A *Very Oil Yellow1* modifier of the *Oil Yellow1-N1989* allele uncovers a cryptic phenotypic impact of cis-regulatory variation in maize

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Abstract

Detecting phenotypically relevant variation outside the coding sequence of genes and distinguishing it from the neutral variants is not trivial partly because the mechanisms by which a subset of the DNA polymorphisms in these regions affect gene regulation are poorly understood. Here we present an approach of using dominant genetic markers with convenient phenotypes to investigate the effect of cis and trans-acting regulatory variations. In the current study, we performed a forward genetic screen for natural variants that suppress or enhance the semi-dominant mutant allele *Oy1-N1989* encoding the magnesium chelatase subunit I of maize. This mutant permits rapid phenotyping of leaf color as a reporter of chlorophyll accumulation, enabling QTL mapping and GWAS approaches to identify natural variation in maize affecting chlorophyll metabolism. Using different mapping approaches, we identified the same modifier locus, *very oil yellow 1* (*vey1*), that was linked to the reporter gene itself. Based on the analysis of OY1 transcript abundance and study of a maize gene expression dataset, *vey1* is predicted to be a cis-acting regulatory sequence polymorphism that causes the differential accumulation of OY1 transcripts encoded by the mutant and wild-type alleles. Fine mapping of the *vey1* genomic region using multiple independent mapping populations demonstrated the value of multiple cycles of early generation random mating to increase recombination. The *vey1* allele appears to be a common polymorphism in the maize germplasm that alters the expression level of a key gene in chlorophyll biosynthesis.

KEYWORDS chlorophyll biosynthesis; cryptic variation; cis-acting; complex traits; epistasis

Introduction

Enzymatic conversion of protoporphyrin IX into magnesium protoporphyrin IX is the first committed step in chlorophyll biosynthesis (Wettstein *et al.* 1995). This is catalyzed by magnesium chelatase, a hetero-oligomeric enzyme consisting of three subunits that are conserved from prokaryotes to plants and are referred to as subunit I, D, and H. The magnesium chelatase subunit I is encoded by the *oil yellow 1* (*oy1*; GRMZM2G419806) gene of maize. Weak loss-of-function alleles at this gene result in recessive yellow-green plants while strong alleles result in the albino seedling-lethal phenotype. Dominant and semi-dominant alleles of this locus arise when amino acid changes in the protein results in the altered assembly of the magnesium chelatase complex. One such allele *Oy1-N1989* carries an amino acid change from leucine to phenylalanine at position 176 (L176F) (Sawers *et al.* 2006). Heterozygous *Oy1-N1989* plants have the eponymous oil-yellow color but are reasonably vigorous and produce both ears and tassels. Homozygotes, however, exhibit the albinism and seedling lethality expected of a loss-of-function mutant. This is consistent with the protein encoded by the mutant allele lacking activity.

In previous work, heterozygotes with a hypomorphic recessive allele of *oy1* and the dominant *Oy1-N1989* allele exhibited increased phenotypic severity as compared to the *Oy1-N1989* heterozygotes with a wild-type *oy1* allele (Sawers *et al.* 2006). Replacement of wild-type *oy1* allele with a recessive hypomorphic allele increased the phenotypic impact of *Oy1-N1989*, suggesting that the mutant protein encoded by *Oy1-N1989* lacks activity and decreased overall magnesium chelatase activity of heterozygotes. *Oy1-N1989* is a dominant-negative neomorphic allele and a recombinant protein containing the orthologous mutation to the *Synecocystis* acted as a competitive inhibitor of magnesium chelatase activity conferred by wild-type subunit I *in vitro* (Sawers *et al.* 2006).

Genetic variation in the coding or regulatory sequences affect differences between genotypes and is fundamental to crop improvement (Springer and Stupar 2007). Maize has an approximate genome size of 2,300 megabase pairs with an estimated 32,000 protein-coding genes (Schnable *et al.* 2009). Forward and reverse genetics approaches have been successful in the identification and characterization of many of these genetic variants. Common among these strategies is the focus on phenotype and gene relationships to determine its function. These methods have proven successful for identifying genes with large impacts following their disruption. Genes with conditional impacts on phenotypes, or requiring genetic interactions or modifiers to express effects on phenotype, are still difficult to observe. Using mutants of known phenotypic impact and physiological mechanism to detect the modifier genes and their mode of action leverages these resources to expand our understanding of biological processes and improve fundamental understanding of gene functions.

Recently, a forward genetics approach called Mutant-Assisted Gene Identification and Characterization (MAGIC) was proposed to detect modifiers and expose cryptic variation affecting traits of interest (Johal et al. 2008). MAGIC uses a mutant trait as a reporter to identify natural variants that encode enhancers or suppressors of that phenotype in germplasm collections. This genetic screen has identified loci from maize involved in the hypersensitive response (Chintamanani et al., 2010; Penning et al., 2004) and plant development (Buescher et al., 2014) among others. In each case, no phenotype

was previously associated to these loci when the mutant genotype was not present. These MAGIC screens exposed loci that altered the mutant phenotypes and encode genes in the same pathway as the mutant reporter. The easy visual scoring, heterozygous transmission, and simplicity of quantifying chlorophyll makes the *Oy1-N1989* allele an excellent reporter which could be used to identify modifier loci in F_1 crosses. By using a mutant that perturbs magnesium chelatase activity, the relative proportion of the phenotypic variance in chlorophyll content contributed by modifier loci of even small effects should be visible. Numerous mechanisms might affect a change in the mutant phenotype. For instance, when *Oy1-N1989* is crossed to multiple genetic backgrounds, expression differences between the wild-type and mutant alleles should change chlorophyll content in the F_1 plants. Similarly, a coding sequence change alters the k_D of the wild-type allele of *oy1* for the other subunits, should increase or decrease the competition between the wild-type and mutant subunits for the magnesium chelatase complex and contribute to variance in chlorophyll biogenesis. In effect, the *Oy1-N1989* phenotype should be modulated by the stoichiometry of both the wild-type and mutant proteins present in the magnesium chelatase complex in heterozygous plants. Any molecular mechanism that alters the quantity of biochemically active protein complex should read out as a change in chlorophyll content and plant color.

The *Oy1-N1989* mutant allele is maintained in the heterozygous state (*Oy1-N1989*/*oy1*). In the exploratory phase of pursuing this study, we detected extreme genetic variation when we crossed *Oy1-N1989* heterozygote with B73 and Mo17, two most prominent inbred lines in maize genetic studies that have been used to generate many mapping populations and other genetic resources (Lee et al. 2002; Hussain et al. 2007; Eichten et al. 2011; Liu et al. 2015). While B73 suppressed the mutant phenotype in a hybrid combination with *Oy1-N1989*, Mo17 dramatically enhanced it. This observation prompted us to dissect the genetic basis of the observed genetic variation using a combination of QTL and GWAS mapping approaches. In this study, we carried out a MAGIC screen using the semi-dominant neomorphic *Oy1-N1989* mutant to identify enhancers or suppressors of this variant. We crossed a *Oy1-N1989* mutant heterozygote in B73 genetic background (*Oy1-N1989*/*oy1*:B73) to intermated B73 x Mo17 recombinant inbred lines (IBM-RILs), B73 x Mo17 doubled haploid lines (Syn10-DH) and a panel of diverse maize inbreds for mapping modifier loci. In each case, the resulting F_1 families were scored for mutant phenotype severity followed by linkage and association mapping to localize variation in leaf chlorophyll contents. In each case, we identified a single quantitative trait locus (QTL) of large effect on chromosome 10 linked to the *oy1* locus itself where the B73 allele suppressed the *Oy1-N1989* phenotype. This locus, which we call *very oil yellow1* (*vey1*), could not be attributed to changes in protein sequence of the *oy1* alleles from the wild-type parent of the F_1 heterozygotes used for phenotyping. However, an expression QTL (eQTL) that was linked to *oy1* locus, referred to as a cis-eQTL, was able to explain the observed phenotypic variation in the mutant siblings in a genotype dependent manner in the IBM-RILs. Remarkably, we also found that the allele expression at *oy1* locus in the mutant heterozygotes was biased towards the *Oy1-N1989* allele in the severe hybrid genetic background. The implications of the discovered cryptic variation, the inheritance of the traits, and the proposed allele expression bias due to a putative cis-acting regulatory element are discussed.

Materials and Methods

Plant materials

The *Oy1-N1989* mutant allele was acquired from the Maize Genetics Cooperation Stock Center (University of Illinois, Urbana/Champaign, IL). The original allele of the *Oy1-N1989* mutation was isolated from an *r1 c1* colorless synthetic stock of mixed parentage (G. Neuffer, personal communication). This allele was introgressed into B73 for eight generations by repeated backcrossing and was maintained as a heterozygote (*Oy1-N1989*/*oy1*:B73) by crossing to wild-type siblings. For line-cross QTL mapping, *Oy1-N1989*/*oy1*:B73 plants were crossed as pollen parents to 216 Intermated B73 x Mo17 recombinant inbred lines (IBM-RILs; Lee *et al*, 2002) and 251 Syn10 double haploid (Syn10-DH; Hussain *et al*, 2007) lines. QTL validation was done using test crosses of pollen from *Oy1-N1989*/*oy1*:B73 with 35 B73-Mo17 Near-Isogenic lines (NILs; Eichten et al., 2011). These NILs consisted of 22 B73-like NILs and 13 Mo17-like NILs. All the F_1 families segregated for the mutant (*Oy1-N1989*/*oy1*) and wild-type (*oy1*/*oy1*) siblings.

For association mapping, *Oy1-N1989*/*oy1*:B73 plants were crossed as a male to 343 inbred lines that included 249 inbreds from maize association panel (Flint-Garcia *et al.* 2005) and 94 inbred lines that included 82 ExPVPs from the Ames panel (Romay *et al.* 2013). For the popcorn lines in the maize association panel, *Oy1-N1989*/*oy1*:B73 was used as a female to avoid the crossing barrier affected by gametophytic factor Ga1-S (first described by Correns in 1902; Mangelsdorf & Jones, 1926). This panel of 343 inbred lines is referred to as maize diversity lines (MDL). The full list of IBM-RILs, Syn10-DH, and MDL used are contained in **Tables S1-S3**.

Field trial

Field experiments were performed at the Purdue Agronomy Center for Research and Education (ACRE) in West Lafayette, Indiana. Test cross populations with IBM-RILs were evaluated in a single replication in Summer of 2013. Test cross population with Syn10-DH lines were evaluated as two replications in a randomized complete block design (RCBD). F_1 progenies of *Oy1-N1989*/*oy1*:B73 crossed with B73 and Mo17 were used as parental checks in each range treated as a block. Test cross F_1 progenies with NILs and parents (B73 and Mo17) were planted in a RCBD with five replications in 2016. In the same year, F_1 families of *Oy1-N1989*/*oy1*:B73 with MDL were evaluated in a RCBD with three replications. Each replication of MDL F_1 population was divided into 10 blocks of the same size and F_1 crosses of *Oy1-N1989*/*oy1*:B73 with B73 and Mo17 were used as checks in each block.

All F_1 families were planted as a single plot of 12-16 plants that were segregating for both mutant and wild-type siblings. Plots were sown in a 3.84 m long row with the inter-row spacing of 0.79 m and an alley space of 0.79 m. No irrigation was applied during the entire crop season as rainfalls were uniformly distributed for satisfactory plant growth. Conventional fertilizer, pest and weed control practices for growing field maize in Indiana were followed.

Phenotyping and data collection

Destructive chlorophyll measurements were performed on a fresh weight basis in 80% acetone solution using a UV-VIS spectroscopic method described in Lichtenthaler & Buschmann, 2001. Due to the suppressing effect of various genetic backgrounds during late developmental stages, mutant plants were tagged at knee height stage so that they can be easily distinguished from the wild-type siblings for trait measurement in the late season. For each F_1 family, two to four plants of each phenotypic class were picked at random for trait measurements. For each trait, measurements were performed on both mutant (reported with a prefix MT) and wild-type (reported with a prefix WT) siblings. Ratios (MT/WT) and differences (WT-MT) were derived for each trait. Non-destructive chlorophyll pigment measurements (CCM) were performed using a chlorophyll meter model CCM-200 plus (Opti-Sciences, Inc., Hudson, NH). Measurements were taken on the leaf lamina of the top fully expanded leaf at 25-30 days after sowing (CCMI) and at 45-50 days after sowing (CCMII). Plant height and stalk width data were collected following the procedure described by Chaikam et al., 2011. Briefly, once plants attained maturity, the height from the soil bed to the flag leaf (abbreviated as FlHT), and ear height (abbreviated as EaHT) was recorded in centimeters (cm). Additional height trait was calculated indirectly by subtracting EaHT from FlHT to get the distance between the top ear and flag leaf (abbreviated as Ea2Fl). EaHT and consequently Ea2Fl were not measured in the F_1 populations with IBM-RILs. For GWAS dataset, ratios were also obtained between EaHT and FlHT of mutants and wild-type separately (abbreviated Ratio_MT_EaHTtoFlHT and Ratio_WT_EaHTtoFlHT). Stalk width (abbreviated as SW) were measured using Vernier calipers at the middle of the first internode above the top ear. Phenotypic data of all the primary traits in both bi-parental and MDL F_1 populations that were measured directly is provided as **Tables S1-S3**.

Public/open-access Genotypic data

Public marker data for the IBM-RILs was obtained from www.maizegdb.org. A total of 2,178 retrieved markers were reduced to 2,156 after the removal of markers with the duplicate assessment. Approximately 13.3% of the marker data were missing. The reads per kilobase of transcript per million mapped reads (RPKM) for the *oy1* locus were obtained from a public repository of the National Science Foundation grant (GEPR: Genomic Analyses of shoot meristem function in maize; NSF DBI-0820610; https://ftp.maizegdb.org/MaizeGDB/FTP/shoot_apical_meristem_data_scanlon_lab/). This data consists of normalized read counts (expressed as RPKM) of the maize genes from the transcriptome of shoot apical meristem of 14 days old IBM-RIL seedlings. Marker data for Syn10 DH lines was obtained from Liu et al., 2015. The Syn10 DH lines were genotyped at 6611 positions (B73 RefGenv2) with SNP markers covering all 10 chromosomes of maize. The entire set of markers were used for linkage analysis as there was no missing data. All B73-Mo17 NILs in both B73 and Mo17 recurrent background that had introgression of the critical region from the opposite parent were selected for QTL validation. Genotyping data of the NILs to select informative lines was obtained from Eichten et al., 2011.

Genotypes for the MDL used in this study is a subset obtained from the maize inbred lines described in Romay et al., 2013. Briefly, these maize lines were genotyped at 681,257 SNP (physical positions from B73 RefGenv2) using a GBS protocol (Elshire *et*

al. 2011) covering all 10 chromosomes of maize. The SNP markers were filtered for ≤15 percent missing data and minor allele frequency of ≥0.05 using TASSEL (Bradbury *et al.* 2007), reducing the marker number to 185,722 SNPs.

Statistical analyses

QTL mapping: Line cross phenotype and marker were used to detect and localize QTL using the R/QTL package version 1.40-8 (Broman et al., 2003). Trait means were used for the QTL analyses. Single interval mapping (SIM) was used for all traits, although composite interval mapping (CIM) was carried out with remarkably similar results (data not shown). Statistical thresholds were computed by 1000 permutations (Churchill and Doerge 1994) of each trait in both bi-parental F_1 populations.

Genome-wide association study (GWAS): GWAS was carried on the phenotypic data from the MDL F_1 crosses. Preliminary data analysis was done using JMP 13.0 (SAS Institute Inc. 2016). Statistical correction on the raw phenotypic data were performed by determining the most significant terms in the model using analysis of variance (Fisher 1921). Genotype and replication were used as a random effect in a linear mixed-effects model built in the lme4 package (Bates et al., 2015) implemented in R (R core team, 2014) to calculate best linear unbiased predictor (BLUP) for each trait.

Broad-sense heritability (line mean basis) were calculated using BLUP values using the method described by Lin & Allaire, 1977. BLUP estimates for each trait were used to perform GWA analysis. GWA analysis was done using the R package GAPIT (Lipka *et al*. 2012) using a compressed mixed linear model. Principle components and kinship matrix were used to correct for false positive associations. A Bonferroni correction (Holm 1979) was used to compute a statistical threshold for the positive association to further control for false positive assessment of association.

Molecular Analyses

Genotyping: DNA analysis to detect recombinants in selected Syn10 DH lines and the BC_1F_1 population was done using three molecular markers. Two markers detecting insertion polymorphisms flanking the *oy1* locus and one dCAPS marker at *oy1* locus were designed for this purpose. Genotyping at indel marker *ftcl1* (flanking an indel polymorphism in intron 4 of *ftcl1*; GRMZM2G001904) was performed using PCR with forward primer 5'- GCAGAGCTGGAATATGGAATGC -3' and reverse primer 5'- GATGACCTGAGTAGGGGTGC -3'. Genotyping at indel marker *gfa2* (flanking an indel polymorphism in the intron of *gfa2*; GRMZM2G118316) was performed using PCR with forward primer 5'- ACGGCTCCAAAAGTCGTGTA -3' and reverse primer 5'- ATGGATGGGGTCAGGAAAGC -3'. A polymorphic SNP in the second intron at *oy1* was used to design a dCAPS (http://helix.wustl.edu/dcaps/dcaps.html; Neff, Turk, & Kalishman, 2002) forward primer 5'- CGCCCCCGTTCTCCAATCCTGC -3' and a gene-specific reverse primer 5'- GACCTCGGGGCCCATGACCT -3'. The PCR products from polymerization reactions with the dCAPS oligonucleotide at *oy1* were digested by *Pst*I restriction endonuclease (New England Biolabs, MA, USA) and resolved on 3.5% agarose gel.

Allele-specific expression analyses: Allelic bias at transcriptional level was quantified using the third leaf of maize seedlings at the V3 developmental stage. Total RNA was extracted using a modified Phenol/Lithium chloride protocol (Eggermont et al., 1996). The modification involved grinding of plant tissue in pestle and mortar into a fine powder using liquid nitrogen, instead of quartz sand and glass beads in the original protocol. Total RNA was subjected to DNase I treatment using Invitrogen Turbo DNA-free kit (Catalog#AM1907, Life Technologies, Carlsbad, CA) and 1 µg of DNase treated RNA from each sample was converted to cDNA using oligo dT primers and a recombinant M-MLV reverse transcriptase provided in iScript™ Select cDNA synthesis kit (catalog#170-8896, Bio-Rad, Hercules, CA) according to the manufacturer's recommendations. Besides the cDNA samples, genomic DNA samples were also prepared as a control to test the sensitivity of the assay. Genomic DNA controls included a 1:1 (F_1 hybrid), 1:2, and 2:1 mixture of B73 and Mo17. PCR were conducted using gene-specific forward primer 5'- CAACGTCATCGACCCCAAGA -3' and reverse primer 5'- GGTTACCAGAGCCGATGAGG -3' for 30 cycles (94˚ for 30s, 56˚ for 30s, 72 ˚ for 30s and final extension for 2 minutes) to amplify the OY1 gene product. These primers flank SNP252 (C->T), which is the causative mutation of *Oy1-N1989*, and SNP317 (C->T) which is polymorphic between B73 and Mo17 but is monomorphic between B73 and *Oy1-N1989* genetic background. Corresponding PCR products were used to generate sequencing libraries using transposon-mediated library construction with the Illumina Nextera® DNA library preparation kit and sequence data were generated on a MiSeq instrument (Illumina, San Diego, CA) at the Purdue Genomics Core Facility. The SNP variation and read counts were decoded from the sequenced PCR amplicons by alignment of the quality controlled reads to the *oy1* reference allele from B73 using the BBMap (Bushnell 2014) and the GATK packages (DePristo *et al.* 2011). Additional analysis was performed using IGV (Robinson *et al.* 2011) to manually quality-check the alignments and SNP calls. Read counts at polymorphic sites obtained from GATK was used to calculate allele-specific expression. Genomic DNA control samples showed bias in the read counts in a dosage dependent manner. DNA from F_1 hybrids between B73 and Mo17 resulted in 1:1 reads at *oy1* demonstrating no bias in the assay to quantify expression.

OY1 sequencing: Coding sequence of *oy1* locus from B73, Mo17, GN:ACR, W22, and *Oy1-N1989* homozygous seedlings was obtained by PCR amplification of the genomic DNA. For rest of the maize inbred lines, the *oy1* locus was amplified from cDNA synthesized from total RNA derived from the shoot tissue of 14 days old maize seedlings. PCR amplification of *oy1* locus from genomic DNA was performed using four primer pairs: (a) forward primer Oy1-FP1 5'- GCAAGCATGTTGGGCACAGCG -3' and reverse primer Oy1-RP12 5'- GGGCGGCGGGATTGGAGAAC -3', (b) forward primer Oy1-FP5 5'- GGTGGAGAGGGAGGGTATCT -3' and reverse primer Oy1-RP6 5'- GGACCGAGGAAATACTTCCG -3', (c) forward primer Oy1-F8 5'- ATGCCCCTTCTTCCTCTCCT -3' and reverse primer Oy1-R8 5'- CGCCTTCTCGATGTCAATGG -3', (d) forward primer Oy1-F9 5'- GGCACCATTGACATCGAGAA -3' and reverse primer Oy1-R9 5'- GCTGTCCCTTCCTTTCAACG -3'. PCR amplification of OY1 transcripts from cDNA was performed using all primer pairs except Oy1-FP1/RP12.

The PCR product from these samples were sequenced either using Sanger or Illumina sequencing. For Sanger sequencing, amplified PCR products were cleaned using homemade filters with sterile cotton plug and Bio-Gel® P-30 gel (Bio-Rad, Hercules, CA) to remove unused dNTPs and primers. Cleaned PCR products were used to perform a cycle reaction using Big Dye version 3.1 chemistry (Applied Biosystems, Waltham, MA) and run on ABI 3730XL sequencer by Purdue genomics core facility. Read with high-quality base pairs from Sanger sequencing were aligned using ClustalW (Thompson et al., 1994). Illumina sequencing was performed as described above except in this case paired-end reads were aligned to the B73 reference of *oy1* gene using bwa version 0.7.12 (Li & Durbin, 2009) and variant calling was done using Samtools (Li et al., 2009).

