87	5.81
	W10004_0098	-0.21	-0.51	-0.54	0.59	1.55	0.25	-12.32	-5.81
	W10004_0066	-0.26	0.30	-0.27	0.11	-1.84	-2.21	4.89	0.48
	W10004_0143	-0.26	0.14	-0.36	0.28	3.47	1.58	5.56	2.26
	W10004_0152	-0.41	-0.15	-0.58	0.06	-1.01	2.40	7.22	3.81
	W10004_0111	-0.63	0.35	-0.66	-0.08	-2.21	-1.97	2.26	5.17
Random SS x PHG72	W10004_0098	0.46	0.09	0.53	-0.01	-0.25	0.90	6.42	1.11
	W10004_0143	0.39	-0.03	0.49	-0.22	-0.38	0.06	-5.53	-1.49
	W10004_0131	0.18	-0.18	0.16	-0.24	1.56	1.30	-1.52	-1.60
	W10004_0066	0.17	0.11	0.34	-0.28	-0.38	1.25	-1.88	-1.05
	W10004_0049	0.14	0.10	0.13	-0.36	2.87	0.57	6.65	2.88
	W10004_0223	0.14	0.24	0.27	0.50	-0.65	-1.01	-2.76	-1.57
	W10004_0063	0.14	-0.03	0.20	0.07	-3.42	-3.52	-5.17	-0.98
	W10004_0120	0.10	0.37	0.20	0.09	1.81	1.94	2.50	-2.52
	W10004_0152	0.04	0.02	0.09	-0.27	1.82	0.03	2.94	3.96
	W10004_0185	0.04	-0.47	-0.09	-0.02	-2.53	-0.85	-2.84	-0.86
	W10004_0208	0.03	-0.03	0.06	0.27	2.77	1.65	5.21	3.77
	W10004_0178	0.01	-0.10	-0.02	0.94	-5.69	-4.53	-1.76	0.82
	W10004_0206	0.01	-0.18	-0.10	-0.87	-2.57	2.10	-0.43	-2.33
	W10004_0007	0.00	0.34	0.05	-0.02	-2.48	-1.57	-2.81	-1.61
	W10004_0169	-0.01	-0.12	-0.15	-0.45	-1.61	-1.70	1.98	2.87
	W10004_0220	-0.02	-0.64	-0.29	-0.31	-0.57	-3.43	-6.91	-8.12
	W10004_0275	-0.10	-0.23	-0.15	0.85	3.13	2.53	4.19	0.61
	W10004_0008	-0.17	0.41	-0.15	-0.20	2.14	-0.35	-3.72	-0.12
	W10004_0181	-0.18	-0.09	-0.25	0.18	2.57	1.57	2.71	1.30
	W10004_0053	-0.19	-0.01	-0.23	0.05	-0.33	-0.84	-2.46	-0.88
	W10004_0217	-0.22	-0.03	-0.34	0.21	5.95	3.99	3.24	2.92
	W10004_0133	-0.23	0.23	-0.20	0.21	-4.17	-2.18	0.32	1.78

	W10004_0013	-0.27	-0.16	-0.29	0.30	-0.94	-0.23	3.10	1.99
	W10004_0087	-0.38	0.30	-0.35	-0.04	-0.87	1.43	-4.59	-2.97
Random SS x PHP02	W10004_0098	0.47	-0.10	0.50	0.02	-0.20	1.89	-1.49	-3.27
	W10004_0053	0.37	-0.06	0.60	-0.08	3.65	3.20	4.58	6.20
	W10004_0169	0.34	0.21	0.46	0.21	-3.09	-1.65	-10.03	-4.51
	W10004_0220	0.31	-0.17	0.38	0.27	3.42	2.66	1.36	3.67
	W10004_0007	0.17	0.11	0.24	-0.28	3.83	1.93	1.05	2.11
	W10004_0111	0.17	-0.29	0.27	-0.25	2.75	2.26	-1.21	-3.89