Results

Mo17 encodes an enhancer of the semi-dominant mutant allele *Oy1-N1989* of maize

The *Oy1-N1989* allele was recovered from a nitrosoguanidine mutant population in a mixed genetic background. The molecular nature of the mutation is a single base pair non-synonymous change (Sawers *et al.* 2006). During the course of introgression of the semi-dominant *Oy1-N1989* allele into B73 and Mo17, we observed a dramatic suppression of the mutant phenotype in F_1 crosses of the stock obtained from the maize genetics cooperative to the B73 background. The difference in phenotype expression was stable and persisted in both genetic backgrounds through all seven backcross generations observed to date. To further explore and quantify this suppression, B73 and Mo17, as well as *Oy1-N1989* crossed with each of these inbred, were grown to the V3 stage in the greenhouse. To improve upon our visual assessment of color and provide quantitation, optical absorbance, which is predicted to strongly correlate with chlorophyll and carotenoid contents, was measured using a Chlorophyll Content Meter-200 plus (CCM; Opti-Sciences, Inc) hand-held LED-based instrument. To confirm that our rapid phenotyping with the CCM would accurately assess chlorophyll and carotenoid levels, we measured these pigments directly using a UV-VIS spectrophotometer following destructive sampling of the same leaves used for CCM measurements (**Table 1**). The non-destructive CCM measurements and destructive pigment quantitation displayed an R-squared value of 0.94 or greater for chlorophyll a, chlorophyll b, and total chlorophyll (**Figure S1**). Given this high correlation between the rapid and non-destructive measurement of leaf greenness using CCM-200 plus instrument and absolute pigment contents in the leaf, we performed all further leaf pigment measurements of *Oy1-N1989* enhancement using CCM values.

Heterozygous maize plants encoding the *Oy1-N1989* allele display reduced stature, yellow-green whole plant phenotype, resulting from reduced Magnesium chelatase and ATPase activity. Contrary to expectations that hybrid vigor might further rescue the mutant phenotype, the B73 inbred background resulted in substantially greener *Oy1-N1989*/*oy1* than heterozygous mutants in B73 x Mo17 F_1 hybrid backgrounds (**Figure 1**). Measurement of CCM at 30 DAS (CCMI), CCM at 55 DAS (CCMII), stalk width (SW), flag leaf height (FlHT), ear height (EaHT), and ear-to-flag-leaf height (Ea2Fl) was done for B73, F_1 B73 x Mo17 hybrids and *Oy1-N1989* heterozygotes in each of these genetic backgrounds. For stalk width, leaf greenness at two time points, and ear height the F_1 hybrid wild-type plants displayed greater trait values than the B73 inbred

indicating hybrid vigor for these characters (**Table 2**). Again, defying the expectation of hybrid vigor, pigmentation, stalk width, and ear height were lower in F_1 hybrid mutants than they were in the B73 inbred mutant heterozygotes (**Table 2**). The increased severity of *Oy1-N1989* in the Mo17 background was observed even after 6 backcrosses (**Figure S2**). This demonstrates the profound negative impact of *Oy1-N1989* on plant growth and the dramatic suppression of this mutant allele by B73.

vey1 maps to a single locus that co-segregates with the *oy1* allele of Mo17 in DH, RIL, BC_1F_1 and NIL families

In order to identify the genetic basis of the suppression of *Oy1-N1989* in Mo17, we performed a series of crosses to two mapping populations. In each case, we crossed a B73 line into which we have introgressed *Oy1-N1989* allele in heterozygous condition (*Oy1-N1989*/*oy1*:B73) as a pollen parent to a population of recombinant lines as female parents (**Figure 2**). We chose two populations to map the very oil yellow trait: Intermated B73 x Mo17 population (IBM), a publically available RIL population (Lee *et al.* 2002) that has been extensively used by the maize community for a variety of mapping experiments, and a doubled haploid population (Syn10) derived from 10 rounds of intermating B73 x Mo17 hybrids followed by fixing alleles using double haploid process (Hussain et al., 2007). These inbred populations differ in the number of rounds of intermating, and therefore the number of recombinants captured and genetic resolution of trait localization that they permit. In the mutant F_1 siblings of these populations both CCMI and CCMII displayed bimodal trait distributions (**Figure 3A and 3B, Figure S3 and S4**) and there was no overlap between wild-type and mutant trait distribution (**Figure S5**) consistent with segregation of a single, effectively Mendelian, suppressor in these B73 x Mo17 populations (**Figure 3**). We name this suppressor locus ***very oil yellow1* (*vey1*).** All mutant traits were positively correlated with CCMI and CCMII in both populations, indicating a common mechanism to the suppression of all traits affected by *Oy1-N1989*. Somewhat surprisingly, CCMI and CCMII traits in the mutant siblings were negatively correlated with stalk width in the wild-type siblings in both populations (**Table 3 and Table 4; Figure S3 and S4**). These associations are inconsistent with each other and therefore cannot be indicative of the *vey1* modifier affecting plant vigor in the absence of *Oy1-N1989*. There might be a linked co-segregating QTL affecting stalk width and pigment accumulation in the wild-type siblings. In addition, to control for variation in genetic potential of each line that was independent of the *Oy1-N1989* modification, we divided the mutant trait value by the congenic wild-type sib values to derive ratios for each trait. Each of the direct measurements, as well as the ratio-metric values, were used as phenotypes in an attempt to detect and localize QTL.

QTL mapping was carried out on all traits using single interval mapping by the EM algorithm as implemented in R/QTL (Broman *et al.* 2003). Tables summarizing the peak positions of all QTL passing a permutation computed threshold are presented for the IBM population in **Table 5** and the Syn10 population in **Table 6**. For all mutant traits, all ratios of mutant to wild-type trait expression, and all differences between mutant and wild-type measurements we identified *vey1* as a QTL of large effect on chromosome 10. A plot of the log of odds (LOD) score and permutation calculated threshold for CCMII from the mutant plants in the Syn10 population is plotted in **Figure 3C and 3D**, and

other mutant related traits showed similar plots at this position. The magnitude of the effects of this position on all of the traits in the mutant siblings, particularly the effects on CCMI and CCMII, were consistent with the prediction of a single Mendelian locus controlling the majority of the phenotypic variance and resulting in the bimodal trait distributions in each population seen in **Figure 3A and 3B**. Only for mutant plant height (MT_FlHT) were any other QTL identified which significantly affected mutant traits. In the case of mutant FlHT, an additional QTL on chromosome 9 was identified in both the IBM-RILs and the Syn10-DH F_1 populations. The position of this QTL matches the position of a QTL of large effect affecting FlHT in the wild-type siblings of both populations (**Table 5 and Table 6**). Additional minor effect alleles influencing stalk width, plant height, and CCMI were identified in the wild-type siblings but not in the mutant populations. However, no QTL affecting the wild-type siblings were detected at the position of *vey1*. Together, these analyses indicate that the *vey1* QTL encodes a single locus with an effect contingent upon the allelic status at *oy1* responsible for the suppression of *Oy1-N1989* in these populations.

The identification the *vey1* modifier as a single mendelian locus variant of large effect in the presence of the *Oy1-N1989* allele, suggested that we could take a similar approach to localization as we had done previously for metabolic QTL (Li et al., 2014). Each F_1 mutant hybrid was classified as high or low CCMII using the bimodal distribution to distinguish the lines into phenotypic categories. We then compared the marker genotypes at each marker under the QTL on chromosome 10 with the phenotypic categories. The top marker in the linkage analysis using Syn10-DH F_1 population was 10.94.5 on chromosome 10. The trait values, marker genotypes, and phenotypic categories for the nine F_1 mutant Syn10-DH line recombinants within the *vey1* region between the flanking markers 10.90.5 and 10.95.5 are presented in **Table 7**. Because of the mendelian segregation of the trait, we interpret a discordance between the marker genotype and F_1 mutant Syn10-DH phenotype for high and low CCMII categorization as recombination between the QTL and that marker. **Figure 4** summarizes data across these flanking markers and additional markers with the physical position of each marker annotated by the number of instances of discordance between these markers and the phenotypic class. Marker genotypes perfectly predicted trait expression only at 10.93. Recombinants separated the trait outcome from the marker genotype in one Syn10-DH line for marker 10.94.5 and for two Syn10-DH lines at 10.90.5, indicating that the QTL resides between 10.94.5 and 10.90.5 (**Figure 4**). This physical position coincides with the location of the *oy1* locus itself, suggesting that *vey1* may be encoded by the Mo17 allele of *oy1* and enhances the impact of the *Oy1-N1989* allele. The three Syn10-DH lines that contained recombination within this critical region were genotyped for a SNP that distinguished *oy1* in Mo17 from both the B73 and *Oy1-N1989* alleles. In all three, the genotype at *oy1* matched the phenotype expression, indicating perfect segregation between the *oy1* allele from B73 or Mo17 in the Syn10-DH and the modified phenotype. In addition, we developed markers for the *ftcl1* locus (GRMZM2G001904) which is two genes upstream of *oy1* and *gfa2* (GRMZM2G118316) which is directly downstream from *oy1*. Two recombinants separated phenotype expression from the *ftcl1* genotype, narrowing the region locating the QTL to within the region between *ftcl1* and 10.94.5. The *ftcl1* marker is closer to *oy1* than the top GWAS SNP associated with suppression,

indicating that the SNP with the lowest p-value is linked to a causative polymorphism but cannot encode or be required for the suppression phenotype. No recombinants were found between the phenotype and marker genotype at *gfa2*. This approach of fine mapping was able to reduce the *vey1* locus to ~227 kb interval that includes *oy1*. In an another attempt to recover additional recombinants, a population of ~1100 BC_1F_1 plants was generated from *Oy1-N1989/oy1*:B73 x (B73 x Mo17). All the mutant siblings from this population were separated into suppressed and enhanced phenotype categories by CCM readings and genotyped at *ftcl1*, *oy1*, and *gfa2*. In a sample of 576 mutants, three recombinants between *vey1* and the *ftcl1* marker were found whereas none at *oy1* and *gfa2* were detected (**Figure 4**). Thus, no further narrowing of the QTL interval was achieved.

A similar analysis was carried out for the data from the F_1 crosses to the IBM-RILs. CCM readings was used to bin IBM-RILs into suppressed and enhanced mutant categories. The number of cases of discordance between each marker genotype in the *vey1* region and the F_1 mutant phenotypic class are summarized in **Figure 4**. For all IBM-RILs with unambiguous genotypes at isu085b, the *Oy1-N1989* suppression or enhancement phenotype was perfectly predicted by marker genotype. A single recombinant between phenotype and genotype was identified for the flanking marker phi059 which is ~372 kb from the *oy1* locus. Twenty-seven recombinants between the phenotype and genotype were noted for the marker flanking isu085b on the distal side (umc2069) with the physical distance of ~3.14 Mb on the opposite side of isu085b. This identified a ~3.51 Mb window in IBM-RILs containing *vey1* on chromosome 10 providing a confirmation of the Syn10 results with no additional resolution.

We performed crosses between *Oy1-N1989/oy1* in the B73 background and a series of nearly isogenic lines (NIL) that contained the *vey1* QTL region introgressed into a homogeneous background of either B73 or Mo17. These clearly displayed the bimodal effect observed in the QTL experiment, but now without segregating all other B73 and Mo17 alleles in the background, eliminating the presence of a globally hybrid background as a requirement for *vey1* expression (**Figure S6**). Thus, our NIL data confirm the expectation of the QTL mapping and the existence of the *vey1* modifier. The recombinants in the NIL were sufficient to identify a 3.01 Mb region that must contain the *vey1* QTL, but this did not further narrow the region from the five gene window, which included the *oy1* locus itself, identified in the Syn10-DH F_1 population. Further mapping resolution will require the isolation of additional recombinants within this region.

Additional QTL detected outside the *vey1* locus have no effect on *Oy1-N1989* expression

Despite the non-normality of some of the trait distributions and apparent thresholds, no QTL for binary traits in the combined two-part models implemented in R/QTL (Broman *et al*. 2003) were detected (data not shown). This is consistent with the strong single QTL affecting the non-normality in the data. In an effort to account for the substantial segregation variance of this QTL, the top marker was extracted and used as a covariate in a one-dimensional scan of the genome to absorb the effect of this QTL.

When this was done, no additional QTL were detected for any traits analyzed. This indicated that removal of this segregation variance did not make visible any additional variation in the genome affecting the residual variance in any of the traits and points to a simple genetic basis for *vey1* in Mo17. The QTL affecting plant height on chromosome 9 was not affected by adding the top marker associated with *vey1* as a covariate, was still detected in both mutant and wild-type data sets, and did not display any epistasis with the B73 or Mo17 allele at *vey1* in the mutant F_1 mapping populations. Consistent with these results no QTL interactions were detected by two-way scans of all pair-wise comparisons across the genome (data not shown). Thus, modification of the *Oy1-N1989* phenotype by *vey1* was inherited as a single QTL, acting alone.

The similar measurements and QTL mapping using bi-parental populations derived using different breeding scheme from same inbred lines permit a comparison for the Syn10-DH and IBM-RIL populations. We previously noted a QTL, on chromosome 9 that affected plant height and ear height in the Syn10-DH populations that was present in wild-type siblings. A QTL at an overlapping position was identified in the IBM-RIL F_1's affecting plant height in both mutants and wild-types. This QTL on chromosome 9 maps to a genetically linked position and the allele from Mo17 at this locus exhibit higher trait expression when combined with the B73 allele which is fixed in each F_1 because of the nature of this population (**Table 5 and 6; Figure 2**). A second QTL was found in both IBM and Syn10 populations, this one on chromosome 1 with effect on the stalk widths of wild-type siblings only. However, this QTL does not co-localize in two populations showing higher trait expression with a Mo17 allele in IBM population and B73 allele in Syn10 population (**Tables 5 and 6**). Ratios and difference of stalk widths in Syn10 crosses detected a QTL on chromosome 9 that was not identified in IBM-RIL populations. Another QTL affecting the early CCM measure was identified in the wild-type siblings (WT_CCMI) in IBM-RIL F_1 populations and also localized to chromosome 1 but at a position unlinked to the QTL for wild-type stalk width. In the Syn10 population, an additional QTL for plant height of the wild-type siblings but not of the mutant was identified on chromosome 3, however, this QTL does not show higher trait expression with the non-reference allele (**Table 6**). Wild-type siblings in Syn10 also detected additional QTL on chromosome 1 affecting the stem length between the ear and the flag leaf (WT_Ea2Fl) which co-localizes with the QTL for plant height and stalk width in the wild-types (**Table 6**). This QTL shows increased additive effect with B73 allele. However, an additional QTL in Syn10 that was linked to this QTL in repulsion phase was also detected for mutant and wild-type flag leaf height with the positive effect from Mo17 allele (**Table 6**). Thus, in addition to repeatedly detecting *vey1*, we were able to reproducibly detect a QTL affecting plant height (FlHT and Ea2Fl) and a QTL affecting stalk width in both the IBM-RILs and Syn10-DH F_1 crosses.

GWAS for chlorophyll content in maize diversity lines (MDL) and *Oy1-N1989/oy1* F_1 genotypes identifies a single QTL

Given the lack of additional recombinants within our line cross populations and finding of a single modifier locus, we undertook genome-wide association mapping of *Oy1-N1989* severity. A population of 343 lines including members of the maize association panel (Flint-Garcia *et al.* 2005) and the Ames panel including ExPVPs

(Romay *et al.* 2013) was crossed to *Oy1-N1989/oy1* in the B73 background. These F_1 progenies were phenotyped for a subset of the most informative traits including CCM measurements (CCMI and CCMII), stalk width, flag leaf height, and ear height on both mutant and wild-type siblings. As we observed in the F_1 test crosses with B73 and Mo17 bi-parental mapping populations (**Figure S5**), there was total separation between mutant and wild-type siblings in the MDL F_1 populations for the CCMI and CCMII traits (**Figure S7**). Additionally, dramatically suppressed mutant F_1 families, much like that seen in F_1 crosses to Mo17, were present within the panel but a strict bimodal trait distribution was not identified for any traits (**Figure S8**). Pairwise correlations between most of the mutant sibling traits measured in MDL F_1 populations showed significant positive correlations except weak negative pairwise correlation was observed between ear height and ear to flag leaf height (**Table S4**). Broad-sense heritability estimates were also calculated for the traits measured on wild-type and mutant siblings in the MDL F_1 population. High heritability estimates for plant and ear height were observed in mutant and wild-type siblings whereas the ratios of these traits exhibited lower repeatability (**Table S5**). Plant stalk width measurements provided much consistent heritability values between the primary trait value and the ratios. Chlorophyll estimates of the leaves (CCMI and CCMII) showed very high heritability estimate in the mutant and ratio traits, whereas wild-type siblings had much lower repeatability.

GWA was performed using the GAPIT (Lipka *et al.* 2012), a package implemented in R (R core team, 2014) using the SNP dataset from Romay et al., 2013. The 500 SNPs with the lowest p-values for each of the trait genome-wide association is graphed in **Figure 5A** along with the Bonferroni threshold for significance. A closer view of these SNPs at the *vey1* locus on chromosome 10 are plotted in **Figure 5B**. GWA tests only identified one locus that passed multiple testing corrections that affected CCMI and CCMII in the *Oy1-N1989* mutant F_1 plants (**Figure 5**). The top SNP from the association testing of the mutant CCM traits was on Chromosome 10 at 9138486 within the coding sequence of *ftcl1*, which was separated from the *vey1* QTL by six recombinants in our Syn10 and BC_1F_1 mapping experiments (**Figure 4; Table 8**). Thus, even by GWA we did not further narrow down the QTL interval and can extend the confirmation of our DH, RIL, and NIL experiment.

In an effort to explore suppression of *Oy1-N1989* by alleles independent of *vey1*, we utilized the top SNP as a covariate to absorb the effect of *vey1* and performed a genome-wide scan for effect on CCMI and CCMII. This did not yield any additional loci affecting *Oy1-N1989* suppression (data not shown). Thus, illuminated no other detectable mechanism of suppression of the dominant *Oy1-N1989* mutant beyond *vey1*. It would appear that the *vey1* locus is responsible suppression of the *Oy1-N1989* mutant in this diverse panel of maize and that the *vey1* polymorphism is relatively common in maize germplasm.

Oy1-N1989 **is a semi-dominant chlorophyll mutant and enhanced by reduced function at** ***oy1***

Recessive hypomorphic alleles at *oy1* have also been reported and heterozygotes between *Oy1-N1989* and hypomorphic *oy1* alleles are more severe than isogenic *Oy1-N1989*/oy1 siblings. To confirm that reduced *oy1* function could determine the differential sensitivity to *Oy1-N1989*, we crossed the dominant and recessive mutants to

each other. The recessive weak hypomorphic allele *oy1-yg* was obtained from the maize genetics coop in an unknown genetic background. These plants were crossed with both B73 and Mo17 to develop F_1 material that would segregate the mutation. F_1 plants were crossed to *Oy1-N1989* in the B73 background as well as backcrossed to the *oy1-yg* mutant to recover plants that had *Oy1-N1989* in combination with the wild-type B73, wild-type Mo17, and *oy1-yg* alleles. Chlorophyll contents were determined by CCM-meter at 21 and 40 days after sowing in the field and a summary of these data are presented in **Table 9**. The *Oy1-N1989* allele was substantially enhanced when combined with the *oy1-yg* allele, demonstrating that reduced function of the *oy1* gene in Mo17 could underlie the *vey1* QTL (**Figure 6**). Missing from our previous understanding of the *Oy1-N1989* allele is whether this allele requires the presence of a functional *oy1* allele, either wild-type or the hypomorphic *oy1-yg*. Selfed progeny from *Oy1-N1989* heterozygotes segregated for albino seedling-lethal *Oy1-N1989* homozygotes with no detectable chlorophyll by either CCM measures or spectrophotometer (**Table 1**). Thus, the *Oy1-N1989* mutation is a dominant-negative neomorphic allele with no evident magnesium chelatase activity. Any QTL that affected increased expression of the *Oy1-N1989* allele or increased the proportion of mutant to wild-type gene product in the hybrids would increase the severity of the heterozygous mutant phenotype.

No coding sequence differences in *oy1* account for *vey1* inheritance

Given that reduced *oy1* activity enhanced the phenotype of *Oy1-N1989*, we sequenced the *oy1* locus from Mo17 and B73 to determine if coding sequence differences could encode the *vey1* modifier. The only non-synonymous changes that distinguish these two alleles is at the site of the previously reported in-frame 6bp insertion (Sawers *et al.* 2006), which adds an alanine and threonine residue to the protein. PCR amplification of *oy1* in 17 maize inbred lines, as well as the *Oy1-N1989* allele, was performed. Sequencing of the amplification products confirmed the absence of 6 bp insertion in *Oy1-N1989* allele and multiple other lines including B73, CML103, and CML322. A polymorphism within the 6 bp indel was also found that resulted in an alternative in-frame insertion encoding an alanine and serine codon in Mo17 and a subset of lines. This *oy1* indel allele's genotypes, phenotypic values, and phenotypic class for the F_1 plants are summarized in **Table 10.** This indel allele at *oy1* did not predict the phenotypic severity of *Oy1-N1989* in the heterozygous condition. Five lines, including Mo17, resulted in dramatic enhancement of the CCMI and ratio of CCMI phenotypes of F_1 plants crossed to *Oy1-N1989/oy1*:B73. These enhanced genotypes encoded all three possible alleles at *oy1*. In addition, the suppressing inbred lines also encoded all three possible indel alleles, demonstrating that the only coding sequence polymorphism between B73 and Mo17 could not be responsible for the *vey1* QTL. Besides this 6 bp indel, enhancing CML322 inbred line had two missense mutations that lead to amino acid change at position 321 (D->E), and 374 (S->I), the suppressing inbred line NC358 had one amino acid change at position 336 from aspartic acid to glycine and the enhancing line Tzi8 had a 15 bp in-frame deletion leading to removal of five amino acids (VMGPE) in the third exon of the coding sequence. Even considering these additional alleles, the coding sequence changes that differentiated B73 and Mo17 cannot be responsible for *vey1*.

Expression level polymorphism at *oy1* in the suppression of *Oy1-N1989*

Differential expression of *oy1* by Mo17 as compared to the B73 alleles was available in public expression polymorphism data. We downloaded the normalized transcript abundance (expressed as RPKM) data tables from assessments of shoot apical meristem transcriptomic data from a NSF GEPR project. Out of 105 IBM-RILs that were assessed for expression level, 74 were among the one that were tested for chlorophyll accumulation and plant growth in IBM-RIL x *Oy1-N1989/oy1*:B73 F_1 hybrid populations. We investigated whether B73 and Mo17 alleles encode cis-acting eQTL affecting the expression of OY1 by using the genotypes at markers linked to *oy1* to predict the RPKM of OY1 in the RILs. Using the genetic markers for the IBM-RIL we determined that a cis-acting eQTL controlled the accumulation of OY1 transcripts **(Table 11)**. This cis-acting eQTL conditioned greater expression of the B73 allele and explained 19 percent of the variation ($p < 0.0001$) in OY1 transcript abundance in the IBM-RILs. A lower expression of the wild-type *oy1* allele from Mo17 is expected to enhance the phenotype of *Oy1-N1989* given the enhancement of *Oy1-N1989* by the *oy1-yg* allele (**Table 9**). Regressions between the RPKM values obtained for the RIL and all mutant phenotypes expressed in IBM-RIL x *Oy1-N1989/oy1*:B73 F_1 hybrids were significant. This indicated that lines with increased Mg-chelatase subunit I transcripts available for protein production and complex assembly could overcome chlorophyll and plant vigor defects caused by the *Oy1-N1989/oy1* genotype in IBM-RIL F_1 hybrids. Consistent with this, full models that included both the *vey1* genotype, and therefore the cis-eQTL, and the residual variation in RPKM at OY1 did a better job of predicting CCMI and CCMII than the *vey1* genotype by itself. If the cis-eQTL at OY1, which results in differential allele accumulation in the inbred lines can affect allele-specific expression in the hybrids, it would explain the better performance of the mutant IBM-RIL F_1 hybrids with the B73 allele at *vey1*.