	W10004_0133	0.13	0.21	0.33	-0.31	1.58	-0.55	6.35	1.09
	W10004_0217	0.12	0.07	0.17	-0.29	-4.25	-2.13	-13.62	-5.58
	W10004_0008	0.09	0.23	0.19	-0.58	2.58	2.24	1.24	2.90
	W10004_0143	0.08	-0.14	0.00	0.21	-2.97	-1.35	-3.47	-1.80
	W10004_0049	0.05	-0.10	0.03	0.14	-0.19	1.16	-0.03	0.57
	W10004_0181	0.05	-0.21	0.01	0.43	-1.77	-3.34	-6.03	-2.59
	W10004_0178	0.01	0.30	0.13	-0.43	1.15	1.09	3.13	-0.12
	W10004_0223	0.01	-0.01	-0.03	-0.13	-3.63	-0.83	3.45	2.76
	W10004_0120	-0.01	0.10	-0.05	0.47	-0.42	-0.05	-3.06	-0.34
	W10004_0206	-0.03	-0.36	-0.20	0.16	-1.95	-0.54	-4.50	-5.63
	W10004_0152	-0.07	-0.26	-0.24	-0.05	1.84	0.92	0.23	-2.79
	W10004_0013	-0.12	-0.04	-0.14	-0.35	-1.02	-1.03	1.27	0.76
	W10004_0131	-0.12	-0.16	-0.20	0.13	-4.19	-2.48	8.65	4.79
	W10004_0063	-0.12	0.11	-0.16	0.44	2.83	0.22	2.33	1.04
	W10004_0208	-0.13	-0.04	-0.22	-0.33	0.61	1.94	3.19	1.08
	W10004_0185	-0.19	0.43	-0.10	0.16	2.53	0.66	0.87	-1.33
	W10004_0087	-0.22	0.47	-0.13	0.63	-3.03	-5.42	3.43	1.83
	W10004_0066	-0.38	-0.36	-0.60	-0.08	1.42	0.70	1.90	1.57
	W10004_0275	-0.55	0.22	-0.85	-0.13	-1.29	-0.42	-1.79	-1.19
Tester	DH	SI	GM	GY	TW	PH	EH	GDDAnt	GDDSilk
Selected SS x DK3IIH6	W10004_0115	0.82	-0.71	0.55	0.01	1.99	1.31	1.04	-1.04
	W10004_0258	0.64	-0.62	0.23	-0.23	1.47	3.39	-3.64	-2.47
	W10004_0313	0.57	0.01	0.60	-0.09	2.91	-0.56	3.64	1.48
	W10004_0119	0.42	-0.07	0.44	0.28	2.55	2.55	-1.75	1.35
	W10004_0041	0.39	0.26	0.56	0.02	1.49	2.04	1.57	2.63
	W10004_0145	0.17	-0.36	0.18	-0.18	2.85	2.80	4.43	7.26
	W10004_0101	0.13	-0.28	0.04	-0.11	4.20	1.53	1.39	0.76
	W10004_0144	0.11	-0.13	0.22	0.04	-2.74	-3.74	-7.75	-11.80
	W10004_0026	0.11	0.20	0.21	-0.06	5.91	3.86	-1.39	2.99
	W10004_0090	0.11	-0.18	-0.01	0.02	-4.75	-4.11	-7.55	-9.82
	W10004_0069	0.10	0.00	0.17	0.04	-4.54	-3.83	0.68	-1.80
	W10004_0038	0.08	-0.38	-0.08	-0.03	0.93	1.48	-3.23	-5.02
	W10004_0232	0.04	-0.22	-0.03	-0.10	-1.77	-3.80	-5.15	-5.66
	W10004_0094	0.04	0.36	0.24	0.09	-1.68	-1.82	-5.25	-3.81
	W10004_0121	0.03	-0.07	0.07	0.20	-2.28	-1.31	-4.50	-6.37