A previous study of allele-specific expression in F_1 hybrid maize seedlings identified preferential expression of alleles in the B73 allele of *oy1* in combination with PH207 and Mo17 but not Oh43 (Waters *et al.* 2017). The bias of OY1 transcript accumulation towards B73 in B73/Mo17 hybrids from this study is shown in **Table 12**. As the original allele of the *Oy1-N1989* mutation was isolated from a *r1 c1* colorless synthetic stock of mixed parentage (G. Neuffer, personal communication) this raises the possibility that the same cis-acting regulatory variation that lowered expression of OY1 from PH207 and Mo17 when combined with the B73 allele might also be present in the *oy1* allele that was the progenitor of *Oy1-N1989*. We tested this possibility by using the SNPs that distinguish B73, Mo17, and the *Oy1-N1989* alleles to measure allele-specific expression in each of the hybrids. In the B73 isogenic crosses, the *Oy1-N1989* and B73 wild-type alleles were accumulated to equal proportions in the F_1 of that cross indicating that the suppressed phenotype was not due to a lowered expression of *Oy1-N1989* relative to the wild-type allele (**Table 12**). Remarkably, mutant siblings from the reciprocal crosses between *Oy1-N1989/oy1*:B73 and Mo17 resulted in greater expression from the *Oy1-N1989* allele than the Mo17 wild-type allele. Allele-specific expression of *Oy1-N1989* was statistically significant in the B73 isogenic material as compared to the Mo17 hybrids. Thus, overexpression of *Oy1-N1989* relative to the wild-type Mo17 allele could account for the *vey1* QTL that distinguished the B73 from the Mo17 hybrids with *Oy1-N1989* allele (**Table 12**). We propose that *vey1* results from cis-acting regulatory

sequence polymorphism that affects the relative proportion of wild-type and mutant transcript accumulation in the *Oy1-N1989/oy1*:B73/Mo17 hybrid cross combination.

GWAS identified additional loci unlinked to *oy1* which impacts mutant phenotype expression

Besides detecting *vey1* as the major loci responsible for the suppression of mutant phenotype expression, association mapping identified novel loci that were unlinked to *vey1* but showed significant association with few traits in the mutant siblings of MDL F_1 population in a likely *vey1* dependent manner. CCMII measurement of mutant siblings (MT_CCMII) identified a SNP on chromosome 4 that was significantly associated with a genomic region containing *adenosyl homocysteine hydrolase1* (*ahh1*), one of the two maize paralogs of *homology-dependent gene silencing 1* (*hog1*) from Arabidopsis encoding S-adenosyl-L-homocysteine hydrolase involved in sulfur amino acid metabolism, one-carbon metabolism, and the maintenance of cytosine methylation of DNA (Rocha *et al.*, 2005; **Table 8**). This gene exhibited biased expression favoring the B73 allele in B73/Mo17 hybrids in maize seedlings (Waters *et al.* 2017), suggesting cis-regulation affecting *AHH1* transcription as a possible mechanism for this QTL. The next strongest association with MT_CCMII was found on chromosome 7 and linked to two candidate genes with roles in primary metabolism (**Table 8**). The maize genes *Isocitrate lyase 1* (*icl1*) and *pyruvate orthophosphate dikinase regulatory protein 1* (*ppdk rp1*) are linked to the identified SNPs and may act by modifying the consequences of *vey1* on metabolism via a light-independent or light-dependent metabolic pathways, respectively. Similarly, ratios and differences of CCMII trait expression identified a SNP associated with a genomic region on chromosome 3. This SNP resides in GRMZM2G461356, an ortholog of At*tho2* and is linked (~65 kbp) to a heme-binding protein GRMZM2G092152 (**Table 8**).

Plant vigor associated traits in the mutant including stalk width, ratio and differences of the mutant to wild-type stalk width were all affected by a gene linked to the same SNP on chromosome 5. This SNP was tightly linked (<2kbp) to a zinc finger homeodomain (ZF-HD) containing protein and a monodehydroascorbate reductase 4 (*mdar4*) protein (**Table 8**).

Plant height traits associated with mutant siblings including ear height and the ratio of ear height to flag leaf height were significantly associated with a region on chromosome 8 (**Table 8**). These traits were un-modified by variation at the *vey1* QTL, yet mutants and not wild-type controls were subject to variation on chromosome 8. This suggests that the second locus with effects contingent on the mutant genotype was present on chromosome 8. Two candidate genes associated with this genomic region are *Zea mays centroradialis* (*zcn8*) and trehalose-6-phosphate synthase 1 (*tps1*).

Discussion

Semi-dominant mutant allele *Oy1-N1989* displays dominant-negative function on the magnesium chelatase enzyme complex (Sawers *et al.* 2006). In heterozygous condition, the negative effect on the enzyme complex hinges on the donor parent of wild-type *oy1* allele. B73 and Mo17 show differential suppression response in mutant heterozygotes resulting in suppressed and severe mutant phenotype, respectively. The reduced chlorophyll accumulation in these genetic backgrounds is directly proportional to

the reduction in vigor of plant measured in terms of plant height and stalk width. Surprisingly, mutant heterozygotes in B73 genetic background exhibited greater plant vigor than B73/Mo17 mutant hybrids indicating the deleterious effect of the Mo17 allele was strong enough to upset the hybrid vigor when combined with *Oy1-N1989* allele. Thus, we have demonstrated that the *Oy1-N1989* mutant allele sensitizes maize plants and exposes a phenotypic consequence for genetic variants that would otherwise be invisible in maize germplasm. Similar methodology has been adopted previously in maize to gain the genetic understanding of various traits (Chintamanani et al., 2010; Buescher et al., 2014; Olukolu et al., 2013; Olukolu et al., 2014). Employing this mutant allele as a reporter to screen for effects of natural variants is a simple and powerful technique to detect standing variation. The *vey1* locus was a pleiotropic major QTL controlling CCM readings, plant height, and stalk width in GWAS and line cross studies of *oy1* mutants. These alleles or variants were common in maize germplasm and yet went unnoticeable for all of these traits in all studies using wild-type plants published to date, including ours. Thus, if experimental procedures, for instance, chlorophyll biosynthesis are not in place these genetic variants are invisible. These cryptic genetic variants, or contingent QTL, permit the reclassification of variants that might otherwise be hypothesized to be neutral or non-functional in plant adaptation. Thus, genetic screens based upon semi-dominant mutant alleles as reporters offer a cost-effective and robust approach to map QTL(s) as it can leverage the publicly available genetic resources, bi-parental populations, and diverse inbred lines.

Alleles affecting even modest fitness consequences may not be visible to researchers working with population sizes even in the thousands, such as in GWAS, and only a few generations. By contrast, evolutionarily relevant segregating variation may have very small phenotypic effects. One of the possible uses of MAGIC is in boosting the fitness consequences, or relative contribution of genetics to a phenotypic variance, to uncover cryptic variation affecting a pathway of interest. Not all of this variation need be fitness-affecting, and interpreting mutant-conditioned phenotypes as non-neutral variation would be a mistake. It is, of course, possible that neutral variants may result in increased severity of a mutant phenotype due to changes not physiologically relevant for all alleles of that gene in the species. Nevertheless, it does identify a new pathway member and inform us about the allelic variation in the species and the pathway topology as a form of gene discovery.

In the current study, use of bi-parental mapping populations derived from the same inbred lines but developed using different intercross and inbreeding schemes provided the opportunity to compare the effect of extra rounds of random interbreeding in the development of mapping population on genetic resolution (**Figure 2**). The comparative fine mapping of *vey1* in the Syn10-DH population, that employed 10 rounds of random mating, provided far better localization of the QTL than the IBM-RIL populations derived after 4 rounds of random mating. This demonstrated the benefits of increased recombination during random intermating of early generations to QTL localization (**Figure 4**). Based on these results, as future RIL are generated we recommend increased intermating generations and DH production rather than relying on further recombination during the selfing generations of RIL production.

We expected that the MDL would provide us fine-scale genetic resolution and assist in mapping *vey1* closer to a quantitative trait nucleotide (QTN) as it utilizes

historical recombination (Flint-Garcia *et al.* 2005). Such populations offer a better understanding of variation in traits across the species, or at least within the diversity of materials sampled in the MDL. The Syn10-DH population detected 3 recombinants at a physical position (marker ftcl1) which was closer to *vey1* than top SNP associated with the same trait in GWAS (**Figure 4 and Table 8**). This case highlights the danger of chasing top SNP linked gene(s) from GWAS to be a candidate. For instance, we might have focused on the gene encoding the position that was the top GWAS hit for CCMII, *ftcl1*, which is ~77 kbp away from *oy1*. The role of this gene in thiamine and one carbon metabolism, that indirectly impact chlorophyll biosynthesis (Michael and Spurr 1975; Pribat *et al.* 2011), make it a reasonable candidate gene. However, the recombinant Syn10 DH and BC_1F_1 line-cross materials eliminated *ftcl1* as a potential cause of *vey1* (**Figure 4 and Table 8**). This displaced signal detection by GWAS could very well be an artifact of erroneous SNPs, imputation inaccuracy, missing markers that are tightly linked to causative variation etc. Future work to identify the nucleotide changes responsible for the differences between B73 and Mo17 that encode *vey1* will retrospectively answer which of these possible limitations prevented the association study from being more effective. While GWAS did not take us closer to *vey1*, the detection of multiple QTL unlinked to *vey1* in GWAS dataset (**Table 8**) demonstrates a value of association panels in the discovery of phenotypically active allelic variation that might be absent (monomorphic) in a particular bi-parental cross. Taking all these pros and cons into account, this study illustrates the complementary nature of line-cross QTL mapping and GWAS to explore the genetics of a trait.

We used a non-destructive, inexpensive, and rapid phenotyping method to measure leaf chlorophyll. Rapid and robust phenotyping is critical and contributed to the strong correlation between the absolute trait measurement and the estimated phenotypes like CCM (**Figure S1**). Previous studies have highlighted the importance of benchmarking such indirect, or proxies, for traits of interest. For instance, using near infrared reflectance spectroscopy (NIRS) to estimate major and total carotenoids in maize kernels could replace a sensitive and accurate but cumbersome, expensive, slow, and destructive measurements by HPLC (Berardo *et al.* 2004). Comparisons of HPLC and NIRS measurements resulted in a correlation of 0.85 for total carotenoids (Berardo *et al.* 2004). A subjective visual score for yellow color was not effective, yielding a correlation of 0.12 with HPLC measurements of total carotenoids (Harjes *et al.* 2008). Thus, developing additional methodologies that rely on non-invasive multispectral or hyperspectral data as proxies for various biochemical compounds in plants or other organisms will accelerate and enable genetic studies that are currently deemed unfeasible due to the arduous task of phenotyping large populations or making multiple observations over time.

Additional loci detected by GWAS implicate carbon metabolism and small RNA regulation to effect mutant traits

Multiple loci exhibited statistically significant associations with phenotypic variation, apart from the *vey1* locus. Loci detected in the GWAS analyses in addition to *vey1* were linked to genes with possible roles in the control of metabolism and gene expression (**Table 8**). Disruption of HOG1, which encodes S-adenosyl-L-homocysteine hydrolase, perturbs methyl donor availability resulting in loss of DNA methylation in

Arabidopsis (Rocha *et al.* 2005). The current study identified a GWAS locus linked to *ahh1*, a maize ortholog of At*hog1*, as a determinant of CCMII in the MDL F_1 mutant siblings. It is possible that DNA methylation affected by *ahh1* variation in the mutant siblings plays a role in modulating the cis-acting regulatory sequences or specifically alters the expression of *vey1*. An alternative mechanism is suggested by GWAS QTL linked to *ICL1*, an enzyme responsible for core metabolic processes particularly important for early stages of seedling development. Prior to sufficient sugar production from photosynthesis, excess isocitrate produced by fatty acid catabolism in the seed is shuttled, by isocitrate lyase activity, between ATP production via the TCA cycle and sugar synthesis (Kornberg & Krebs, 1957; Beevers, 1961). In *Oy1-N1989*/*oy1* seedlings, the low net capture of carbon by photosynthesis may make the ability to shuttle carbon skeletons from fatty acids to sugar and amino acid metabolism, such as to produce the glycine and glutamate required for chlorophyll biosynthesis, even more critical. Similarly, *PPDK RP1* is a plastid-localized protein that is involved in the C_4 cycle in the mesophyll cells to regenerate phosphoenol-pyruvate via de-phosphorylation (activation in light) and phosphorylation (inactivation in dark) of *PPDK* (Hatch 1987; Astley *et al.* 2011). As *PPDK RP1* regulates one of the light reactions of maize photosynthesis, it is an obvious candidate gene that might modify the sufficiency of photosynthetic capacity in *oy1* mutants thereby altering leaf pigment.

Besides detecting *vey1* locus, ratio and differences of CCMII trait identified a GWAS locus on chromosome 3 linked to GRMZM2G461356 and GRMZM2G092152 (heme binding protein) on as the candidate genes (**Table 8**). Each of these loci might explain some or all of the effect of the QTL at this position. THO2 protein which is an Arabidopsis ortholog of GRMZM2G461356 is part of the *THO*/*TREX* complex that is involved in small interfering RNA (siRNA) biosynthesis (Yelina *et al.* 2010). Thus, this RNA silencing machinery which is part of trans-acting small interfering RNA (tasiRNA) pathway could be a component of the transcriptional regulation of the *oy1* locus. GRMZM2G092152, a homolog of a protein from *Arabidopsis thaliana* that binds heme *in vitro*, has been hypothesized to play a role in redox reactions and reactive oxygen species signal transduction (Bianchetti et al., 2010). Thus, this protein could protect mutant seedlings from photo-damage visible in most penetrant juvenile plants that likely results from superoxide production by phototoxic metabolites such as protoporphyrin IX (PPIX) (Matringe et al., 1990) or simply stabilize heme and thus permit greater chlorophyll biosynthesis.

Plant growth measured as stalk width for mutant siblings and related traits identified an unlinked region to *vey1* with two candidate genes, ZF-HD and MDAR4, that are proposed to impact the development of the mutant siblings (**Table 8**). Zinc finger homeodomain (ZF-HD) protein family have been demonstrated to bind in vitro to the promoter sequence of C_4 specific PEP Carboxylase (PEPCase) gene (Windhövel et al., 2001) and may modulate the C_4 cycle, operating by a mechanism similar to that proposed for PPDK RP1. The MDAR4 protein, however, is involved in redox balance and may help detoxify reactive oxygen species and damaged metabolites (Lisenbee et al., 2005).

Surprisingly, another plant developmental trait in mutant siblings (MT_EaHT and Ratio_MT_EaHTtoFlHT) did not detect *vey1* but did find a genomic region on chromosome 8 (**Table 8**). Two candidate genes associated with this genomic region, *Zea mays centroradialis* (*zcn8*) and trehalose-6-phosphate synthase 1 (*tps1*) are proposed to

impact ear height of the mutant siblings. The *ZCN8* protein, a member of the gene family which is substantially expanded in maize, homologous to the flowering locus T (FT) protein of Arabidopsis and has been previously demonstrated to impact photoperiod sensitivity and leaf number in maize and is linked to a GWAS QTL controlling leaf number (Meng et al., 2011; Bouchet et al., 2017). *TPS1* is less than 100 kbp away from the top associated SNP. In Arabidopsis, *tps1* mutants display altered vegetative growth, starch synthesis, and flowering time (Gómez et al., 2010; Lunn et al., 2006; Wahl et al., 2013) and this may alter ear height in maize.

Additional QTLs that were unlinked to *vey1* were also detected in this study. A QTL on chromosome 9 for flag leaf height and ear height traits in Syn10, and flag leaf height trait in IBM co-localized to same genomic location (**Table 5 and Table 6**) except the flag leaf height QTL on chromosome 9 for mutant siblings in Syn10 F_1 population. This common QTL is tightly linked to a physical position previously reported by Haase et al., 2015 in IBM and Syn14 population and Liu et al., 2015 in IBM and Syn10 for plant height. This QTL shows positive additive effect with Mo17 allele just as reported previously (Haase *et al.* 2015). More QTL were detected for plant height traits only in the Syn10 population (**Table 6**). Two QTLs linked in repulsion phase were detected on chromosome 1 for plant height in wild-type F_1 siblings in Syn10. A previous study detected a QTL co-localizing with this common flag leaf height QTL on chromosome 1 detected in mutant and wild-type siblings with greater additive effect from Mo17 allele (Liu *et al.* 2015). However, none of the studies discussed here made use of F_1 population for mapping these QTLs. Failure to detect same QTLs in IBM F_1 population could be due to experimental error as these QTLs account for small variation in plant height. Another reason could be that the IBM-RILs still have some residual heterozygosity as the alleles in this population were fixed using the single seed descent method, whereas, Syn10 is highly homozygous due to double haploid induction (Liu *et al.* 2015). In the presence of a residual heterozygosity, small phenotypic variation in highly quantitative traits like plant height can be quantified inaccurately.

What is *vey1*?

The *vey1* gene may yet turn out to be the *oy1-vey1* allele, as the only remaining possibilities are regulatory polymorphisms within the cis-acting control regions. Previous studies have utilized test-crosses to loss-of-function alleles (Dilkes *et al.* 2008) to provide single-locus tests of additive QTL alleles in an otherwise identical hybrid background. Protein-null alleles of *oy1* isolated directly from the B73 and Mo17 backgrounds could be used to carry out a similar test. If hybrids between B73 and Mo17, with null mutants from either side, were identical it would demonstrate that *vey1* is the *oy1* locus. Maize intergenic space is spanned by transposable elements and can be highly divergent between different inbred lines due to large insertions/deletions polymorphisms (Sanmiguel and Bennetzen 1998). The region upstream of *oy1* but before the next gene *gfa2* contains numerous large insertions and deletions adding ~139 kb of DNA sequence in Mo17 compared to B73, except a short stretch of sequence ~12 kb upstream of *oy1* is conserved to some extent (data not shown). Thus, the molecular determination of the cis-acting sequence encoding an eQTL responsible for *vey1* will require substantial additional experimentation. It is conceivable that intragenic recombinants between *Oy1-N1989* and either B73 or Mo17, or between B73 and Mo17 themselves could be

identified and used to test the effects of upstream or downstream regulatory sequences. In the absence of such recombinants, we can only consider what mechanisms might be consistent with the observed suppression of the chlorophyll biosynthesis defects, cis-acting effects on OY1 transcript abundance, and allele-specific gene expression. In aggregate, these data point to an allele-specific regulation of OY1 transcript abundance encoded by a cis-acting regulatory element. Most remarkable and relevant to the *vey1* QTL as opposed to overall *Oy1-N1989* phenotype suppression, is the cis-eQTL at *oy1*. This is noteworthy that the RPKM data is derived from shoot apical meristems of two weeks old IBM-RILs, whereas the CCM readings were derived from the leaf tissue of three to six weeks old IBM-RILs F_1 plants that were grown in completely different environments. So, even though when we compared the OY1 transcript abundance of the maize inbreds with the phenotypic outcome of F1 hybrid seedlings from a different tissue at a different developmental stage, we were still able to detect the cis-eQTL. Though only encoding 19 percent of the variation in OY1 RPKM, the *vey1* QTL accounted for more than 80 percent of the variation in chlorophyll content. Whereas the remaining 81 percent of the RPKM variation in the IBM-RILs only accounted for a tiny, but significant proportion of the remaining variation in phenotype. This is, again, consistent with our stoichiometric model and previous work (Sawers et al., 2006) that demonstrate that *Oy1-N1989* is a competitive inhibitor of magnesium chelatase complex formation. A cis-acting eQTL would result in a greater or lesser proportion of wild-type OY1 protein accumulation. By contrast, trans-acting effects or environmental effects which affected each copy independently would have a lesser effect on suppression of the deleterious *Oy1-N1989* allele.

The reciprocal crosses between *Oy1-N1989*/*oy1*:B73 and Mo17 did not result in different phenotypes, thus, *vey1* does not exhibit imprinting (**Table 2**). Allele-specific expression at *oy1* locus in the *Oy1-N1989* heterozygous mutants demonstrated the existence of functional cis-acting regulatory polymorphism between *Oy1-N1989* and both the B73 and Mo17 *oy1* wild-type loci. In addition, *oy1* is affected by a cis-eQTL in the IBM (**Table 11**). Together with our other data, the allele-specific expression at OY1 that was visible when we re-analyzed the data from Waters et al., 2017 (**Table 12**) and the large 5' upstream polymorphism at *oy1*, we propose that *vey1* is encoded by a cis-acting regulatory DNA sequence variation (**Figure S9**).

We intend to test this further using NILs in B73 and Mo17 background that have introgression of *the vey1* allele in a reciprocal fashion to characterize the expression polymorphism of the cis-acting element at *oy1* locus. This experiment would eliminate the trans eQTL that contribute to a significant variation in RPKM visible in the IBM-RIL data. Allele-specific expression assays at *oy1* using crosses with this material will provide additional molecular evidence that *vey1* encodes a cis-acting regulatory polymorphism capable of modulating allele-specific expression. As *vey1* was the only major locus detected in GWAS, other inbred lines that enhance and suppress the phenotype should also exhibit this differential expression polymorphism at *oy1* in the mutant hybrids (**Figure 5; Table 8**) and variation in the 5' upstream sequence at *oy1*. Ultimately, inspection of assembled maize genomes that include the upstream and downstream sequence of *oy1* gene from *Oy1-N1989*, Mo17, and the enhancing and suppressing backgrounds will help identify structural variation underlying this cis-acting DNA sequence polymorphism.

We propose that the approach we have taken is not likely to be unique to *oy1*. As a core component of chlorophyll biosynthesis, we expected strong purifying selection on magnesium chelatase subunit I, which would eliminate most phenotypically affective polymorphisms. Indeed, there was no effect of the *vey1* locus on CCMI or CCMII in wild-type plants. The presence of the mutant allele at *oy1* exposed cryptic variation and rendered previously invisible highly heritable sequence variation. We propose that the use of semi-dominant mutant alleles as reporters will not only detect novel cis-acting gene regulatory elements but also functionally validate previously-detected cis-eQTL from the genome-wide eQTL studies.

Conclusions

In this study, we used a semi-dominant mutant allele *Oy1-N1989* in maize to mine for natural variation that impacts chlorophyll biosynthesis. This genetic screen, like similar studies in past, demonstrate a way to leverage existing public genotypic data sets to understand the genetic variation for a trait of interest. The genetic variation uncovered by this approach may be invisible otherwise as it requires a mutant allele in the trait of your interest as a reporter. In the current study, we identified the *vey1* locus that exists as a common polymorphism in the maize germplasm. Transcriptional regulation mediated by *vey1* can be explained by a cis-acting enhancer resulting in the allele-specific expression at *oy1*. This molecular mechanism involves a lower expression of the wild-type *oy1* allele of Mo17 (*oy1*-Mo17) due to disruption of a putative cis-acting enhancer element (*vey1*-Mo17) which is intact in *the Oy1-N1989* mutant allele. A similar bias in the expression is also seen in B73 and Mo17 F_1 hybrids mediated by a functional cis-acting enhancer element present in B73 (*vey1-B73*) which is very similar to the one present in *Oy1-N1989* mutant allele background. Besides *vey1*, this study identified various repeated QTLs in the F_1 hybrid wild-type traits like plant height and stalk width that can be subjected to further analyses.

Acknowledgements

We thank past undergraduate and graduate students of Johal lab who were involved with field operation and data collection of part of the material used in this study. Authors also acknowledge the help of the staff at Purdue ACRE farm for assistance with planting and crop management of all the field experiments described in this study. R.S.K was supported by USAID Feed the Future CGIAR-US Initiative grant “Heat stress resilient maize for South Asia through a public-private partnership” to G.S.J.. This work was supported by NSF grant 1444503 awarded to G.S.J. and B.P.D.

Tables

Table 1. Chlorophyll accumulation in the third leaf at V3 stage of maize seedlings.

Genotype	CCM (CCM units)	Chlorophyll a (mg/g FW)	Chlorophyll b (mg/g FW)	Total Chlorophyll (mg/g FW)	Chl a/b ratio	Total Carotenoids (mg/g FW)
Mo17/B73	27.04±2.11[a]	1.48±0.10[a]	0.42±0.026[a]	1.90±0.12[a]	3.50±0.05[d]	0.20±0.011[a]
Oy1-N1989/oy1:Mo17/B73	5.74±0.11[e]	0.38±0.02[d]	0.07±0.005[d]	0.45±0.02[d]	5.48±0.16[b]	0.04±0.002[e]
B73/Mo17	22.86±0.29[b]	1.15±0.04[b]	0.32±0.015[b]	1.47±0.05[b]	3.57±0.10[d]	0.16±0.004[b]
Oy1-N1989/oy1:B73/Mo17	4.35±0.22[e]	0.36±0.03[d]	0.06±0.008[d]	0.42±0.04[d]	6.03±0.25[a]	0.05±0.002[de]
B73	25.19±1.12[ab]	1.13±0.03[b]	0.32±0.008[b]	1.47±0.04[b]	3.54±0.03[d]	0.16±0.003[bc]
Mo17	16.18±0.97[c]	0.98±0.03[b]	0.29±0.008[b]	1.27±0.04[b]	3.44±0.03[d]	0.14±0.001[c]
Oy1-N1989/oy1:B73	10.18±0.42[d]	0.57±0.03[c]	0.13±0.008[c]	0.70±0.03[c]	4.40±0.07[c]	0.06±0.003[d]
Oy1-N1989/Oy1-N1989[&]	1.00±0.00[f]	n.d	n.d	-	-	0.01±0.001[f]

Data are represented as means and SD. The values are means of 3 biological replicates except Mo17 with 2 biological replicates. Superscript connecting letter report between genotypes within each trait was determined using ANOVA with posthoc analysis using Tukey's HSD at $p<0.05$. CCM meter reads value of 1.00 for blank.

[&]Homozygote seedlings were obtained in B73 background and the measurements were performed on first leaf of 10 days old seedlings, n=5.

Table 2. Pigment Absorbance and plant traits affected by suppression of *Oy1-N1989/oy1* genotype.

Genotype	CCMI[a]	CCMII	SW	FlHT	EaHT	Ea2Fl
B73	57.3±8.0[a]	67.0±5.2[a]	22.5±1.2[a]	214.8±10.0[a]	100.6±9.3[a]	114.3±6.4[a]
B73/Mo17	57.8±7.3[a]	76.4±5.6[b]	27.4±1.1[b]	239.1±8.9[b]	109.6±6.5[b]	129.5±8.9[b]
Oy1-1989/oy1:B73	6.8±1.3[b]	27.7±3.2[c]	19.5±1.3[c]	234.6±8.4[b]	120.3±7.4[c]	114.3±7.1[a]
Oy1-1989/oy1:B73/Mo17	2.3±0.5[c]	9.8±1.7[d]	17.7±1.4[d]	250.6±9.1[c]	110.8±8.5[b]	139.8±8.5[c]

[a]All traits are presented as means and SD calculated from 39 experimental replications with 2-3 mutant or wild-type siblings in each replication. Connecting letter report presented as superscripts between genotypes within each trait was determined using ANOVA with posthoc analysis using Tukey's HSD at $p<0.01$. See materials and methods for trait description.

Table 3. Trait correlations in IBM-RILs x *Oy1-N1989/oy1*:B73 F_1 test cross populations.

	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT
MT_CCMI		0.069	0.875	0.059	0.685	-0.257	0.370	-0.128
WT_CCMI	0.312		0.062	0.368	0.013	0.035	0.059	0.025
MT_CCMII	<.0001	0.361		0.136	0.671	-0.278	0.350	-0.134
WT_CCMII	0.390	<.0001	0.046		0.039	0.103	-0.038	-0.064
MT_SW	<.0001	0.848	<.0001	0.571		0.163	0.418	-0.024
WT_SW	0.000	0.614	<.0001	0.130	0.017		-0.028	0.156
MT_FlHT	<.0001	0.387	<.0001	0.576	<.0001	0.684		0.657
WT_FlHT	0.062	0.714	0.049	0.350	0.729	0.022	<.0001	

Lower half contains correlation p-values and upper half contains Pearson's correlation coefficient for each pairwise trait comparison. Self-comparisons (diagonal) are left blank.

Table 4. Trait Correlations in Syn10-DH x *Oy1-N1989/oy1*:B73 F_1 test cross populations.

	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT	MT_Ea2Fl	WT_Ea2Fl
MT_CCMI		0.127	0.911	0.009	0.844	-0.167	0.548	0.071	0.437	0.118	0.448	-0.030
WT_CCMI	0.045		0.118	0.293	0.054	0.033	0.074	-0.090	0.012	-0.144	0.128	0.027
MT_CCMII	<.0001	0.064		0.006	0.864	-0.208	0.550	0.036	0.422	0.062	0.472	-0.018
WT_CCMII	0.893	<.0001	0.931		0.010	-0.046	-0.012	-0.146	-0.003	-0.146	-0.020	-0.065
MT_SW	<.0001	0.400	<.0001	0.877		0.018	0.614	0.107	0.481	0.139	0.515	0.008
WT_SW	0.008	0.606	0.001	0.467	0.775		0.066	0.268	0.038	0.147	0.074	0.280
MT_FlHT	<.0001	0.242	<.0001	0.847	<.0001	0.301		0.603	0.870	0.540	0.713	0.362
WT_FlHT	0.265	0.154	0.574	0.021	0.092	<.0001	<.0001		0.603	0.825	0.319	0.689
MT_EaHT	<.0001	0.852	<.0001	0.966	<.0001	0.551	<.0001	<.0001		0.672	0.274	0.193
WT_EaHT	0.062	0.023	0.330	0.021	0.029	0.020	<.0001	<.0001	<.0001		0.097	0.160
MT_Ea2Fl	<.0001	0.043	<.0001	0.753	<.0001	0.243	<.0001	<.0001	<.0001	0.125		0.431
WT_Ea2Fl	0.638	0.671	0.772	0.308	0.898	<.0001	<.0001	<.0001	0.002	0.011	<.0001	

Lower half contains correlation p-values and upper half contains Pearson's correlation coefficient for each pairwise trait comparison. Self-comparisons (diagonal) are left blank.

Table 5. Summary of the QTL detected in IBM-RILs x *Oy1-N1989/oy1*:B73 F_1 test cross populations.

Trait Identifier	QTL[a]	Chr[b]	LOD[c]	Position[d]	Left Marker	Right Marker	LOD-2 Interval[e] Left	LOD-2 Interval[e] Right	PVE[f]	Mean±SE[g] B73	Mean±SE[g] Mo17	Greater Allele
Chlorophyll												
MT_CCMI	1	10	46.9	139	AI795367	AY109994	137	141	53.68	8.81±0.188	4.16±0.226	B73
WT_CCMI	1	1	3.6	523	bnl5.59a	php20654	519	534	7.12	47.27±0.548	43.51±0.734	B73
MT_CCMII	1	10	45.0	139	AI795367	AY109994	128	141	51.48	18.27±0.448	7.38±0.585	B73
WT_CCMII	0											
Ratio_CCMI	1	10	39.7	139	AI795367	AY109994	137	145	50.19	0.19±0.004	0.09±0.005	B73
Ratio_CCMII	1	10	44.4	139	AI795367	AY109994	137	142	55.38	0.36±0.009	0.14±0.01	B73
Diff_CCMI	1	10	6.6	145	phi059	isu85b	126	153	13.18	36.89±0.576	42.24±0.724	B73
Diff_CCMII	1	10	22.4	138	AI795367	AY109994	129	142	36.80	32.95±0.687	44.77±0.912	B73
Morphology												
MT_FlHT	2	9	4.1	298	bnlg1012	ufg66	273	302	8.34	197.05±1.729	207.54±1.639	Mo17
		10	7.5	137	AI795367	AY109994	125	154	15.08	207.98±1.467	193.64±1.91	B73
WT_FlHT	1	9	7.6	257	bnl5.04	umc1267	238	272	14.32	194.82±1.276	205.89±1.311	Mo17
Ratio_FlHT	1	10	16.9	139	AI795367	AY109994	135	145	28.54	1.04±0.005	0.96±0.006	B73
Diff_FlHT	1	10	16.7	139	AI795367	AY109994	135	145	27.97	-8.22±1.052	6.44±1.299	B73
MT_SW	1	10	26.9	144	phi059	isu85b	137	148	43.35	22.36±0.189	18.56±0.233	B73
WT_SW	1	1	6.8	810	nfc103a	AY109506	802	821	13.43	23.3±0.15	24.4±0.118	Mo17
Ratio_SW	1	10	35.3	145	isu85b	rz900c(ahh)	126	147	52.58	0.94±0.007	0.76±0.009	B73
Diff_SW	1	10	35.1	139	AI795367	AY109994	125	147	48.98	1.44±0.196	5.62±0.235	B73

[a]Number of QTL detected for a given trait
[b]Chromosome location of a QTL
[c]LOD score at the peak of a given QTL
[d]Peak position and [e]LOD-2 interval of the QTL in terms of genetic position in centiMorgan(cM)
[f]PVE is percent of variance explained by the QTL at this position as estimated by regression and reported as an R^2 value*100
[g]Mean and standard error of the trait with B73 and Mo17 genotype at the peak marker of the detected QTL

Table 6. Summary of the QTL detected in Syn10-DH lines x *Oy1-N1989/oy1*:B73 F_1 test cross populations.

Trait	QTL[a]	Chr[b]	LOD[c]	Position[d]	Left Marker	Right Marker	LOD-2 Interval[e] Left	LOD-2 Interval[e] Right	PVE[f]	Mean±SE[g] B73	Mean±SE[g] Mo17	Greater allele
Chlorophyll												
MT_CCMI	1	10	59.9	189	chr10.90.5	chr10.93	189	193	65.2	7.00±0.117	2.65±0.174	B73
WT_CCMI	0											
Ratio_CCMI	1	10	54.0	189	chr10.90.5	chr10.93	189	192	62.1	0.14±0.002	0.05±0.003	B73
Diff_CCMI	0											
MT_CCMII	1	10	83.6	192	chr10.94.5	chr10.95.5	190	193	66.5	29.07±0.478	8.39±0.731	B73
WT_CCMII	0											
Ratio_CCMII	1	10	78.1	192	chr10.94.5	chr10.95.5	190	193	66.9	0.40±0.006	0.11±0.010	B73
Diff_CCMII	1	10	52.1	189	chr10.90.5	chr10.93	189	191	60.3	42.46±0.623	63.39±0.926	B73
Morphology												
MT_FlHT	3	1	3.8	622	chr01.808	chr01.809.5	612	638	6.7	226.50±1.585	237.6±2.084	Mo17
		9	4.1	57	chr09.36.5	chr09.37.5	41	68	7.5	225.77±1.661	237.03±1.927	Mo17
		10	16.7	191	chr10.94.5	chr10.95.5	187	195	26.4	237.51±1.338	214.28±2.05	B73
WT_FlHT	5	1	3.9	538	chr01.519.5	chr01.522	517	553	6.9	218.40±1.043	226.9±1.678	Mo17
		1	4.6	622	chr01.808	chr01.809.5	612	629	8.1	217.62±1.106	226.21±1.454	Mo17
		1	5.1	779	chr01.1843	chr01.1860	751	832	8.9	224.45±1.149	215.65±1.355	B73
		3	4.0	565	chr03.1591	chr03.1592.5	554	579	7.1	225.67±1.431	217.74±1.126	B73
		9	4.4	466	chr09.1039.5	chr09.1050.5	458	475	7.9	217.29±1.164	225.45±1.351	Mo17
Ratio_FlHT	1	10	24.4	189	chr10.90.5	chr10.93	174	194	35.7	1.07±0.004	0.97±0.006	B73
Diff_FlHT	1	10	25.3	189	chr10.90.5	chr10.93	174	194	36.7	-16.48±1.013	5.03±1.508	B73
MT_EaHT	1	10	9.1	191	chr10.94.5	chr10.95.5	166	198	15.4	113.60±1.046	100.69±1.603	B73
WT_EaHT	1	9	7.4	465	chr09.1039.5	chr09.1050.5	457	470	12.7	97.52±0.829	105.2±0.961	Mo17
Ratio_EaHT	1	10	11.3	178	chr10.70.5	chr10.72	172	197	18.7	1.12±0.007	1.01±0.011	B73
Diff_EaHT	1	10	11.7	178	chr10.70.5	chr10.72	171	196	19.3	-12.26±0.767	-1.71±1.132	B73
MT_Ea2Fl	1	10	12.4	184	chr10.80.5	chr10.82.5	179	195	20.4	124.38±0.745	114.35±1.005	B73

WT_Ea2Fl	2	1	4.4	781	chr01.1 874.5	chr01.1 875.5	774	791	7.8	121.89± 0.656	117.17± 0.787	B73
		9	4.0	237	chr09.1 30.5	chr09.1 32	230	252	7.0	118.63± 0.589	123.64± 0.987	Mo17
Ratio_Ea2Fl	1	10	16.9	187	chr10.8 8.5	chr10.9 0.5	175	195	26.6	1.04±0.005	0.94±0.008	B73
Diff_Ea2Fl	1	10	17.4	187	chr10.8 8.5	chr10.9 0.5	176	194	27.3	-4.65±0.677	6.78±0.963	B73
MT_SW	1	10	62.3	189	chr10.9 0.5	chr10.9 3	189	193	68.2	21.74±0.138	15.93±0.209	B73
WT_SW	2	1	6.2	1645	chr01.2 976.5	chr01.2 977.5	1642	1653	10.8	25.70±0.096	24.75±0.144	B73
		1	5.3	786	chr01.1 877	chr01.1 878.5	775	808	9.3	25.72±0.1	24.86±0.134	B73
Ratio_SW	2	9	3.9	280	chr09.1 59.5	chr09.1 61	261	877	6.9	0.81±0.01	0.75±0.011	B73
		10	69.1	190	chr10.9 3	chr10.9 4.5	189	193	70.9	0.86±0.005	0.61±0.008	B73
Diff_SW	2	9	4.1	280	chr09.1 59.5	chr09.1 61	261	294	7.2	4.59±0.286	6.47±0.315	B73
		10	65.5	190	chr10.9 3	chr10.9 4.5	189	193	69.4	3.55±0.147	9.83±0.225	B73

[a]Number of QTL detected for a given trait
[b]Chromosome location of a QTL
[c]LOD score at the peak of a given QTL
[d]Peak position and [e]LOD-2 interval of the QTL in terms of genetic position in centiMorgan(cM)
[f]PVE is percent of variance explained by the QTL at this position as estimated by regression and reported as an R^2 value*100
[g]Mean and standard error of the trait with B73 and Mo17 genotype at the peak marker of the detected QTL

Table 7. Recombinants within the *vey1* region derived from Syn10-DH x *Oy1-N1989/oy1*:B73 F_1 populations.

Line ID	MT_CCMI	Ratio_CCMI	MT_CCMII	Ratio_CCMII	MT_SW	Ratio_SW	chr10.90.5	chr10.93	chr
IBM_31	7.0	0.13	33.2	0.46	24.0	0.92	B	A	
IBM_41	2.3	0.05	7.0	0.10	16.0	0.61	B	B	
IBM_149	1.7	0.03	5.7	0.09	15.7	0.65	B	B	
IBM_144	1.7	0.03	5.6	0.07	14.7	0.58	B	B	
IBM_199	8.9	0.20	30.1	0.41	22.3	0.96	A	A	
IBM_201	8.5	0.15	32.0	0.40	20.8	0.82	A	A	
IBM_214	1.8	0.03	5.5	0.07	15.0	0.60	B	B	
IBM_217	2.4	0.04	7.3	0.10	15.7	0.56	B	B	
IBM_229	9.7	0.17	34.8	0.49	23.0	0.90	B	A	

Table 8. Summary of the significant SNP markers associated with different traits detected in GWAS.

Trait	SNP marker[1]	P.value	MAF[2]	FDR_Adjusted_P-values	PVE[3]	Bonferroni[4]	Candidate gene[5]
MT_CCMI	S10_9138486	1.87E-07	0.31	0.019056	6.2	No	GRMZM2G419806 (*oy1*)
	S10_8856702	2.05E-07	0.37	0.019056	6.1	No	"
MT_CCMII	S10_9138486	6.00E-11	0.31	0.000011	10.2	Yes	GRMZM2G419806 (*oy1*)
	S10_8856702	1.93E-10	0.36	0.000012	9.6	Yes	"
	S10_9212946	1.98E-10	0.20	0.000012	9.6	Yes	"
	S10_9141634	5.29E-10	0.32	0.000025	9.1	Yes	"
	S10_8856870	8.13E-10	0.23	0.000030	8.9	Yes	"
	S10_8852672	2.41E-09	0.22	0.000075	8.4	Yes	"
	S10_9216485	2.99E-09	0.49	0.000079	8.3	Yes	"
	S10_9223914	1.01E-08	0.21	0.000235	7.7	Yes	"
	S10_8852732	1.78E-08	0.24	0.000368	7.4	Yes	"
	S10_8858297	6.11E-08	0.24	0.001134	6.8	No	"
	S10_8932692	7.40E-08	0.34	0.001250	6.7	No	"
	S10_8931408	1.19E-07	0.48	0.001847	6.5	No	"
	S10_9401386	1.94E-07	0.21	0.002647	6.3	No	"
	S10_9216503	2.05E-07	0.35	0.002647	6.3	No	"
	S10_9397873	2.14E-07	0.27	0.002647	6.2	No	"
	S10_9373288	3.07E-07	0.28	0.003560	6.1	No	"
	S10_8856651	3.72E-07	0.25	0.004067	6.0	No	"
	S10_8853527	6.24E-07	0.39	0.006103	5.7	No	"
	S10_8853571	6.24E-07	0.39	0.006103	5.7	No	"
	S10_8852556	6.68E-07	0.35	0.006207	5.7	No	"
	S10_8852	9.25E	0.2	0.008183	5.6	No	"

Trait	SNP marker[1]	P.value	MAF[2]	FDR_Adjusted_P-values	PVE[3]	Bonferroni[4]	Candidate gene[5]
	733	-07	4				
	S10_8853640	1.12E-06	0.16	0.009419	5.5	No	“
	S10_9214837	1.34E-06	0.34	0.010549	5.4	No	“
	S4_21320898	1.36E-06	0.08	0.010549	5.4	No	GRMZM2G015295 (*ahh1*)
	S10_8931792	1.97E-06	0.49	0.014629	5.2	No	GRMZM2G419806 (*oy1*)
	S10_9223788	2.21E-06	0.27	0.015768	5.2	No	“
	S10_8761158	2.86E-06	0.26	0.019705	5.0	No	“
	S10_9380089	4.95E-06	0.08	0.031190	4.8	No	“
	S10_9376277	5.37E-06	0.30	0.031190	4.8	No	“
	S10_9376296	5.37E-06	0.30	0.031190	4.8	No	“
	S10_9376305	5.37E-06	0.30	0.031190	4.8	No	“
	S10_9376292	5.37E-06	0.30	0.031190	4.8	No	“
	S7_154267281	7.93E-06	0.25	0.043305	4.6	No	GRMZM2G056369 (icl1) also linked to GRMZM2G004880 (ppdk regulatory protein1)
	S7_154267310	7.93E-06	0.25	0.043305	4.6	No	“
	S7_143697110	8.95E-06	0.24	0.047502	4.5	No	“
	S10_8761117	9.68E-06	0.26	0.049928	4.5	No	GRMZM2G419806 (*oy1*)
Ratio_CCMII	S10_9138486	7.05E-11	0.31	0.000013	10.9	Yes	GRMZM2G419806 (*oy1*)
	S10_8856702	1.70E-10	0.36	0.000014	10.4	Yes	“
	S10_9212946	2.28E-10	0.20	0.000014	10.3	Yes	“
	S10_9141634	7.25E-10	0.32	0.000034	9.6	Yes	“
	S10_8856870	1.79E-09	0.23	0.000066	9.2	Yes	“
	S10_8852	1.38E	0.2	0.000426	8.1	Yes	“

Trait	SNP marker[1]	P.value	MAF[2]	FDR_Adjusted_P-values	PVE[3]	Bonferroni[4]	Candidate gene[5]
	672	-08	2				
	S10_8932692	3.88E-08	0.34	0.001030	7.6	Yes	“
	S10_9213109	7.76E-08	0.21	0.001801	7.2	No	“
	S10_9397873	8.79E-08	0.27	0.001815	7.2	No	“
	S10_9216485	1.18E-07	0.49	0.002186	7.0	No	“
	S10_9223914	1.41E-07	0.21	0.002188	6.9	No	“
	S10_8858297	1.41E-07	0.24	0.002188	6.9	No	“
	S10_8852732	1.55E-07	0.24	0.002216	6.9	No	“
	S10_8853527	2.58E-07	0.39	0.003189	6.6	No	“
	S10_8853571	2.58E-07	0.39	0.003189	6.6	No	“
	S10_9401386	3.00E-07	0.21	0.003482	6.6	No	“
	S10_9376292	7.14E-07	0.30	0.006629	6.1	No	“
	S10_9376277	7.14E-07	0.30	0.006629	6.1	No	“
	S10_9376296	7.14E-07	0.30	0.006629	6.1	No	“
	S10_9376305	7.14E-07	0.30	0.006629	6.1	No	“
	S10_9380089	8.81E-07	0.08	0.007486	6.0	No	“
	S10_9373288	9.20E-07	0.28	0.007486	6.0	No	“
	S10_8931408	9.65E-07	0.48	0.007486	6.0	No	“
	S10_9214837	9.67E-07	0.34	0.007486	6.0	No	“
	S10_8856651	1.14E-06	0.25	0.008472	5.9	No	“
	S10_8853640	1.26E-06	0.16	0.008979	5.8	No	“
	S10_8852733	2.65E-06	0.24	0.018255	5.5	No	“
	S10_8852556	4.46E-06	0.35	0.029604	5.2	No	“
	S3_208837596	4.76E-06	0.08	0.030455	5.2	No	GRMZM2G461356 (tho2) also