	W10004_0105	0.03	-0.28	-0.05	-0.04	-0.62	-0.02	-3.20	-5.23
	W10004_0225	0.03	0.23	0.12	-0.10	0.66	-1.07	0.16	0.94
	W10004_0142	0.01	-0.09	0.10	0.11	-2.81	-0.49	2.66	0.21
	W10004_0212	-0.11	0.13	-0.04	0.06	2.97	0.07	-0.65	1.46
	W10004_0080	-0.14	-0.40	-0.27	-0.08	2.79	1.95	2.68	2.10
	W10004_0192	-0.16	-0.02	-0.22	-0.02	-3.99	-2.61	-1.50	-6.95
	W10004_0140	-0.30	-0.35	-0.45	0.00	4.02	6.33	1.64	7.33
	W10004_0045	-0.31	0.25	-0.22	-0.08	0.93	2.47	0.18	5.83
	W10004_0148	-0.36	0.03	-0.47	0.09	-0.44	-1.78	4.41	3.64
	W10004_0202	-0.42	0.82	-0.12	-0.03	-4.37	-4.22	2.21	4.41
	W10004_0031	-0.43	0.03	-0.40	0.12	0.21	1.72	5.47	6.01
	W10004_0123	-0.44	0.13	-0.36	0.18	0.43	0.00	2.89	-6.11
	W10004_0064	-0.51	0.18	-0.40	-0.08	-5.92	-6.12	-0.41	1.77
	W10004_0306	-0.64	-0.23	-0.75	0.06	3.96	4.42	-2.23	-5.34
	W10004_0095	-1.06	1.40	-0.46	-0.10	-2.71	2.34	13.45	21.02
Selected SS x LH185	W10004_0202	0.72	-0.61	0.43	-0.08	-0.60	2.44	-5.31	-3.68
	W10004_0105	0.62	-0.04	0.64	0.10	1.44	-2.00	-7.27	-9.55
	W10004_0064	0.54	-0.22	0.51	-0.13	5.51	-0.21	1.32	4.10
	W10004_0192	0.46	0.05	0.48	-0.11	2.68	3.69	6.93	9.82
	W10004_0142	0.42	0.07	0.56	-0.01	5.37	2.00	2.96	3.99
	W10004_0090	0.34	-0.40	0.04	-0.28	1.15	3.55	-2.27	-7.03
	W10004_0225	0.32	0.32	0.51	0.14	-1.59	0.64	-3.61	-1.25
	W10004_0123	0.29	-0.37	0.08	-0.08	1.17	1.17	-1.41	1.30
	W10004_0148	0.28	0.23	0.39	0.10	-7.09	-5.60	-3.31	-5.01
	W10004_0080	0.25	0.61	0.61	-0.24	-3.08	-0.43	5.99	0.87
	W10004_0101	0.18	-0.39	-0.05	0.17	2.37	1.55	-5.52	-8.15
	W10004_0121	0.17	-0.07	0.15	0.26	4.10	2.86	3.51	4.05
	W10004_0026	0.16	0.16	0.23	-0.12	-5.77	-5.44	7.63	3.64
	W10004_0115	0.12	-0.02	0.15	-0.16	7.90	1.87	-4.18	-5.39
	W10004_0306	0.11	-0.27	-0.05	0.11	-2.35	-4.10	0.69	-0.74
	W10004_0031	0.11	-0.28	-0.02	-0.17	1.11	2.53	-2.49	-1.06
	W10004_0140	0.10	-0.50	-0.19	0.18	1.03	0.75	-5.93	-12.13
	W10004_0041	0.03	-0.11	-0.05	0.10	3.26	0.33	0.41	1.10
	W10004_0212	0.02	-0.23	-0.12	-0.01	-0.73	-3.51	-5.72	-2.76
	W10004_0045	0.00	0.43	0.14	-0.07	-2.63	-1.60	4.23	2.37