Trait	SNP marker[1]	P.value	MAF[2]	FDR_Adjusted_P-values	PVE[3]	Bonferroni[4]	Candidate gene[5]
							linked to heme binding protein GRMZM2G092152
	S10_9213139	5.99E-06	0.35	0.037100	5.1	No	GRMZM2G419806 (*oy1*)
	S10_9216503	7.27E-06	0.35	0.043552	5.0	No	"
Diff_CCMII	S10_8856702	5.53E-10	0.36	0.000053	9.6	Yes	GRMZM2G419806 (*oy1*)
	S10_9138486	5.76E-10	0.31	0.000053	9.6	Yes	"
	S10_9141634	7.63E-09	0.32	0.000473	8.3	Yes	"
	S10_9212946	2.35E-08	0.20	0.001093	7.7	Yes	"
	S10_9401386	4.27E-08	0.21	0.001457	7.4	Yes	"
	S10_9213109	4.71E-08	0.21	0.001457	7.4	Yes	"
	S10_8856870	7.05E-08	0.23	0.001871	7.2	No	"
	S10_8932692	1.59E-07	0.34	0.003697	6.8	No	"
	S10_8852672	3.20E-07	0.22	0.006595	6.4	No	"
	S10_9397873	1.01E-06	0.27	0.017804	5.8	No	"
	S3_208837596	1.05E-06	0.08	0.017804	5.8	No	GRMZM2G461356 (tho2) also linked to heme binding protein GRMZM2G092152
	S10_9214837	1.22E-06	0.34	0.018958	5.7	No	GRMZM2G419806 (*oy1*)
	S10_9373288	3.45E-06	0.28	0.049311	5.2	No	"
MT_SW	S5_201229725	3.80E-08	0.08	0.007055	7.0	Yes	GRMZM2G417229 (*zhd12*) and linked to GRMZM2G320307 (*mdar4*)
	S10_9212946	1.54E-07	0.20	0.014323	6.4	No	GRMZM2G419806 (*oy1*)

Trait	SNP marker[1]	P.value	MAF[2]	FDR_Adjusted_P-values	PVE[3]	Bonferroni[4]	Candidate gene[5]
	S10_9138486	4.52E-07	0.31	0.023091	5.9	No	“
	S10_9141634	6.20E-07	0.32	0.023091	5.7	No	“
	S10_9380089	6.44E-07	0.07	0.023091	5.7	No	“
	S10_8856702	7.46E-07	0.37	0.023091	5.6	No	“
Ratio_SW	S5_201229725	1.62E-08	0.08	0.001918	8.3	Yes	GRMZM2G417229 (*zhd12*) and linked to GRMZM2G320307 (*mdar4*)
	S10_9380089	2.64E-08	0.07	0.001918	8.0	Yes	GRMZM2G419806 (*oy1*)
	S10_9212946	3.10E-08	0.20	0.001918	7.9	Yes	“
	S10_8852672	2.67E-07	0.22	0.011727	6.8	No	“
	S10_9138486	3.16E-07	0.31	0.011727	6.7	No	“
	S10_8852732	3.80E-07	0.24	0.011775	6.6	No	“
	S10_9141634	4.83E-07	0.32	0.011860	6.5	No	“
	S10_8856702	5.11E-07	0.37	0.011860	6.5	No	“
	S10_9216485	8.54E-07	0.49	0.017615	6.2	No	“
Diff_SW	S5_201229725	3.62E-08	0.08	0.004884	7.6	Yes	GRMZM2G417229 (*zhd12*) and linked to GRMZM2G320307 (*mdar4*)
	S10_9380089	5.26E-08	0.07	0.004884	7.4	Yes	GRMZM2G419806 (*oy1*)
	S10_9212946	3.16E-07	0.20	0.019548	6.5	No	“
	S10_8852672	1.18E-06	0.22	0.046292	5.9	No	“
	S10_8852732	1.35E-06	0.24	0.046292	5.8	No	“
	S10_9216485	1.50E-06	0.49	0.046292	5.7	No	“
	S10_9138486	1.86E-06	0.31	0.049217	5.6	No	“

Trait	SNP marker[1]	P.value	MAF[2]	FDR_Adjusted_P-values	PVE[3]	Bonferroni[4]	Candidate gene[5]
MT_EaHT	S10_9397873	2.13E-06	0.27	0.049506	5.6	No	"
	S8_123506087	3.98E-08	0.44	0.002299	3.5	Yes	GRMZM2G179264 (*zcn8*) also linked to GRMZM2G068943 (*tps1*)
	S8_123506089	3.98E-08	0.44	0.002299	3.5	Yes	"
	S8_123506141	3.98E-08	0.44	0.002299	3.5	No	"
	S8_123509373	4.95E-08	0.47	0.002299	3.5	No	"
	S8_123512155	1.12E-06	0.48	0.041754	2.7	No	"
Ratio_MT_EaHT toFlHT	S8_123509373	3.76E-08	0.47	0.002799	4.6	Yes	GRMZM2G179264 (*zcn8*) also linked to GRMZM2G068943 (*tps1*)
	S8_123506087	7.41E-08	0.44	0.002799	4.4	No	"
	S8_123506089	7.41E-08	0.44	0.002799	4.4	No	"
	S8_123506141	7.41E-08	0.44	0.002799	4.4	No	"
	S8_123512155	7.54E-08	0.48	0.002799	4.4	No	"

[1]SNP marker associated with the respective traits. Numerical digit followed by S in the name of the marker indicates the chromosome number and physical position of the marker is indicated by number followed by underscore.
[2]Minor allele frequency (MAF) of the marker
[3]Phenotypic variance explained by the marker
[4]Yes/No indicates if marker crossed the genome wide Bonferroni threshold value

Table 9. Chlorophyll quantification of populations segregating for the allelic interaction between *Oy1-N1989* and *oy1-yg* alleles at *oy1*.

Cross	Days after planting	*Oy1-N1989/oy1-yg*	*Oy1-N1989/+*	*oy1-yg/+*	*oy1-yg/oy1-yg*
(Mo17 X *oy1-yg/oy1-yg*) X *Oy1-N1989*/+:B73	21	1.7±0.4[a]	3.0±0.6[a]	.	.
(B73 X *oy1-yg/oy1-yg*) X *Oy1-N1989*/+:B73	21	2.9±0.5[b]	5.1±0.8[b]	.	.
(Mo17 X *oy1-yg/oy1-yg*) X *Oy1-N1989*/+:B73	40	3.7±0.6[c]	7.0±0.3[c]	.	.
(B73 X *oy1-yg/oy1-yg*) X *Oy1-N1989*/+:B73	40	7.5±0.9[d]	17.1±3.3[d]	.	.
(Mo17 X *oy1-yg/oy1-yg*) X *oy1-yg/oy1-yg*	21	.	.	27.6±5.7[a]	7.6±2.8[a]
(B73 X *oy1-yg/oy1-yg*) X *oy1-yg/oy1-yg*	21	.	.	27.8±6.8[a]	8.1±2.8[a]
(Mo17 X *oy1-yg/oy1-yg*) X *oy1-yg/oy1-yg*	40	.	.	32.2±4.9[b]	16.7±5[b]
(B73 X *oy1-yg/oy1-yg*) X *oy1-yg/oy1-yg*	40	.	.	38.7±6.1[b]	21±6.2[b]

Data is presented as means and standard deviations. Sample size in each category vary from 5-20 plants. Comparisons to declare statistical significance were done only between the crosses with B73 and Mo17 as a parent within each genotype class of the progeny quantified on the same day (i.e. within 21 or 40 days after planting). Connecting letter report between two samples indicate significance at $p < 0.05$ using student's t-test.

Table 10. Trait expression of the F_1 populations of inbred lines crossed with *Oy1-N1989/oy1*:B73 along with the allelic state at the 6 bp indel in the coding sequence of OY1 transcript in the respective parental inbred lines.

Inbred	Indel[a]	MT_CCMI	WT_CCMI	Ratio_CCMI	MT_CCMII	WT_CCMII	Ratio_CCMII	Category[b]
NC350	AT	12.7	68.1	0.19	36.2	76.6	0.48	sup
NC358	AT	12.6	53.3	0.24	36.9	70.3	0.54	sup
CML69	AT	9.9	71.0	0.14	27.5	69.9	0.39	sup
B97	AS	9.9	59.7	0.17	31.5	76.9	0.41	sup
Mo18W	AS	9.1	68.1	0.13	24.4	75.2	0.33	sup
Oh43	AS	8.7	58.4	0.15	24.3	57.9	0.42	sup
W22	AT	8.5	64.4	0.13	37.8	74.6	0.51	sup
IL144	AT	7.7	50.3	0.15	22.5	68.8	0.33	sup
B73	-	7.0	57.2	0.12	26.3	69.4	0.38	sup
MS71	AS	6.9	60.3	0.11	12.9	71.1	0.18	sup
P39	AT	6.5	41.6	0.16	16.9	64.7	0.26	sup
Oh7b	AS	6.5	54.2	0.12	24.6	70.4	0.35	sup
CML103	-	6.3	55.1	0.12	17.6	75.6	0.23	sup
CML322	-	4.6	61.9	0.07	21.1	72.4	0.29	enh
Ki3	AT	4.0	59.5	0.07	19.9	70.2	0.28	enh
CML247	AT	3.1	70.6	0.04	14.1	79.1	0.18	enh
Tzi8	AT	2.4	71.0	0.03	5.4	78.8	0.07	enh
Mo17	AS	2.0	53.7	0.04	9.6	76.5	0.13	enh
Linear Fit (R^2)[c]		**0.009**	**0.00003**	**0.005**	**0.002**	**0.008**	**0.0009**	

[a]Coding sequence polymorphism in the third exon of OY1 transcripts with three alternate alleles. Abbreviated symbols are A:Alanine, T:Threonine, S:Serine, -:Deletion of both amino acids.
[b]Category of the genotypes in terms of the severity of *Oy1-N1989/oy1*:B73/inbred F_1 mutant individuals assigned based on CCMI and Ratio_CCMI trait value. Abbreviated symbols are sup:suppressed mutants, enh:enhanced/severe mutants.
[c]R^2 of the linear model using indel as an explanatory variable onto a given trait as a response variable.

Table 11. Linear regression of the top *vey1* linked marker (isu085b) and CCM traits from wild-type and mutant siblings of IBM-RIL x *Oy1-N1989/oy1*:B73 F_1 populations on to OY1 transcript RPKM values of the respective IBM-RILs (n=74).

Trait/Marker	R^2 (%)	P-value
isu085b	19.2	<0.0001
MT_CCMI	25.2	<0.0001
WT_CCMI	4.8	0.06
MT_CCMII	27.3	<0.0001

WT_CCMII	0.9	0.40
Ratio_CCMI	31.3	<0.0001
Ratio_CCMII	22.5	<0.0001

Table 12. Determination of allele expression bias at *oy1* in leaf tissue from third leaf at V3 stage from wildtype and mutant sibs of B73(B)/ Mo17(M) F_1 hybrid and mutant B73 genetic backgrounds.

Genotype	SNP_252[1]	SNP252_Ref[2]	SNP_252_Alt[3]	SNP_317	SNP317_Ref	SNP317_Alt	Rati
B/M[&]	.	.	.	.	.	.	.
B/M	C/C	.	.	C/T	2635±51.60	2430±67.28	.
Oy1-N1989/oy1:M/B	C/T	2044±149.77	2291±152.87	C/T	2782±120.79	2522±67.29	1.12
Oy1-N1989/oy1:B/M	C/T	2138±142.51	2456±122.46	C/T	2677.33±99.71	2425±95.50	1.15
Oy1-N1989/oy1:B	C/T	2261±109.33	2290±76.62	C/C	.	.	1.01

[1]SNP position 252 with two alternate alleles. C corresponds to the wildtype/reference allele and T corresponds to the mutant/alternate allele. Same applies to SNP_317 column, except this SNP is polymorphic only between B73 and Mo17; *Oy1-N1989* allele is monomorphic with B73 at SNP_317.

[2]Mean ± standard deviation of allele count for the reference allele using three biological replications. Same applies to SNP317_Ref column. Same applies to SNP317_Ref column.

[3]Mean ± standard deviation of allele count for the alternate allele using three biological replications. Same applies to SNP317_Alt column. Same applies to SNP317_Alt column.

[&]Data obtained from Waters et al, 2017. Allele bias at *oy1* locus for plants grown under control condition.

[Ψ]Mean ± standard deviation of the ratios of the read count from reference allele to the alternate allele at SNP252. Connecting letters report indicate statistical significance calculated using ANOVA with posthoc analysis using Tukey's HSD with $p<0.01$.

[+] Mean ± standard deviation of the ratios of the read count from reference allele to the alternate allele at SNP317. Connecting letters report indicate statistical significance calculated using ANOVA with posthoc analysis using Tukey's HSD with $p<0.01$.

[%]Mean ± standard deviation of the average of the ratios at SNP position 252 and 317. Connecting letters report indicate statistical significance calculated using ANOVA with posthoc analysis using Tukey's HSD with $p<0.01$.

Supplemental Table 1. Primary trait mean values of the wild-type (WT) and mutant (MT) siblings of F_1 test crosses of *Oy1-N1989/oy1*:B73 with respective IBM-RILs.

RIL Identifier	MT_CCMI	WT_CCMI	WT_CCMII	MT_CCMII	MT_FlHT	WT_FlHT	MT_SW	WT_SW
MO001	6.30	45.30	49.60	17.50	202.70	190.80	22.70	24.00
MO003	8.30	35.50	37.30	16.20	212.00	194.20	18.90	22.80
MO007	4.00	46.80	54.80	5.80	163.30	193.00	20.50	25.30
MO008	10.30	47.40	51.90	16.10	202.50	191.30	20.50	24.00
MO010	11.40	48.20	42.90	18.60	225.00	211.50	21.00	21.30
MO013	8.70	33.70	47.70	16.30	206.50	196.50	21.60	23.50
MO014	3.50	54.60	47.30	5.10	184.30	185.70	17.80	24.30
MO016	3.20	52.30	43.90	6.20	179.00	192.80	19.00	23.80
MO017	9.30	54.30	67.90	21.40	224.00	212.30	22.90	23.20
MO018	8.00	34.30	51.20	18.20	177.00	173.00	24.50	22.80
MO019	8.40	36.90	40.90	14.50	198.00	188.70	20.60	22.70
MO021	3.60	50.10	65.40	5.40	198.50	194.50	15.50	24.30
MO022	8.60	46.30	45.70	15.80	220.50	210.80	24.40	23.60
MO023	3.10	47.90	55.20	3.80	172.50	201.80	14.80	25.50
MO024	8.60	47.10	50.30	19.20	234.50	224.50	23.80	23.00
MO025	3.60	49.60	57.90	6.90	160.70	185.00	15.80	22.60
MO028	4.30	35.00	52.50	5.50	180.80	187.20	15.60	23.00
MO029	11.80	47.80	41.90	19.60	199.00	201.80	21.40	20.90
MO031	3.20	41.90	54.90	5.20	207.80	207.00	17.80	25.80
MO032	4.00	57.90	52.30	7.10	212.30	223.40	18.80	23.10
MO033	12.00	46.50	52.90	19.50	208.00	203.40	22.80	25.70
MO036	3.30	39.00	54.00	4.60	199.20	223.00	19.20	25.30
MO039	4.10	52.60	52.40	5.70	207.40	212.00	17.50	21.90
MO040	11.00	42.20	62.90	22.50	243.00	219.50	24.80	25.10
MO042	10.00	53.00	47.40	18.60	211.00	191.30	22.00	23.50
MO044	2.80	42.80	52.70	4.40	151.00	191.00	20.00	26.00
M0045	6.90	41.80	42.40	12.60	196.00	193.50	26.80	26.50
MO047	4.00	35.70	36.70	8.10	196.00	193.00	20.60	25.00
MO048	6.40	30.30	35.50	18.20	226.20	221.00	26.80	29.00
MO051	4.00	40.20	45.60	7.30	198.50	205.40	14.30	21.90
MO052	10.70	53.10	56.30	15.50	196.50	182.80	23.00	22.80
MO054	8.40	50.60	43.70	13.90	229.00	215.80	24.80	23.80
MO055	16.90	38.60	37.70	24.50	205.50	192.30	23.30	24.00
MO056	8.80	41.60	44.90	18.00	200.40	190.40	24.20	22.60
MO057	9.20	47.90	45.40	19.60	221.30	208.00	24.50	24.00
MO060	3.70	44.30	54.90	6.00	200.80	202.20	18.70	25.30
MO061	11.20	43.30	64.70	29.30	215.80	201.20	21.30	21.50
MO062	11.40	43.00	62.00	20.60	209.30	206.70	22.50	24.80
MO063	11.60	55.50	55.20	20.50	170.80	158.80	20.40	22.50

RIL Identifier	MT_CCMI	WT_CCMI	WT_CCMII	MT_CCMII	MT_FlHT	WT_FlHT	MT_SW	WT_SW
MO066	9.10	47.90	50.40	21.50	196.20	188.60	23.00	23.60
MO067	8.60	41.30	44.90	13.60	206.00	212.30	23.10	23.80
MO074	3.70	48.50	48.50	4.90	195.30	187.00	21.80	23.00
MO076	3.90	56.00	64.00	6.50	193.30	186.50	21.80	24.00
MO077	3.10	49.10	44.00	6.70	207.80	226.80	16.10	24.10
MO079	9.90	42.90	46.40	18.30	245.60	229.80	22.30	22.20
MO080	6.10	39.20	52.60	15.40	205.00	196.80	20.60	25.00
MO081	3.30	41.00	58.30	5.40	203.30	210.30	19.50	25.00
MO082	3.20	45.50	58.00	4.90	198.30	208.60	16.70	25.20
MO083	9.90	49.20	54.70	22.80	206.30	194.50	20.80	23.80
MO085	3.80	41.70	36.30	3.70	187.00	203.00	18.50	22.50
MO086	9.50	58.40	65.20	24.80	223.40	199.20	22.40	24.00
MO088	11.40	48.20	53.80	27.00	234.30	207.80	21.30	24.00
MO092	10.40	53.70	60.50	27.50	200.00	199.00	20.40	23.10
MO093	6.70	51.40	51.90	12.60	234.50	220.80	24.00	24.50
MO097	4.90	48.00	56.90	7.40	177.80	194.30	18.60	23.50
MO098	7.40	49.50	64.90	17.50	193.80	189.00	22.00	24.00
MO099	3.10	59.80	55.00	6.00	217.20	218.00	20.30	27.80
MO101	8.40	41.80	50.10	22.70	215.40	207.60	21.20	23.10
MO106	5.50	44.10	51.00	16.80	225.60	217.00	20.50	23.50
MO109	7.30	43.10	52.90	18.40	235.50	220.50	21.30	23.50
MO110	4.00	43.90	46.50	7.10	198.50	211.80	18.30	23.80
MO113	10.10	53.80	59.40	24.50	211.00	195.50	22.30	22.00
MO114	7.40	36.30	52.30	20.80	197.20	182.80	21.60	21.70
MO116	8.70	46.60	50.20	16.50	218.60	201.40	24.30	27.00
MO118	10.10	43.20	39.80	18.70	202.60	200.00	21.20	23.20
MO119	4.30	42.70	46.50	6.40	210.00	199.30	20.50	24.30
MO121	10.00	51.80	43.70	19.50	196.00	186.00	19.90	22.50
MO124	8.00	35.80	39.40	18.00	183.00	173.50	22.80	23.00
MO125	10.60	39.60	40.10	16.00	220.20	213.20	20.10	23.70
MO127	7.00	57.40	49.60	24.10	183.00	200.50	20.50	23.50
MO129	3.60	49.40	41.50	6.00	202.40	214.60	17.80	26.00
MO130	8.10	45.70	51.50	23.30	230.00	213.60	21.40	22.70
MO131	10.00	39.50	62.20	26.00	192.80	194.60	21.50	23.00
MO133	2.80	43.20	56.30	4.70	189.30	187.50	16.30	25.30
MO134	6.30	43.20	42.90	11.20	231.80	215.50	20.60	23.40
MO138	9.80	50.30	47.90	24.70	187.80	192.00	24.10	25.10
MO141	2.00	37.50	41.80	3.70	168.30	218.00	15.00	25.00
MO142	8.40	45.30	62.30	15.50	198.20	182.60	22.90	24.50
MO146	9.80	48.80	52.30	15.90	231.80	214.80	23.80	23.00
MO147	3.50	44.80	46.30	6.70	224.30	213.30	18.90	26.50

RIL Identifier	MT_CCMI	WT_CCMI	WT_CCMII	MT_CCMII	MT_FlHT	WT_FlHT	MT_SW	WT_SW
MO153	9.70	52.10	47.30	14.50	204.80	200.50	24.40	24.90
MO154	3.30	49.00	55.60	6.00	201.00	201.30	16.50	25.50
MO156	10.30	51.40	74.10	16.00	209.20	198.40	23.40	24.80
MO157	9.70	49.40	61.30	20.70	207.80	188.20	20.00	23.20
MO159	10.20	47.00	50.00	12.30	213.50	205.50	24.50	25.00
MO160	4.20	36.30	57.00	7.50	199.80	215.60	17.40	22.80
MO161	3.30	44.80	53.90	7.40	212.50	227.80	19.90	25.60
M0162	3.80	54.00	56.70	5.60	215.80	205.30	19.80	25.80
MO165	3.20	51.30	51.00	6.00	189.80	199.00	16.80	25.50
MO168	4.10	46.40	45.90	8.40	210.00	193.00	21.80	24.30
MO169	11.70	44.80	49.10	21.00	196.80	191.50	23.00	22.30
MO170	8.10	43.10	46.10	25.00	216.00	214.50	23.80	22.90
MO171	8.50	45.90	48.70	26.70	209.00	211.50	23.50	24.00
MO174	3.50	54.00	60.90	8.70	198.80	196.00	17.00	23.80
MO176	3.50	30.10	49.10	5.10	184.00	194.50	19.60	24.30
MO177	3.50	40.60	53.10	5.20	183.40	198.60	20.20	24.50
MO178	8.80	45.90	55.10	23.40	206.00	194.00	21.30	25.80
MO180	8.10	45.00	52.50	17.90	199.50	195.50	21.30	23.00
MO181	8.30	38.70	72.70	17.00	192.00	185.30	25.00	28.70
MO182	3.50	37.10	48.60	7.00	203.80	217.50	22.50	26.00
MO183	7.50	42.00	44.30	16.50	222.50	208.30	21.40	23.80
MO184	4.70	55.00	56.40	8.60	230.50	229.00	15.80	21.00
MO185	6.60	35.70	38.60	12.00	213.60	209.00	21.80	22.80
MO186	2.50	25.00	51.70	3.80	158.00	173.50	16.00	24.00
MO189	13.00	50.10	50.80	17.30	227.30	216.50	24.80	23.40
MO191	3.80	50.20	55.40	6.00	185.60	204.20	19.50	24.40
MO192	2.60	42.50	46.20	3.90	160.00	185.20	17.80	25.80
MO194	12.40	48.20	51.80	17.80	218.20	196.20	23.80	26.10
MO195	8.60	43.00	43.50	18.30	210.50	202.00	22.30	24.30
MO196	10.50	46.10	62.50	26.30	224.50	226.00	21.80	22.90
MO197	8.30	52.80	60.50	22.20	199.30	179.50	24.90	27.10
MO198	8.90	55.40	65.50	21.90	230.80	226.80	23.80	21.80
MO199	9.20	49.70	50.40	21.40	228.30	224.50	23.30	24.80
MO200	9.10	41.40	45.40	19.10	203.30	197.50	23.50	23.00
MO201	3.40	40.60	40.10	5.70	205.00	203.30	18.00	26.30
MO204	3.80	35.90	38.90	5.90	179.20	191.30	18.40	23.60
MO205	5.70	39.40	41.80	13.60	189.50	184.00	24.00	24.90
MO206	9.70	53.20	45.30	18.00	190.80	180.50	20.30	23.00
MO208	10.10	54.70	53.20	18.60	226.00	214.00	23.80	23.80
MO209	10.90	54.70	52.20	18.80	189.50	181.00	25.00	24.00
MO214	9.50	51.10	59.80	19.80	194.20	185.60	20.60	22.10

RIL Identifier	MT_CCMI	WT_CCMI	WT_CCMII	MT_CCMII	MT_FlHT	WT_FlHT	MT_SW	WT_SW
MO215	4.00	45.00	60.20	6.20	190.20	204.80	18.60	24.20
MO216	10.30	42.20	51.40	23.00	211.40	198.20	20.50	21.10
MO218	3.30	52.10	56.10	5.40	167.80	212.60	12.90	22.70
MO219	10.20	43.40	53.50	14.10	226.00	207.00	25.00	26.00
MO220	8.30	42.70	51.10	18.20	215.00	194.00	23.10	24.00
MO222	11.20	49.00	42.60	21.90	190.50	169.00	22.50	19.80
MO223	7.70	47.70	67.00	18.40	206.80	193.80	23.80	23.00
MO224	8.70	50.00	58.50	28.60	186.00	175.50	28.00	26.50
MO225	3.60	44.20	45.10	5.50	211.70	231.60	15.00	23.30
MO228	9.90	36.60	38.80	15.50	199.40	193.80	19.10	22.20
MO229	10.90	45.70	45.90	20.10	198.60	188.80	22.30	22.70
MO232	9.90	42.60	45.40	17.50	221.30	202.80	22.30	23.00
MO233	6.70	39.90	48.60	15.10	215.50	200.80	19.80	23.80
MO237	3.50	59.30	47.00	6.60	227.80	203.50	18.00	24.30
MO240	3.20	57.30	57.60	6.70	182.30	189.30	17.80	25.50
MO241	8.90	42.70	49.00	15.30	202.50	207.30	21.50	22.70
MO244	4.10	54.60	51.80	5.30	178.00	178.00	20.40	26.20
MO248	10.60	44.30	66.40	22.30	187.80	172.00	21.40	22.70
MO250	3.00	44.30	61.50	3.80	186.00	209.50	16.80	25.50
MO253	2.90	47.30	41.50	4.60	179.30	188.50	13.00	21.30
MO255	3.10	39.90	44.80	4.80	201.40	236.80	18.60	26.70
MO256	3.20	48.80	57.70	5.40	194.50	207.30	16.80	24.50
MO258	6.60	41.90	54.20	24.80	173.00	171.50	17.00	21.00
MO262	3.70	48.80	56.00	5.00	186.20	192.20	17.60	24.60
MO263	3.20	40.90	63.20	4.50	186.00	194.30	17.50	23.50
MO264	3.70	50.20	50.70	5.50	172.60	182.00	20.70	24.30
MO265	7.40	43.10	56.80	15.50	199.30	186.30	26.30	25.30
MO266	9.00	44.10	52.20	17.50	199.80	189.00	23.00	24.80
MO267	7.60	47.90	45.70	13.70	208.80	201.20	21.90	25.20
MO269	8.60	44.00	50.10	18.60	207.70	195.50	25.30	24.50
MO270	12.30	66.20	56.50	23.60	213.30	204.80	21.30	22.80
MO271	12.70	47.40	51.40	21.80	199.20	193.60	22.30	24.00
MO272	4.00	43.60	55.50	4.80	205.30	209.50	19.90	24.90
MO274	8.90	43.10	46.50	23.50	200.20	201.80	20.80	22.60
MO275	5.90	52.90	47.10	13.70	176.00	191.40	20.00	23.60
MO276	7.00	50.60	57.20	14.60	195.80	191.20	23.30	24.70
MO277	9.10	47.40	52.30	27.80	199.00	200.00	23.80	23.80
MO279	3.50	38.80	40.00	6.10	223.00	186.30	19.40	23.10
MO280	9.00	43.60	36.20	15.80	221.00	205.00	24.70	24.50
MO282	3.20	44.80	42.60	5.90	191.20	196.00	18.00	25.00
MO286	3.10	61.70	48.40	5.10	177.00	204.50	17.80	25.00

RIL Identifier	MT_CCMI	WT_CCMI	WT_CCMII	MT_CCMII	MT_FlHT	WT_FlHT	MT_SW	WT_SW
MO287	3.40	47.40	46.20	5.50	223.50	223.50	18.00	26.10
MO292	3.70	46.60	42.00	6.20	177.80	191.40	17.20	22.10
MO295	9.10	53.50	51.00	18.10	210.00	196.30	21.00	22.30
MO296	3.20	56.70	58.00	7.20	198.50	199.80	18.80	24.00
MO297	8.80	44.90	53.70	13.80	203.50	200.80	20.10	24.30
MO298	8.40	50.30	48.50	22.40	201.20	185.80	22.20	23.80
MO300	6.00	43.50	46.70	19.80	234.00	214.50	22.00	23.50
MO301	8.40	45.60	45.40	17.20	222.80	211.00	22.30	23.50
MO304	3.50	45.70	53.80	5.40	178.20	203.80	17.80	25.10
MO305	6.90	43.30	42.30	17.70	200.30	186.30	19.80	21.30
MO307	2.90	27.90	40.20	3.40	185.30	201.00	17.80	24.00
MO311	8.10	37.90	52.30	18.60	229.40	226.30	19.40	21.90
MO313	3.40	43.30	50.70	5.60	191.00	198.00	16.80	25.60
MO314	9.50	39.00	42.00	18.40	227.80	213.30	24.60	24.10
MO318	3.90	44.30	56.90	6.20	199.00	209.60	19.30	24.00
MO321	3.40	59.30	55.10	4.60	177.50	199.40	20.30	27.30
MO322	8.20	41.70	38.90	18.50	218.00	211.80	21.60	22.60
MO325	7.20	44.80	58.00	19.00	229.80	217.30	21.10	22.30
MO326	4.10	58.50	56.10	8.50	201.50	200.00	19.30	24.00
MO328	3.00	45.40	48.70	4.50	199.20	211.20	19.40	23.80
MO331	6.20	44.40	49.30	11.20	218.60	221.40	23.10	25.10
MO334	8.80	50.70	60.30	18.50	178.00	165.70	23.30	21.70
MO335	6.50	36.20	44.40	11.50	220.30	209.30	23.40	23.80
MO337	10.70	46.70	48.40	25.20	223.50	220.30	24.00	25.50
MO340	10.00	49.00	54.60	22.40	217.40	183.30	22.70	23.70
MO341	3.20	45.30	48.60	4.10	172.60	187.00	16.20	22.80
MO344	3.80	51.70	45.60	5.80	206.00	217.20	20.00	23.80
MO345	9.30	42.70	49.00	16.20	208.80	195.40	22.80	25.90
MO346	10.10	46.20	48.40	19.80	219.30	209.00	24.10	24.40
MO347	4.20	53.50	60.10	8.80	217.00	203.00	19.00	22.30
MO349	4.30	52.80	59.20	6.90	224.30	204.50	21.50	24.80
MO351	7.30	34.40	59.80	25.50	199.80	191.00	23.80	23.50
MO352	11.50	40.90	52.30	24.10	184.30	168.30	23.60	24.30
MO353	10.10	52.90	60.10	23.40	236.80	215.00	21.50	23.30
MO354	3.40	45.40	56.20	5.60	184.20	189.80	17.80	25.20
MO355	9.50	48.40	58.50	20.10	221.20	201.40	20.00	22.10
MO356	4.50	49.70	59.70	7.00	196.40	210.80	17.90	23.70
MO357	10.60	53.40	46.20	18.00	200.20	188.60	21.70	23.30
MO358	7.20	44.50	50.40	17.20	196.80	187.00	22.00	23.80
MO360	11.40	39.10	52.30	18.90	197.30	196.50	23.30	23.80
MO361	3.50	29.70	41.80	4.90	201.30	193.50	17.50	22.30

RIL Identifier	MT_CCMI	WT_CCMI	WT_CCMII	MT_CCMII	MT_FlHT	WT_FlHT	MT_SW	WT_SW
MO362	8.90	36.80	56.40	15.10	237.00	235.00	25.60	26.00
MO364	11.40	46.20	60.20	17.80	189.50	189.80	21.00	25.00
MO368	6.90	51.10	55.30	19.80	208.00	202.60	24.50	24.80
MO369	10.20	48.70	49.40	17.30	192.30	184.30	24.70	25.00
MO372	3.70	44.30	42.70	6.30	211.00	202.00	19.60	24.30
MO373	3.60	49.40	59.20	4.90	202.30	214.00	17.50	24.00
MO378	7.40	53.40	64.50	16.20	232.50	237.00	27.00	27.00
MO379	3.00	42.60	52.70	3.80	157.20	172.60	15.10	23.60
MO380	12.20	49.70	70.30	30.40	171.80	172.80	23.60	23.80
MO381	9.50	40.00	43.60	28.90	187.50	179.30	24.00	23.00
MO382	8.60	48.70	57.20	20.60	195.60	189.80	21.40	22.50
MO383	2.70	55.70	50.10	4.90	181.80	200.80	19.40	26.40
MO384	2.50	27.30	46.80	4.20	182.30	190.00	17.50	21.80

Supplemental Table 2. Primary trait mean values of the wildtype (WT) and mutant (MT) siblings of F_1 test crosses of *Oy1-N1989*/*oy1*:B73 with respective Syn10-DH line.

Line ID	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT	MT_SW	WT_SW
M0001	2.48	61.60	6.48	88.70	228.50	206.75	100.50	85.00	16.50	24.83
M0002	6.95	63.63	31.85	63.52	238.50	215.50	105.50	99.75	21.67	26.00
M0009	7.93	43.13	28.33	77.85	236.25	214.50	120.50	108.50	20.83	23.00
M0010	3.02	62.70	8.97	78.75	211.75	210.50	107.00	94.25	16.17	25.67
M0011	6.12	41.67	25.72	70.70	248.75	237.00	145.00	121.00	22.50	27.17
M0012	7.13	51.43	30.13	67.83	234.00	226.25	118.50	100.50	20.00	24.33
M0015	6.50	43.57	25.20	64.53	225.25	213.75	112.75	104.25	22.00	24.83
M0019	1.87	53.63	5.27	77.97	200.50	211.50	91.50	96.50	14.17	26.33
M0020	2.03	56.82	6.05	73.58	225.75	218.00	114.75	104.25	15.83	24.67
M0023	7.20	55.87	27.42	75.42	226.00	207.75	111.00	88.50	21.33	25.50
M0024	8.05	47.42	29.90	63.79	251.25	239.25	123.00	112.50	21.50	25.50
M0025	9.50	51.28	25.88	69.18	261.00	245.00	130.75	125.50	25.67	27.67
M0027	2.10	42.02	6.00	70.55	198.00	197.50	92.00	99.00	16.83	24.83
M0029	6.52	55.58	25.62	63.40	242.25	205.25	113.50	95.75	19.50	22.50
M0030	5.95	54.60	22.88	69.72	260.75	219.00	136.75	103.50	19.33	23.83
M0032	7.90	54.28	33.97	68.08	245.00	219.75	110.75	102.25	23.83	28.33
M0034	6.80	58.70	33.10	78.75	212.50	196.00	103.50	82.00	21.17	23.33
M0036	2.27	56.42	8.30	89.33	219.50	212.50	102.25	91.75	15.67	24.33
M0038	10.80	51.83	34.07	64.40	237.00	219.50	112.25	103.00	22.50	24.67
M0041	4.72	50.20	25.40	57.35	212.00	209.75	90.50	92.00	21.33	25.83
M0042	6.48	47.48	34.02	73.33	242.75	219.75	124.50	111.50	19.67	23.67
M0043	7.57	46.65	30.68	67.40	261.25	240.00	130.00	112.25	21.67	24.50
M0047	2.75	53.45	6.85	59.08	171.00	229.00	73.00	105.25	16.17	27.33
M0049	2.40	41.42	7.62	72.32	231.25	227.00	107.25	106.00	17.33	24.33
M00	8.95	56.25	33.12	75.12	236.5	229.00	104.50	111.25	21.33	25.67

Line ID	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT	MT_SW	WT_SW
50					0					
M0053	7.65	47.47	30.73	76.62	231.50	210.25	111.00	99.25	21.17	24.67
M0054	6.98	52.93	33.18	72.35	244.00	228.75	109.75	103.50	24.00	26.17
M0055	2.75	57.95	6.08	74.55	232.25	216.75	114.50	97.25	16.67	26.67
M0056	5.38	54.38	26.03	73.98	247.00	234.50	111.25	106.75	20.67	25.83
M0057	6.00	43.82	26.43	70.92	236.75	225.75	115.75	105.75	20.83	25.50
M0061	1.57	45.27	4.67	64.03	177.50	220.25	69.50	94.50	13.67	26.00
M0062	5.82	56.05	21.98	73.72	231.50	223.50	105.75	100.75	22.17	26.00
M0068	1.72	56.32	5.55	70.68	205.50	213.00	95.50	105.50	15.67	24.00
M0069	13.27	48.58	32.48	74.30	231.00	204.25	96.00	84.50	24.17	26.83
M0070	2.30	48.43	6.97	73.15	232.25	239.50	112.00	112.75	16.00	26.50
M0074	1.82	53.02	6.42	76.63	236.50	205.50	107.25	88.00	16.17	24.67
M0076	2.58	46.47	7.85	74.67	230.25	242.50	114.25	116.75	15.00	24.17
M0078	6.85	57.53	27.07	74.27	253.50	230.25	135.25	110.00	22.83	24.50
M0084	1.75	52.07	4.33	80.42	205.25	221.75	90.75	102.25	13.50	26.17
M0090	7.13	49.07	30.32	67.05	243.75	235.25	123.75	116.25	24.00	27.00
M0091	7.72	38.28	31.47	72.65	242.00	220.75	118.50	103.25	20.67	24.00
M0092	8.28	48.08	45.65	66.43	238.00	229.00	107.75	99.00	21.50	23.67
M0093	7.07	55.40	32.85	68.63	230.00	211.75	113.00	97.50	24.00	26.50
M0095	6.13	53.27	27.83	70.05	282.00	251.75	147.25	116.75	22.50	27.50
M0105	6.47	60.37	33.78	61.80	235.25	210.50	106.00	94.25	20.67	23.33
M0108	7.47	40.58	29.22	64.13	231.75	221.00	113.50	103.25	22.33	23.83
M0109	5.77	50.32	25.20	62.47	262.50	236.00	136.75	110.00	20.67	24.50
M0111	7.33	45.63	31.27	82.28	218.00	204.25	95.50	93.75	21.00	23.17
M0116	6.35	48.72	25.85	72.90	256.25	238.50	122.00	105.75	22.83	26.50
M0118	7.85	52.32	31.90	63.05	232.25	225.25	104.75	91.75	23.67	26.17
M01	6.68	50.62	30.12	70.95	240.7	228.50	119.75	104.25	21.67	25.83

Line ID	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT	MT_SW	WT_SW
19					5					
M0120	6.75	49.90	33.57	69.55	214.00	219.50	103.00	103.25	22.67	24.50
M0126	5.70	47.63	32.02	70.72	236.25	225.25	114.50	107.00	22.67	27.33
M0130	.	51.00	.	71.08	225.00	228.00	116.25	100.00	.	23.33
M0136	6.73	49.98	28.55	74.30	228.50	204.75	119.25	97.25	22.17	24.00
M0317	8.10	52.90	28.58	79.77	240.00	216.75	109.00	93.50	22.33	28.33
M0316	5.35	47.23	25.22	71.78	226.25	221.75	115.50	114.00	21.00	25.67
M0315	1.65	60.88	5.67	65.95	215.50	201.75	99.00	83.00	15.67	24.33
M0312	7.48	48.80	23.83	70.07	261.50	233.50	131.75	110.50	20.67	25.17
M0305	1.68	50.60	5.60	76.28	203.00	219.50	97.25	102.50	14.67	25.33
M0298	6.25	44.60	28.63	70.28	244.25	229.50	113.75	103.25	22.83	25.00
M0296	7.18	47.62	25.70	69.92	259.00	239.00	109.25	105.25	22.00	26.33
M0295	9.92	57.23	31.70	75.47	241.25	228.25	125.50	117.75	23.83	26.83
M0293	2.38	50.68	7.75	69.17	220.00	215.00	90.00	92.25	17.50	27.33
M0290	8.70	46.50	28.65	64.85	271.75	265.50	139.25	127.00	24.67	28.67
M0285	5.52	47.28	26.97	70.60	223.75	216.00	103.25	102.00	22.50	25.83
M0272	6.82	53.27	29.03	63.68	236.50	215.00	111.75	107.00	18.67	23.50
M0267	8.60	45.87	31.93	71.52	241.00	217.25	118.50	100.50	22.67	25.33
M0266	2.10	55.32	4.48	73.52	190.25	201.50	76.00	77.00	15.67	26.83
M0264	6.17	56.15	29.72	75.85	229.75	209.00	102.25	91.00	22.00	23.00
M0262	6.37	47.27	35.73	69.78	213.75	213.00	91.75	97.50	20.50	23.83
M0258	6.10	47.32	22.58	63.32	227.75	201.00	101.50	91.00	20.17	23.67
M0256	5.60	44.07	23.98	68.58	241.25	218.75	114.25	103.50	20.83	24.00
M0253	6.07	48.80	21.50	71.77	254.50	233.75	108.50	99.25	21.00	25.67
M0252	6.03	36.88	33.90	70.33	226.25	208.75	106.25	95.50	22.33	26.00
M0250	2.27	51.53	6.67	75.92	223.75	214.00	109.00	92.75	16.17	26.00
M02	1.87	44.30	4.72	60.27	194.7	222.00	90.00	102.00	14.50	27.83

Line ID	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT	MT_SW	WT_SW
49					5					
M0245	8.55	51.08	32.10	70.38	227.50	208.75	107.00	95.50	21.17	24.50
M0243	7.90	44.28	33.73	73.25	252.00	217.75	118.75	102.25	23.17	27.33
M0240	2.02	36.15	6.57	76.32	204.25	223.75	104.25	102.75	19.33	27.17
M0237	6.83	44.67	28.33	67.78	223.50	227.50	111.00	105.75	23.00	24.00
M0234	8.12	48.87	24.95	75.62	225.50	207.00	105.25	89.25	21.83	24.50
M0231	2.88	54.68	6.00	83.48	213.25	200.50	94.00	92.50	16.17	27.83
M0230	6.33	52.75	28.87	74.83	229.00	210.50	111.50	98.25	21.83	26.50
M0227	1.85	43.10	5.58	70.48	222.50	223.00	120.00	102.25	16.17	25.50
M0223	2.33	41.03	7.30	68.05	246.50	228.25	123.50	112.25	15.83	26.17
M0221	7.90	49.03	26.78	66.18	239.00	231.75	112.75	107.75	22.83	26.83
M0218	7.63	43.58	35.08	64.90	262.25	241.50	122.50	113.00	21.00	24.83
M0217	9.65	48.13	30.12	71.27	231.75	208.00	101.75	79.75	22.00	24.17
M0215	9.38	47.88	35.68	60.53	240.75	235.00	111.50	98.25	24.17	24.83
M0212	8.73	54.03	33.65	78.37	240.50	226.25	109.75	106.25	21.50	24.00
M0210	5.53	43.23	26.13	68.23	248.50	231.25	129.25	114.25	24.50	26.50
M0209	7.55	57.28	37.03	73.48	213.00	201.75	101.75	87.25	20.33	23.83
M0208	7.42	56.32	28.10	66.25	227.75	208.75	113.50	103.75	21.17	24.50
M0206	6.17	47.27	26.03	70.88	231.75	210.00	101.25	87.00	22.83	25.33
M0202	2.15	51.02	7.50	72.88	224.00	225.75	113.50	100.00	13.83	26.33
M0198	5.98	51.87	35.22	77.87	217.75	206.00	101.25	92.25	21.33	25.67
M0196	10.48	50.05	39.60	67.02	232.25	215.00	112.25	94.25	20.17	23.83
M0195	8.12	70.67	26.82	85.57	229.00	201.00	104.50	89.75	22.33	26.50
M0193	6.98	44.08	31.60	66.80	247.75	223.50	109.75	107.75	22.67	25.50
M0189	8.82	64.22	29.77	75.55	223.50	209.25	101.25	94.00	21.50	26.83
M0188	8.08	45.37	22.22	69.07	239.75	231.00	115.50	100.25	21.67	23.83
M01	7.43	57.68	36.22	69.73	238.2	220.50	103.25	97.50	22.50	24.50