	W10004_0313	-0.20	0.37	-0.12	0.19	-5.12	-3.87	-3.51	-2.38
	W10004_0038	-0.20	0.01	-0.29	0.05	-5.01	-1.80	-0.39	-0.54
	W10004_0258	-0.27	-0.21	-0.49	-0.17	-0.12	-0.86	1.41	-0.49
	W10004_0094	-0.34	0.08	-0.36	0.10	-2.52	-2.06	4.37	-0.13
	W10004_0069	-0.37	0.33	-0.29	0.19	2.71	2.20	1.39	7.85
	W10004_0119	-0.37	0.32	-0.35	-0.31	0.86	2.18	4.50	9.70
	W10004_0232	-0.41	0.09	-0.46	-0.16	4.99	5.66	6.31	7.35
	W10004_0145	-0.44	0.81	-0.17	0.50	-2.16	-1.18	-2.06	-5.91

	W10004_0095	-0.54	-0.07	-0.53	-0.36	-2.08	-0.58	-1.56	-1.00
	W10004_0144	-0.91	0.05	-0.95	0.17	-4.36	-2.10	5.83	20.36
Selected SS x PHG72	W10004_0148	0.67	-0.16	0.60	0.11	4.16	4.69	0.91	4.41
	W10004_0145	0.41	-0.73	0.21	-0.47	-0.26	-2.46	-0.63	-1.70
	W10004_0045	0.38	-0.28	0.32	0.18	5.31	2.42	1.80	-1.91
	W10004_0080	0.37	-0.24	0.35	0.27	-0.65	-0.87	-8.21	-6.84
	W10004_0069	0.35	-0.23	0.28	-0.10	-0.50	1.57	-2.75	-3.06
	W10004_0225	0.34	0.05	0.42	0.02	0.73	0.92	2.55	-4.61
	W10004_0202	0.31	-0.32	0.22	0.14	2.57	0.58	-2.64	-4.00
	W10004_0094	0.28	-0.19	0.28	-0.06	3.10	1.82	-0.74	-1.62
	W10004_0115	0.25	0.06	0.30	-0.16	-2.63	0.42	4.25	8.88
	W10004_0258	0.20	0.07	0.15	0.13	-3.83	-0.92	1.04	3.09
	W10004_0041	0.16	-0.32	0.03	-0.45	-1.89	-1.05	-4.68	-5.44
	W10004_0123	0.16	0.03	0.20	-0.04	-1.34	-1.11	-0.73	4.50
	W10004_0306	0.16	0.43	0.35	0.10	-0.75	-1.28	1.26	1.33
	W10004_0140	0.15	0.83	0.46	0.01	0.32	-2.75	4.98	6.66
	W10004_0232	0.09	0.19	0.19	-0.01	-3.95	-0.34	-0.19	1.57
	W10004_0095	0.02	-0.68	-0.09	0.01	4.69	0.79	-0.08	-4.01
	W10004_0038	-0.04	0.23	0.00	-0.21	-1.12	-1.79	2.80	5.39
	W10004_0031	-0.06	0.28	0.06	0.17	0.29	-3.10	1.71	2.12
	W10004_0313	-0.10	-0.50	-0.37	-0.11	-1.37	1.75	-2.52	-4.37
	W10004_0090	-0.12	-0.11	-0.23	-0.36	0.43	-0.18	2.16	2.52
	W10004_0192	-0.15	0.16	-0.17	0.16	0.38	-2.18	-3.14	-2.68
	W10004_0212	-0.19	0.19	-0.15	0.19	4.17	4.38	4.60	0.97
	W10004_0026	-0.24	0.03	-0.24	0.55	-1.33	1.37	-3.35	-3.49
	W10004_0142	-0.34	0.18	-0.27	0.08	-1.13	-1.37	-6.73	-6.49
	W10004_0064	-0.35	-0.57	-0.53	0.15	0.30	1.90	-8.64	-17.59