Line ID	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT	MT_SW	WT_SW
84					5					
M0179	9.25	51.85	34.78	80.60	240.00	222.00	129.00	115.25	22.83	23.67
M0178	6.40	46.08	36.05	78.50	252.75	228.50	140.25	110.25	18.67	23.33
M0175	7.90	53.80	40.65	79.70	242.00	225.50	114.00	99.75	23.33	27.33
M0173	5.15	50.12	28.38	64.60	213.25	200.75	92.25	83.00	22.00	26.33
M0172	3.00	40.22	6.92	68.17	231.75	244.75	115.50	114.25	17.50	26.50
M0171	2.63	53.13	7.03	72.98	220.50	225.00	106.50	99.25	17.67	26.50
M0169	2.08	49.82	7.08	67.88	186.25	221.00	71.75	90.25	14.67	27.50
M0166	5.27	53.28	24.98	82.12	230.00	214.00	106.75	94.00	21.17	25.33
M0162	8.60	46.07	26.57	57.95	216.75	208.50	104.50	99.75	22.67	24.50
M0159	2.03	41.42	5.05	67.48	195.50	228.75	72.25	102.00	15.33	27.17
M0156	2.27	35.48	7.23	59.70	189.75	190.25	85.50	98.00	12.50	19.83
M0155	6.88	52.38	34.25	71.03	210.75	199.50	87.25	91.75	23.17	25.50
M0152	2.00	39.67	4.42	69.10	203.25	230.00	95.75	104.25	12.67	27.83
M0145	2.17	52.87	7.12	67.30	241.00	261.25	127.25	119.50	16.67	25.17
M0138	8.98	60.95	37.67	72.48	219.75	216.00	108.00	100.00	22.50	25.33
M0319	7.65	47.40	31.78	71.78	227.50	217.50	107.50	96.75	21.00	23.67
M0324	7.67	44.90	30.53	76.93	234.25	208.00	93.75	79.25	20.33	25.50
M0328	2.50	40.57	6.97	68.15	209.50	232.25	91.75	104.75	15.00	24.83
M0330	2.80	51.43	9.32	66.87	242.00	224.50	115.25	108.75	19.67	26.50
M0332	7.72	55.77	34.78	74.23	243.25	225.25	117.00	94.75	21.00	24.83
M0335	6.30	45.13	29.42	66.22	233.75	221.50	104.50	101.00	20.33	24.50
M0336	5.62	54.95	24.33	66.20	237.50	219.75	109.75	102.50	23.33	23.83
M0340	6.42	50.07	32.45	70.92	249.75	238.00	113.75	104.25	22.17	25.50
M0341	5.88	45.77	29.02	66.17	254.00	244.50	122.25	109.75	21.83	26.50
M0345	2.00	39.53	5.43	66.82	186.75	223.50	87.75	101.00	13.83	25.33
M03	6.58	47.03	26.65	78.90	238.5	218.25	113.25	101.00	19.50	24.83

Line ID	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT	MT_SW	WT_SW
47					0					
M0349	7.65	48.20	33.42	80.10	238.25	223.25	110.50	92.75	22.50	24.50
M0356	1.57	51.57	5.28	75.72	201.75	203.00	93.25	90.25	14.67	25.67
M0357	5.68	44.47	23.17	69.68	227.75	221.00	101.75	101.00	21.33	25.17
M0358	5.88	67.85	34.42	82.13	229.75	195.00	108.50	87.75	20.83	24.33
M0366	2.47	55.93	6.35	73.63	205.00	209.50	75.50	80.75	14.67	26.00
M0372	9.13	51.37	34.88	77.35	248.50	233.75	121.50	112.25	23.83	26.67
M0373	1.78	37.92	4.80	72.35	195.50	201.25	90.50	88.00	14.83	26.33
M0374	1.80	41.17	5.58	66.05	197.00	215.25	100.25	100.00	14.83	26.17
M0375	6.23	46.17	29.42	67.58	220.75	205.25	92.75	92.25	20.83	24.67
M0376	2.32	58.53	8.18	74.37	226.75	222.00	104.75	100.00	14.50	25.17
M0381	2.27	50.28	6.95	57.35	229.75	230.25	120.50	105.50	15.67	25.00
M0382	4.85	52.32	21.68	77.27	239.00	225.25	107.50	98.00	22.83	26.50
M0385	5.25	34.77	24.52	71.38	234.75	229.25	128.00	111.75	20.50	24.00
M0388	6.83	60.67	26.62	71.70	271.50	256.25	139.25	118.75	20.50	27.67
M0389	7.87	48.78	29.97	70.38	253.00	229.25	116.25	104.00	21.83	23.00
M0390	1.70	39.53	5.02	72.97	211.00	229.50	106.00	101.75	16.00	26.50
M0391	2.32	52.42	6.62	79.38	222.25	220.25	121.75	112.00	14.17	27.17
M0396	6.05	51.53	33.27	79.13	240.50	213.00	116.00	102.00	24.00	24.83
M0401	7.20	60.02	32.05	71.75	244.00	235.50	118.00	108.00	21.17	24.67
M0404	1.77	53.32	5.95	75.68	192.00	213.25	82.50	100.75	15.00	26.00
M0405	1.93	53.60	6.07	70.52	193.50	212.75	76.75	98.25	14.33	25.83
M0407	7.75	47.50	30.65	77.98	232.50	213.25	109.00	95.25	21.00	26.67
M0412	7.05	37.87	30.13	74.98	214.00	191.50	102.50	85.50	23.67	27.17
M0414	6.57	42.75	27.23	68.87	204.25	193.25	102.75	95.25	19.50	23.67
M0422	1.82	47.47	7.70	77.98	245.25	244.75	113.50	117.50	15.83	28.00
M04	4.88	45.82	23.18	67.33	223.2	199.75	95.50	77.75	19.33	24.17

Line ID	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT	MT_SW	WT_SW
24					5					
M0427	8.50	47.42	39.40	77.37	224.00	207.75	110.75	87.75	22.83	24.83
M0428	8.77	49.53	30.78	74.85	248.50	246.75	122.75	111.75	23.67	26.83
M0429	6.95	51.37	29.80	74.28	261.25	241.75	134.25	111.25	21.50	24.50
M0430	8.85	42.72	30.12	74.15	219.00	214.50	118.75	106.00	22.33	23.33
M0431	1.98	46.80	6.02	77.30	222.25	212.00	93.00	93.75	20.17	26.33
M0433	8.47	57.42	32.02	79.95	254.25	227.25	123.00	96.25	20.83	25.33
M0434	6.88	48.87	28.70	68.75	261.25	238.75	128.25	107.00	22.33	26.67
M0436	5.48	39.53	25.87	68.33	261.00	232.75	121.50	105.50	23.00	24.67
M0438	9.07	52.88	33.87	69.20	241.25	230.50	113.75	103.50	24.50	25.83
M0443	1.98	58.77	5.62	72.68	218.00	217.50	93.50	96.25	16.50	24.50
M0444	5.62	44.07	26.90	68.47	250.75	228.25	112.50	109.00	20.33	23.00
M0448	8.03	59.33	26.55	67.35	249.75	224.25	118.75	102.75	21.33	24.50
M0450	1.60	47.35	5.78	71.05	189.25	193.00	79.75	79.25	14.67	25.17
M0453	7.80	55.88	32.80	70.57	246.75	218.50	116.75	104.00	23.50	27.67
M0454	6.72	50.42	28.43	79.88	208.50	198.00	95.25	85.50	23.00	25.67
M0457	1.77	53.98	5.48	73.25	209.50	189.25	107.00	90.25	15.00	24.83
M0461	6.00	43.08	31.33	61.73	233.00	212.50	116.25	88.50	22.17	27.17
M0463	8.72	63.50	43.48	75.70	230.50	222.75	108.75	100.50	20.67	22.17
M0465	2.38	56.58	7.30	71.60	245.50	251.25	130.50	125.75	15.67	27.83
M0466	7.50	49.73	35.80	74.17	233.25	213.00	114.75	92.75	23.33	24.83
M0469	7.00	55.50	38.10	76.85	232.75	217.75	112.50	98.75	21.67	25.83
M0471	1.82	48.37	4.25	68.92	213.25	210.00	104.00	87.00	15.50	25.17
M0472	7.40	58.10	29.22	86.20	258.00	230.75	124.50	95.50	20.67	25.17
M0474	7.60	52.17	32.75	80.38	220.25	203.75	100.00	94.00	18.83	24.33
M0476	2.15	50.08	7.72	73.85	207.00	213.25	97.50	93.00	15.33	24.00
M04	1.88	44.30	6.10	74.03	227.0	235.25	105.25	105.75	14.83	25.33

Line ID	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT	MT_SW	WT_SW
77					0					
M0479	2.08	46.82	6.63	67.73	219.00	217.75	103.75	101.50	16.00	25.00
M0481	6.23	57.62	34.83	78.85	225.25	214.50	99.25	88.00	24.67	26.00
M0487	9.67	58.18	34.77	70.98	233.75	216.75	111.00	100.00	23.00	25.50
M0489	2.52	51.77	7.58	79.43	214.75	226.75	113.75	96.75	15.67	27.17
M0491	5.70	50.05	27.10	77.30	249.00	239.75	125.50	109.25	23.00	25.17
M0492	6.88	59.90	24.15	78.62	203.75	200.25	84.25	84.75	19.67	25.50
M0494	7.95	54.70	26.23	66.37	229.00	221.75	106.50	115.75	22.33	25.50
M0630	2.05	46.58	6.13	63.67	134.50	202.50	55.25	89.75	12.00	24.33
M0624	7.05	52.67	37.15	73.20	264.50	233.25	113.75	99.75	21.83	27.33
M0623	6.38	49.22	22.20	72.95	226.50	195.50	115.25	82.75	22.67	26.17
M0619	2.72	55.02	7.10	67.22	228.75	227.75	110.75	104.00	17.50	26.67
M0618	5.50	49.95	24.63	73.27	233.25	205.75	101.25	87.00	22.83	25.00
M0617	8.30	51.43	37.12	76.12	253.00	234.00	121.75	113.50	26.50	27.83
M0614	7.52	53.55	30.65	78.38	263.50	239.25	124.25	115.50	20.33	23.50
M0613	5.87	43.05	28.18	72.65	234.25	229.25	116.50	100.00	21.17	25.83
M0611	7.92	52.82	23.88	67.73	255.50	233.25	132.50	113.50	20.50	26.33
M0609	1.78	49.28	5.13	76.05	188.25	219.25	99.25	107.25	13.67	24.17
M0597	7.60	59.10	39.93	72.33	246.00	219.50	111.75	88.50	23.00	26.33
M0594	9.05	50.00	35.20	74.63	232.25	219.00	104.00	90.50	20.50	23.33
M0590	8.20	53.37	25.10	73.02	227.75	201.50	111.00	97.75	21.00	24.67
M0589	6.27	64.10	35.68	83.17	249.00	229.00	126.25	112.75	22.83	25.67
M0588	2.07	49.58	5.52	74.22	181.75	220.25	73.00	88.25	13.33	25.33
M0587	1.85	43.30	4.98	71.37	209.50	221.25	91.25	98.00	16.17	27.17
M0583	7.30	48.10	30.25	67.75	240.50	223.00	119.00	98.75	22.83	25.33
M0581	6.40	55.30	23.52	66.83	235.00	225.50	116.50	106.75	21.50	25.17
M05	7.73	60.83	29.42	82.37	230.0	215.25	108.50	95.00	23.67	25.17

Line ID	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT	MT_SW	WT_SW
80					0					
M0577	6.43	47.55	29.13	72.72	272.50	253.75	148.00	128.50	22.33	26.00
M0566	5.47	39.68	30.62	68.43	253.25	232.25	129.25	105.75	24.17	26.00
M0565	7.87	51.77	27.38	74.60	263.25	235.50	140.00	115.00	19.67	26.00
M0564	8.68	48.85	28.65	70.23	251.25	245.75	125.25	119.00	21.17	25.00
M0563	2.15	47.48	6.87	61.13	228.50	225.25	113.75	113.25	16.50	26.17
M0562	2.32	53.05	6.98	81.25	208.75	223.00	88.25	92.75	13.83	26.00
M0575	1.97	50.62	7.50	73.17	242.00	235.25	110.00	109.75	16.50	25.67
M0574	7.15	63.78	33.68	64.95	233.50	206.50	114.50	91.50	19.67	23.83
M0573	4.35	47.10	31.70	61.40	229.00	192.00	99.50	70.00	23.00	26.00
M0571	2.28	62.95	7.73	78.53	199.75	207.50	86.00	82.25	16.67	26.00
M0561	7.95	46.85	25.65	67.33	240.00	231.00	124.00	112.25	21.33	23.83
M0560	8.60	53.15	26.17	75.43	260.50	246.75	133.25	128.75	23.50	27.00
M0559	7.05	53.45	29.92	70.15	240.75	219.25	124.50	98.50	21.17	25.00
M0558	1.73	47.20	5.62	76.55	191.00	212.25	104.25	97.00	12.33	25.00
M0557	5.43	43.90	23.43	73.72	242.50	236.25	125.25	125.00	23.00	24.00
M0556	2.37	52.18	6.35	75.47	207.00	194.25	91.75	79.50	16.50	25.83
M0553	6.78	55.60	28.51	67.70	234.75	209.75	106.25	95.00	21.67	25.50
M0551	1.97	48.08	5.35	69.63	204.50	237.00	91.25	111.75	13.50	24.33
M0550	7.97	56.22	27.78	63.90	247.00	224.75	121.50	108.25	21.50	26.50
M0549	6.65	52.95	34.95	69.82	248.75	232.75	117.25	108.75	21.50	25.00
M0548	1.85	45.02	6.27	66.40	207.00	197.00	87.00	84.00	15.00	25.83
M0546	7.28	51.12	29.15	71.68	237.00	218.00	125.25	103.00	22.00	27.83
M0545	5.18	56.37	27.17	71.33	218.25	212.75	107.25	99.50	20.33	25.00
M0543	5.27	33.47	24.73	69.93	264.25	247.50	133.75	128.75	21.33	27.83
M0544	1.90	50.23	5.58	71.18	196.00	219.75	82.75	91.25	16.33	28.67
M05	7.93	51.05	36.37	68.37	248.2	219.50	127.25	101.50	22.83	25.33

Line ID	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT	MT_SW	WT_SW
40					5					
M0538	5.37	51.43	28.32	74.03	241.50	205.25	107.00	87.75	22.17	26.67
M0537	7.05	47.58	25.87	77.18	230.00	220.75	118.00	114.00	22.50	24.33
M0535	8.45	43.63	35.52	75.20	253.00	225.75	128.50	101.00	21.00	24.67
M0534	7.48	39.33	32.98	73.89	243.25	225.50	107.50	104.75	24.00	25.17
M0533	6.48	50.97	23.78	76.43	256.00	224.00	124.00	101.25	21.00	25.00
M0532	5.43	47.42	25.87	68.35	263.50	233.50	143.25	116.00	20.67	27.00
M0527	6.47	53.48	27.63	70.17	274.75	264.50	133.00	124.75	20.17	24.50
M0525	6.68	45.15	28.92	64.40	233.25	218.75	108.50	93.75	19.50	24.33
M0519	7.33	48.28	25.50	68.20	250.25	228.75	139.25	115.25	21.17	25.83
M0517	5.85	40.85	25.77	70.12	231.00	203.25	98.25	78.75	22.83	23.83
M0513	6.35	45.65	31.82	73.33	216.50	218.25	95.75	100.00	18.67	23.00
M0512	6.50	50.07	22.70	87.50	194.00	182.50	93.00	90.50	23.00	25.67
M0510	7.77	45.90	24.77	75.77	227.00	206.75	104.50	93.25	19.67	24.33
M0509	1.92	56.47	6.35	76.90	227.50	241.75	120.25	107.25	14.33	25.67
M0506	2.00	53.73	6.23	68.63	246.00	257.25	127.00	117.50	18.50	26.33
M0502	5.27	43.95	24.40	67.95	211.00	193.50	92.75	88.50	19.50	23.17
M0500	7.27	42.13	28.00	76.82	219.75	207.25	103.25	95.25	24.00	25.33
M0498	1.82	44.35	4.98	71.73	235.50	234.50	102.50	103.25	16.50	27.67

Supplemental Table 3. Primary trait BLUP value of the wild-type (WT) and mutant (MT) siblings of F_1 test crosses of *Oy1-N1989/oy1*:B73 with respective maize inbred line from maize diversity lines (MDL). Information on the inbred lines from maize association panel (referred to as 302 panel) was adapted from Flint-Garcia *et al.* 2005.

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FIHT	WT_FIHT	MT_EaHT	WT_EaHT
F10	Puy-de-Dome, France	Ames Panel	Etoile de Normandie variety	10.67	54.91	32.81	76.84	26.11	26.95	225.40	197.44	90.18	82.28
F431	.	Ames Panel	.	9.09	66.77	38.01	78.97	21.18	27.34	224.66	240.00	103.54	106.77
GE440	North Carolina	Ames Panel	Hastings Prolific	9.42	60.34	22.56	68.42	22.01	24.46	317.38	276.92	158.81	125.79
Hi33	Hawaii	Ames Panel	(M14 x CI187-2)Oh45)BC1	8.56	62.22	28.31	68.15	21.25	25.36	264.87	247.99	120.54	104.55
HY2	.	Ames Panel	.	2.74	57.83	9.63	67.11	15.90	24.91	258.75	252.62	134.10	126.58
IA5125B	Iowa	Ames Panel	Unknown	5.67	54.52	14.98	71.69	20.53	27.34	265.03	254.86	115.85	114.06
Mo16W	Missouri	Ames Panel	Pipe Corn	13.77	58.03	46.03	71.67	24.58	27.52	297.24	270.69	146.05	126.26
Mo20W	Missouri	Ames Panel	N6/Mo22	8.23	68.39	24.42	70.64	21.15	25.81	285.16	252.30	141.85	118.02
Mo48	Missouri	Ames Panel	(NC33/B52) S6	12.54	56.85	41.86	74.12	23.34	26.26	269.22	255.02	125.38	115.80
PH9	.	Ames Panel	.	7.83	58.96	19.26	67.32	21.15	24.91	241.99	231.36	94.54	100.42
W32	Wisconsin	Ames Panel	Unknown	9.15	56.78	29.23	69.73	22.20	27.16	277.43	241.59	136.36	112.95
Yu796	North Carolina	Ames Panel	Unknown	10.62	61.29	20.03	76.65	22.20	25.45	232.65	210.58	97.12	84.57
LH1	USA	Ames Panel	Check PVP certificate	7.96	66.76	21.81	78.59	22.20	27.61	227.50	204.19	94.86	85.21
LH119	USA	Ames Panel	Check PVP certificate	8.70	58.75	29.71	69.25	21.53	24.10	222.99	198.91	94.86	82.19
LH123HT	USA	Ames Panel	Check PVP certificate	11.22	59.51	30.15	73.16	19.91	24.19	281.78	267.49	134.26	128.33
LH127	USA	Ames Panel	Check PVP certificate	11.91	65.34	24.35	68.43	22.58	24.91	229.27	218.25	103.10	99.16
LH128	USA	Ames Panel	Check PVP certificate	10.02	58.63	44.43	72.83	21.15	24.55	270.50	249.75	133.78	119.45
LH132	USA	Ames Panel	Check PVP certificate	9.53	56.58	37.39	70.95	21.82	23.28	227.82	210.10	100.84	89.17
LH145	USA	Ames Panel	Check PVP certificate	8.90	55.76	21.03	72.41	19.53	23.46	233.94	216.34	107.78	104.39

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT
LH146Ht	USA	Ames Panel	Check PVP certificate	7.62	54.14	22.08	67.33	19.84	24.82	234.69	222.41	99.42	95.51
LH149	USA	Ames Panel	Check PVP certificate	7.94	60.00	26.35	71.48	21.63	24.55	210.75	191.56	91.47	80.61
LH150	USA	Ames Panel	Check PVP certificate	7.06	66.99	17.30	75.47	19.72	25.45	285.97	274.36	140.56	122.30
LH160	USA	Ames Panel	Check PVP certificate	8.89	61.48	29.55	78.30	21.82	25.27	243.28	226.41	101.16	96.62
LH193	USA	Ames Panel	Check PVP certificate	9.03	61.83	29.83	64.83	21.34	24.28	217.83	209.94	104.87	84.73
LH194	USA	Ames Panel	Check PVP certificate	8.04	60.00	22.98	74.28	20.67	24.91	240.06	232.16	110.36	103.12
LH195	USA	Ames Panel	Check PVP certificate	10.07	63.47	40.72	71.50	22.29	25.45	227.01	209.46	112.78	91.70
LH196	USA	Ames Panel	Check PVP certificate	6.81	53.16	32.44	70.76	20.20	22.38	219.93	212.34	90.02	85.84
LH202	USA	Ames Panel	Check PVP certificate	5.03	56.62	25.99	66.06	19.24	23.55	227.34	206.10	109.07	84.41
LH205	USA	Ames Panel	Check PVP certificate	NA	55.33	NA	69.58	18.49	24.91	NA	218.57	NA	97.41
LH208	USA	Ames Panel	Check PVP certificate	10.84	61.71	24.58	76.11	20.96	24.10	243.61	220.49	114.56	95.83
LH220Ht	USA	Ames Panel	Check PVP certificate	5.98	56.60	23.18	71.61	19.00	24.46	213.79	202.27	87.12	83.94
LH38	USA	Ames Panel	Check PVP certificate	NA	65.04	NA	69.64	17.38	24.19	NA	227.21	NA	100.11
LH39	USA	Ames Panel	Check PVP certificate	6.99	54.78	16.94	62.94	19.81	25.18	236.68	230.40	115.85	108.19
LH51	USA	Ames Panel	Check PVP certificate	2.98	64.66	13.26	73.93	17.24	25.90	260.52	235.20	123.77	122.62
LH52	USA	Ames Panel	Check PVP certificate	2.56	56.92	9.10	70.89	18.10	24.19	232.26	226.25	95.06	110.89
LH54	USA	Ames Panel	Check PVP certificate	3.10	49.70	10.90	75.02	16.38	25.09	219.28	214.90	98.25	97.57
LH57	USA	Ames Panel	Check PVP certificate	3.17	58.93	10.82	75.36	17.14	25.27	244.41	225.45	106.16	97.89
LH59	USA	Ames Panel	Check PVP certificate	3.68	60.65	13.59	69.38	17.66	24.46	244.30	229.12	114.47	104.55
LH61	USA	Ames Panel	Check PVP certificate	2.53	59.40	10.60	77.87	17.81	25.45	226.85	224.97	89.37	99.00
LH65	USA	Ames Panel	Check PVP certificate	2.56	64.17	11.05	75.25	18.77	25.81	249.08	242.55	114.72	108.19
LH74	USA	Ames Pan	Check PVP certificate	6.97	56.16	32.74	70.42	19.91	22.38	210.75	190.28	94.70	83.94