	W10004_0105	-0.41	0.47	-0.31	0.03	-0.95	0.95	8.78	13.08
	W10004_0119	-0.46	0.05	-0.45	0.12	-4.18	-5.42	-0.26	-7.36
	W10004_0144	-0.59	0.31	-0.38	-0.03	-0.10	0.94	1.60	5.42
	W10004_0101	-0.61	0.04	-0.68	-0.15	-2.96	-0.84	-0.38	2.50
	W10004_0121	-0.82	0.67	-0.67	-0.15	-0.08	-1.14	5.26	9.81
Selected SS x PHP02	W10004_0121	0.63	-0.50	0.49	-0.21	-1.72	-0.04	-2.13	-2.64
	W10004_0212	0.56	0.07	0.65	-0.21	-4.62	-0.58	0.80	0.33
	W10004_0306	0.54	0.13	0.65	-0.17	-2.44	-0.04	1.05	6.05
	W10004_0038	0.49	-0.15	0.42	0.05	3.93	3.03	-0.28	-1.58
	W10004_0192	0.48	-0.07	0.50	-0.04	3.93	2.79	1.65	9.85
	W10004_0101	0.38	0.38	0.60	-0.03	-5.90	-3.75	2.52	3.22
	W10004_0232	0.38	0.08	0.47	0.11	0.95	-2.01	-0.29	-0.53
	W10004_0119	0.37	-0.21	0.38	-0.07	0.09	0.08	-3.61	-6.54
	W10004_0140	0.31	-0.38	0.11	-0.19	-3.21	-2.01	0.85	3.23
	W10004_0258	0.22	0.29	0.35	0.18	3.87	-0.67	0.79	-2.27
	W10004_0031	0.18	0.11	0.29	0.10	1.06	1.42	-0.82	-1.47

W10004_0045	0.16	0.02	0.19	0.02	-1.10	-0.09	-2.52	-3.26
W10004_0105	0.13	0.06	0.16	0.05	2.40	2.85	5.55	4.51
W10004_0144	0.12	-0.25	0.14	-0.07	3.47	2.56	-2.61	-10.40
W10004_0090	0.11	0.05	0.09	0.48	-1.07	-2.42	1.88	0.91
W10004_0026	0.11	-0.23	0.00	-0.16	1.38	-0.16	-2.95	-5.04
W10004_0095	0.05	-0.67	-0.08	0.30	1.32	-0.81	-9.13	-8.79
W10004_0123	0.01	0.05	0.01	0.01	1.63	1.32	0.34	-0.73
W10004_0313	-0.09	-0.27	-0.22	-0.05	0.38	1.27	-0.65	0.95
W10004_0094	-0.18	0.04	-0.17	0.09	3.04	1.07	2.05	6.12
W10004_0148	-0.21	-0.25	-0.36	-0.12	5.11	3.92	0.00	-0.20
W10004_0064	-0.24	0.39	-0.10	-0.08	-1.89	3.16	3.56	1.77
W10004_0069	-0.24	-0.22	-0.35	-0.19	0.75	-1.40	-0.97	-3.74
W10004_0202	-0.26	0.18	-0.23	-0.07	1.11	0.38	3.08	-1.20
W10004_0041	-0.32	0.36	-0.24	0.30	-4.15	-2.17	1.12	0.09
W10004_0225	-0.38	-0.06	-0.47	-0.12	-1.49	-0.52	-2.30	-2.82
W10004_0080	-0.49	0.69	-0.30	-0.05	1.63	0.41	3.31	9.25
W10004_0145	-0.59	0.49	-0.45	0.13	-0.63	0.33	-0.98	-0.03
W10004_0142	-0.60	0.02	-0.67	-0.07	-1.10	-0.92	1.37	2.02
W10004_0115	-1.54	0.13	-1.60	0.06	-6.23	-5.56	-1.94	-3.20