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT
		el											
LH82	USA	Ames Panel	Check PVP certificate	8.39	53.95	26.02	69.38	22.58	25.99	239.26	220.33	110.20	104.70
LH85	USA	Ames Panel	Check PVP certificate	7.77	61.12	18.38	76.72	22.10	25.54	230.72	218.57	98.09	89.96
PHG29	USA	Ames Panel	Check PVP certificate	8.80	59.27	26.16	77.11	22.20	24.73	242.80	223.05	111.01	108.67
PHG35	USA	Ames Panel	Check PVP certificate	7.96	61.89	22.92	75.05	20.86	25.09	256.33	241.91	124.25	102.80
PHG39	USA	Ames Panel	Check PVP certificate	11.79	59.66	39.07	73.06	22.58	25.54	255.52	243.83	114.40	103.91
PHG47	USA	Ames Panel	Check PVP certificate	8.55	61.17	25.62	72.70	23.34	24.73	241.35	241.59	98.57	103.12
PHG50	USA	Ames Panel	Check PVP certificate	8.83	56.31	32.05	72.97	21.48	25.72	240.97	233.28	113.51	112.00
PHG71	USA	Ames Panel	Check PVP certificate	11.54	59.68	25.19	72.62	21.72	24.55	220.09	218.73	103.42	97.89
PHG72	USA	Ames Panel	Check PVP certificate	10.24	63.76	28.22	73.25	20.48	23.28	236.36	223.37	109.72	107.72
PHG83	USA	Ames Panel	Check PVP certificate	2.77	61.61	10.75	72.02	19.34	26.71	253.11	233.12	113.43	96.78
PHG86	USA	Ames Panel	Check PVP certificate	5.70	59.73	15.39	68.41	21.05	24.82	239.42	221.13	115.05	106.29
PHH93	USA	Ames Panel	Check PVP certificate	10.16	61.40	29.12	70.23	22.77	25.00	242.16	219.21	110.36	98.20
PHJ31	USA	Ames Panel	Check PVP certificate	21.74	64.20	43.57	74.87	22.58	26.08	289.19	280.44	121.67	105.18
PHJ33	USA	Ames Panel	Check PVP certificate	2.49	59.09	9.10	73.34	18.48	26.80	254.72	252.94	124.41	114.22
PHJ40	USA	Ames Panel	Check PVP certificate	20.14	56.78	41.25	71.19	21.83	24.01	237.44	225.13	124.66	96.94
PHJ70	USA	Ames Panel	Check PVP certificate	9.39	67.27	37.60	74.11	20.48	25.18	272.44	255.66	136.85	122.14
PHJ75	USA	Ames Panel	Check PVP certificate	9.06	58.96	24.75	73.04	21.72	25.36	242.16	236.64	104.23	102.64
PHK05	USA	Ames Panel	Check PVP certificate	11.01	52.00	28.09	71.58	22.96	25.63	244.89	228.80	108.42	105.66
PHK29	USA	Ames Panel	Check PVP certificate	2.89	56.69	8.04	67.55	16.48	26.80	235.71	237.44	115.21	112.00
PHK35	USA	Ames Panel	Check PVP certificate	10.87	63.40	44.11	72.36	20.48	24.73	252.79	236.32	119.08	112.16
PHK42	USA	Ames Panel	Check PVP certificate	12.08	62.88	28.36	71.26	21.25	24.91	245.05	214.74	112.46	97.73

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT
PHK76	USA	Ames Panel	Check PVP certificate	4.02	68.64	13.00	74.93	18.86	25.81	254.24	229.28	123.12	100.42
PHM49	USA	Ames Panel	Check PVP certificate	6.41	59.58	25.16	77.91	21.72	25.90	260.36	250.55	116.50	107.88
PHM57	USA	Ames Panel	Check PVP certificate	22.90	65.84	47.74	76.98	21.91	24.28	294.50	286.51	146.05	138.00
PHN11	USA	Ames Panel	Check PVP certificate	9.53	59.10	26.29	69.96	20.86	23.92	249.89	226.89	114.88	102.96
PHN29	USA	Ames Panel	Check PVP certificate	7.60	62.41	25.19	75.93	20.39	24.55	267.77	249.91	127.64	114.69
PHN37	USA	Ames Panel	Check PVP certificate	8.41	61.86	27.21	75.80	22.58	25.90	244.41	233.92	101.32	93.13
PHN73	USA	Ames Panel	Check PVP certificate	9.69	56.93	NA	62.67	NA	24.55	NA	247.35	NA	107.24
PHN82	USA	Ames Panel	Check PVP certificate	11.59	65.23	32.56	74.08	19.91	23.64	250.05	232.48	111.33	106.29
PHP02	USA	Ames Panel	Check PVP certificate	9.50	63.62	30.14	75.68	21.44	25.00	249.73	232.64	108.91	99.00
PHP55	USA	Ames Panel	Check PVP certificate	10.85	61.07	27.85	75.52	21.72	25.00	261.64	240.15	120.21	107.72
PHP60	USA	Ames Panel	Check PVP certificate	9.97	63.94	36.72	74.06	21.15	25.63	305.13	281.72	152.35	128.01
PHR25	USA	Ames Panel	Check PVP certificate	8.39	54.72	28.40	72.50	21.82	26.62	230.24	235.20	93.89	99.47
PHR32	USA	Ames Panel	Check PVP certificate	9.21	62.30	33.19	77.68	20.58	24.91	287.58	264.77	144.76	118.66
PHR36	USA	Ames Panel	Check PVP certificate	8.73	62.41	27.43	71.79	21.25	26.17	282.10	258.22	139.43	124.20
PHR47	USA	Ames Panel	Check PVP certificate	8.86	55.99	33.25	70.19	23.73	25.72	259.71	254.86	112.14	109.62
PHR62	USA	Ames Panel	Check PVP certificate	8.39	63.80	22.80	67.50	23.34	26.71	278.88	268.29	122.96	120.40
PHT10	USA	Ames Panel	Check PVP certificate	9.54	63.58	31.09	72.95	19.62	24.64	231.04	216.02	106.16	97.89
PHT22	USA	Ames Panel	Check PVP certificate	9.01	58.87	35.29	77.02	21.91	25.90	258.10	236.96	118.92	105.18
PHT55	USA	Ames Panel	Check PVP certificate	9.71	66.95	37.16	75.85	22.39	25.27	283.23	269.25	133.13	122.30
PHT60	USA	Ames Panel	Check PVP certificate	7.82	57.74	23.09	70.04	20.96	26.53	269.22	254.06	128.93	118.81
PHT77	USA	Ames Panel	Check PVP certificate	15.64	59.59	42.53	72.39	21.44	25.18	267.12	238.40	124.41	116.44
PHV37	USA	Ames Pan	Check PVP certificate	2.34	56.88	8.61	68.31	15.33	26.98	224.28	230.40	94.54	93.29

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT
		el											
PHV63	USA	Ames Panel	Check PVP certificate	2.46	58.98	8.35	72.33	16.38	26.08	214.61	227.05	105.52	101.38
PHV78	USA	Ames Panel	Check PVP certificate	10.15	59.66	30.85	74.08	22.49	26.17	282.91	264.45	145.57	125.47
PHW03	USA	Ames Panel	Check PVP certificate	10.50	56.41	41.70	71.84	21.82	25.09	271.95	236.80	122.64	95.51
PHW17	USA	Ames Panel	Check PVP certificate	8.29	64.98	31.87	68.71	22.77	25.45	255.20	243.51	124.09	107.88
PHW20	USA	Ames Panel	Check PVP certificate	10.81	62.60	19.40	71.14	20.67	24.28	269.05	246.87	124.73	117.23
PHW43	USA	Ames Panel	Check PVP certificate	6.19	52.32	18.80	69.27	21.82	26.08	247.95	230.88	107.94	86.95
PHW52	USA	Ames Panel	Check PVP certificate	11.59	61.06	35.32	70.70	20.01	23.64	243.93	223.05	106.16	92.66
PHW65	USA	Ames Panel	Check PVP certificate	11.37	58.45	32.06	77.79	21.63	26.26	271.15	263.97	119.57	116.75
PHW79	USA	Ames Panel	Check PVP certificate	9.75	61.33	34.47	73.38	20.29	24.28	279.52	264.13	135.39	114.37
PHZ51	USA	Ames Panel	Check PVP certificate	9.08	58.98	31.88	75.11	21.53	24.91	266.64	258.06	113.75	106.13
33-16	Indiana	302 Panel	Lux Johnson Country white	9.77	61.98	31.92	74.69	22.58	26.62	268.89	262.70	132.65	123.25
38-11	Indiana	302 Panel	Outcross in line from 176A	9.11	56.79	21.05	69.26	21.72	27.25	296.92	294.03	161.55	137.20
81-1	USDA	302 Panel	Iowa 60*Edisto	8.35	56.71	24.61	70.84	20.96	24.64	294.99	278.20	154.61	138.95
A188	Minnesota	302 Panel	[(4-29*64)4-29(4)]	6.30	61.37	20.40	79.69	22.87	26.35	231.85	223.85	88.89	92.18
A214N	South Africa	302 Panel	(B68*HtN)B68(3)	10.37	64.40	30.15	71.92	21.53	23.92	256.17	238.72	126.83	117.23
A239	Minnesota	302 Panel	A73*A347	8.70	57.08	19.54	67.52	21.63	24.91	273.40	261.26	134.59	122.94
A441-5	South Africa	302 Panel	Robyn*Leamming yellow dent	8.72	58.32	23.86	66.67	22.96	27.88	292.09	275.80	159.94	139.26
A554	Minnesota	302 Panel	[(WD*Wf9)WD(2))]	7.06	53.57	20.96	72.85	20.77	25.27	238.77	226.25	100.84	97.73
A619	Minnesota	302 Panel	[(A171*Oh43)Oh43]	6.28	53.91	17.91	65.60	20.67	25.81	250.53	221.93	103.90	91.86
A632	Minnesota	302 Panel	[(Mt42*B14)B14(3)]	11.52	60.64	29.32	72.47	20.48	23.28	251.82	236.32	113.43	107.72
A634	Minnesota	302 Panel	[(Mt42*B14)B14(2)]	9.93	57.20	26.91	73.72	22.58	24.55	236.03	215.70	108.75	97.73
A635	Minnesota	302 Panel	ND203xB14(3)	10.07	53.68	33.52	76.54	20.10	23.64	208.97	194.91	86.14	77.12
A641	Minnesota	302 Panel	ND203*B14	8.20	57.75	22.08	75.71	20.77	24.37	202.69	195.39	98.25	83.30
A654	Minnesota	302 Panel	A116*Wf9	6.93	54.13	16.01	66.82	21.82	25.18	213.16	207.22	93.25	95.19
A659	Minnesota	302 Panel	Minnesota Synthetic 3	8.13	61.39	34.13	69.12	21.25	25.90	265.35	244.47	117.63	105.34

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT
A661	Minnesota	302 Panel	Minnesota Synthetic AS-A	6.47	51.08	21.78	70.80	21.82	25.63	257.62	239.36	124.41	112.95
A679	Minnesota	302 Panel	[(A662*B73) B73(3)]	8.82	55.61	28.38	70.01	20.77	23.37	246.34	220.81	126.67	106.29
A680	Minnesota	302 Panel	[(A662*B73) B73(3)]	6.07	59.44	27.73	69.20	20.29	24.01	245.54	218.09	132.16	102.17
A682	Minnesota	302 Panel	[(AS-D*Mo17) Mo17 (2)]	2.26	59.04	10.21	68.78	17.43	25.27	257.62	246.07	114.72	118.81
Ab28A	Alabama	302 Panel	GT152*38-11	17.19	62.70	51.23	77.43	23.92	27.52	307.23	298.50	155.42	139.90
B10	Iowa	302 Panel	Iowa Stiff Stalk Synthetic	8.49	55.86	32.63	72.58	21.44	25.00	252.62	236.32	122.64	101.69
B103	Iowa	302 Panel	CIMMYT Pool 41 [Northern Temperate Ranges -1 (NTR-1)]	8.78	57.27	25.35	70.16	21.91	25.63	254.72	249.27	116.82	112.31
B104	Iowa	302 Panel	BS13(S)C5	7.31	60.10	37.17	68.92	22.68	27.52	231.69	222.09	119.73	102.49
B105	Iowa	302 Panel	BSSS®C9	5.94	60.84	22.51	73.65	21.53	26.26	259.55	230.88	116.34	96.14
B109	Iowa	302 Panel	[B73 * BS20(S)C1]B73	9.53	62.81	29.01	70.99	21.34	22.92	240.38	227.21	123.12	103.44
B14A	Iowa	302 Panel	Cuzco*B14(8)	16.62	60.95	42.63	71.32	23.25	25.09	285.32	262.54	149.60	127.37
B164	Minnesota	302 Panel	Indiana Reid (Pioneer)	4.99	56.08	15.52	72.85	21.72	26.17	256.65	239.36	127.16	113.90
B2	Missouri	302 Panel	Reid Yellow Dent	3.39	61.22	15.20	75.90	21.63	26.35	278.72	255.34	132.81	115.96
B37	Iowa	302 Panel	Iowa Stiff Stalk Synthetic	7.75	68.69	31.11	76.37	23.25	25.36	256.01	253.58	118.60	110.25
B46	Iowa	302 Panel	W22*B10	3.99	61.09	16.66	71.68	21.72	26.08	261.48	240.47	121.34	101.06
B57	Iowa	302 Panel	Midland	9.85	53.59	30.06	69.66	22.49	25.54	253.22	239.20	116.36	102.33
B64	Iowa	302 Panel	41.2 504B*B14(3)	5.02	61.87	15.63	71.07	20.10	26.98	246.18	229.92	118.11	113.58
B68	Iowa	302 Panel	41.2 504B*B14(3)	8.66	59.76	26.42	74.93	19.34	23.82	255.69	230.72	116.34	108.67
B73	Iowa	302 Panel	Iowa Stiff Stalk Synthetic C5	6.84	57.43	27.67	67.19	19.55	22.55	234.69	214.95	120.29	100.62
B73 Htrhm	Iowa	302 Panel	Ht1 and rhm1 conversion of B73	7.77	63.03	30.75	68.45	19.43	23.73	242.80	216.34	120.21	91.23
B76	Iowa	302 Panel	[(Cl.31A*B37)B37]	7.35	57.09	24.07	72.53	22.68	26.17	238.45	226.25	109.56	99.79
B77	Iowa	302 Panel	Pioneer Two-Ear composite(BS11)	8.40	59.36	23.29	71.02	23.25	26.26	289.03	268.93	142.17	123.09
B79	Iowa	302 Panel	Iowa Two-Ear Synthetic No.1(BSTE)	7.94	54.85	21.75	67.24	21.15	24.37	253.75	211.06	140.56	109.46
B84	Iowa	302 Panel	BS13(S2)C0	10.22	62.57	40.73	74.93	22.01	24.28	263.26	233.60	144.92	112.79
B97	Iowa	302 Panel	BSCB1®C9	9.83	59.83	31.34	75.17	22.87	26.08	277.91	265.41	134.10	124.20
C103	Connecticut	302 Panel	Lancaster Surecrop (from Noah Hershey)	2.45	66.54	12.69	70.16	18.19	26.89	260.20	267.33	107.29	120.08
C49A	Minnesota	302 Panel	Minn 13	10.26	59.91	34.57	68.52	22.39	25.54	234.42	224.81	103.58	97.57
CH70 1-30	Canada - Harrow	302 Panel	unknown	3.74	63.79	12.19	75.33	18.19	26.35	255.36	238.40	132.16	115.01
CH9	Canada - Harrow	302 Panel	Funk's G176	7.22	63.08	19.47	78.91	23.25	26.89	247.15	226.57	95.67	87.58

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT
CI187-2	USDA	302 Panel	Krug	13.71	63.56	44.70	75.76	23.63	26.44	250.21	226.73	128.13	115.80
CI21E	USDA	302 Panel	Hy*C.I.21	16.08	60.84	36.02	69.99	24.01	25.99	284.36	264.29	143.95	126.90
CI28A	USDA	302 Panel	Recovered Blight Resistance B2	4.11	58.17	16.30	75.88	19.15	27.34	266.32	254.54	155.58	129.75
CI31A	USDA	302 Panel	Midland OP	7.91	60.45	24.96	64.94	22.49	26.80	288.54	273.73	147.83	136.25
CI3A	USDA	302 Panel	[(C.I.3*related inbred) C.I.3 (2)]	7.67	49.55	25.01	70.63	22.49	25.99	301.11	284.28	147.50	133.40
CI44	USDA	302 Panel	L97*Oh07(2)	5.27	56.54	21.40	70.45	20.58	25.90	288.22	261.58	162.84	132.13
CI64	USDA	302 Panel	K64*Mo21A	5.48	54.98	19.94	69.49	22.20	26.98	289.99	259.50	154.93	132.13
CI66	USDA	302 Panel	L97*K55 (2)	7.29	59.06	19.74	73.93	19.62	25.00	274.05	261.42	146.37	127.22
CI7	USDA	302 Panel	[(L317*33-16)33-16(2)]	6.56	58.49	18.74	70.70	21.63	25.72	295.15	296.75	148.96	162.09
CI90C	USDA	302 Panel	CI90A = L97* M14	7.88	62.79	24.17	76.14	21.53	26.71	271.47	246.23	140.72	113.90
CI91B	USDA	302 Panel	L97*A71	13.98	58.21	40.98	77.83	25.25	28.16	272.76	250.07	145.73	128.48
CM105	Canada-Morden	302 Panel	CMV3xB14(2)	2.56	63.47	5.87	72.23	19.24	27.34	260.03	288.75	163.81	163.20
CM174	Canada-Morden	302 Panel	CMV3xB14(2)	6.95	57.27	18.45	73.59	20.29	24.37	210.91	203.07	85.49	87.90
CM37	Canada-Morden	302 Panel	KE3	9.31	59.22	22.51	80.90	23.53	27.79	228.30	205.15	89.21	78.23
CM7	Canada-Morden	302 Panel	W85*CMV3	8.75	66.55	21.20	79.58	24.20	27.52	235.23	220.97	94.54	84.10
CML10	Mexico	302 Panel	Pop.21 = Tuxpeño	11.89	62.06	38.38	64.26	23.34	25.90	313.19	302.98	175.76	165.74
CML103	Mexico	302 Panel	Pop. 44	6.43	57.10	18.01	74.36	19.34	24.91	293.86	286.51	182.22	163.04
CML108	Mexico	302 Panel	Pop. 44	3.00	55.48	10.96	61.44	18.57	25.27	261.64	274.20	137.01	123.25
CML154Q	Mexico	302 Panel	Pop. 62	20.31	65.55	47.79	75.77	24.11	24.91	296.11	293.87	155.09	149.57
CML157Q	Mexico	302 Panel	Pop. 62	4.63	61.28	13.10	72.21	20.96	25.45	309.48	297.38	178.19	163.84
CML158Q	Mexico	302 Panel	Pop. 62	4.47	66.27	18.79	75.18	19.53	27.34	292.25	295.79	176.09	158.76
CML218	Mexico	302 Panel	EV = Streak resist. source	16.62	59.32	44.61	75.69	22.58	25.36	302.07	282.20	155.58	127.69
CML228	Mexico	302 Panel	Suwan-1/SR	6.65	62.14	28.45	70.61	22.58	26.17	299.17	289.55	168.17	151.47
CML247	Mexico	302 Panel	Pool 24 (Tuxpeño)	3.37	66.25	14.70	76.57	20.77	27.61	286.93	277.88	156.87	134.98
CML254	Mexico	302 Panel	Pop. 21 = Tuxpeño Sequia	4.41	59.30	14.61	73.09	20.96	25.72	299.50	308.10	186.74	177.63
CML277	Mexico	302 Panel	Pop. 43 = La Posta (Tux.)	6.02	63.36	16.30	69.61	20.01	26.26	309.64	306.66	194.82	160.98
CML311	Mexico	302 Panel	Pop. 500 = Inter. Mat. Wh. Dent Mix	8.25	61.10	32.21	79.29	21.39	26.44	318.34	305.86	177.22	158.92
CML314	Mexico	302 Panel	Pop. 600 = Late Mat. Wh. Dent Mix	16.98	60.27	34.86	73.43	22.10	24.64	277.75	269.73	157.68	153.85
CML321	Mexico	302 Panel	Pop. 502 = Mex. DK + US	4.36	59.25	11.21	70.57	18.48	25.36	279.52	306.82	165.91	154.32

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT
CML322	Mexico	302 Panel	Recyc. US + Mex	4.83	61.10	21.38	72.34	20.10	24.28	285.32	278.68	152.51	145.61
CML323	Mexico	302 Panel	Pop. 33 Amar. Subtrop. Mix	7.48	57.09	24.61	71.55	22.10	25.18	289.35	266.53	152.19	139.42
CML331	Mexico	302 Panel	Suwan/Pop.47 * Mp78:518	8.07	58.16	21.71	69.91	22.39	26.44	304.49	302.34	171.40	157.34
CML332	Mexico	302 Panel	Suwan/Pop.47 * Mp78:518	8.76	62.01	19.03	66.04	22.10	25.18	281.46	265.73	161.55	140.22
CML333	Mexico	302 Panel	Pop. 590	2.84	57.37	12.82	71.12	18.10	25.99	272.44	289.07	177.38	162.57
CML341	Mexico	302 Panel	Pop. 43 = La Posta (Tux.)	3.19	60.23	9.37	75.88	16.29	27.25	258.75	320.72	168.34	177.79
CML38	Mexico	302 Panel	Pop. 32	17.38	61.54	45.41	70.83	22.29	25.63	281.30	273.09	170.43	153.22
CML45	Mexico	302 Panel	Pop. 43 = La Posta (Tux.)	2.91	56.35	9.89	79.84	16.76	27.16	265.67	301.86	160.42	153.69
CML52	Mexico	302 Panel	Pop. 79 = STA ROSA	7.28	61.78	19.12	69.73	22.01	25.36	323.98	329.20	196.11	183.49
CML69	Mexico	302 Panel	Pop. 36 = Cogollero (Caribbean)	9.85	66.51	27.43	70.75	22.49	25.99	315.12	301.70	175.76	155.59
CML91	Mexico	302 Panel	Pop. 42 Northern Temp./German Mix	13.54	61.61	36.41	72.14	22.96	25.99	292.25	266.85	146.37	132.29
CML92	Mexico	302 Panel	Pop. 42 Northern Temp./German Mix	10.45	60.28	31.62	71.72	24.68	26.80	309.16	300.10	162.84	142.12
CMV3	Minnesota	302 Panel	A21*W185	6.42	55.23	20.90	68.41	21.15	25.45	215.74	209.46	90.98	92.50
Co106	Canada-Ottawa	302 Panel	University of Wisconsin CR11	7.90	51.81	22.44	74.51	22.39	25.99	225.57	216.50	111.82	103.12
Co125	Canada-Ontario	302 Panel	unknown	5.44	57.04	14.53	74.53	19.05	26.62	252.95	227.05	102.45	93.45
Co255	Canada-Ottawa	302 Panel	INRA 258	12.23	60.58	37.28	80.68	21.25	25.00	242.96	234.40	111.01	99.95
D940Y	South Africa	302 Panel	BO60W(A166NxB566Y-B560Y)B557Y	12.91	61.40	28.54	68.22	23.25	26.71	313.19	276.44	156.06	128.33
DE1	Delaware B	302 Panel	P3140*P3751	6.84	56.48	22.49	70.30	22.20	25.45	267.77	256.14	125.22	117.86
DE2	Delaware B	302 Panel	P3140*P3751	7.30	56.78	23.87	68.88	20.96	26.35	276.14	252.14	127.16	109.30
DE811	Delaware	302 Panel	[B68*[B37Ht*(C103*Mp3204 double cross) Selection]]	2.42	66.41	9.14	72.05	18.38	25.81	256.81	238.40	130.39	103.12
E2558W	South Africa	302 Panel	N6*M162W^3	11.82	53.53	34.47	71.70	25.16	26.44	291.60	272.45	138.46	121.98
EP1	Spain	302 Panel	Spanish population 'Lizargarate'	10.60	53.66	49.75	82.44	20.77	23.82	213.97	217.93	97.61	96.94
F2	Puy-de-Dome, France	302 Panel	OP Lacaune	18.41	59.08	50.25	69.57	21.10	24.19	231.52	229.92	104.39	97.10
F2834T	South Africa	302 Panel	Teko Yellow	5.35	60.56	21.35	72.68	19.62	24.91	297.89	284.76	160.75	142.12
F44	Florida	302 Panel	Smith (Old Florida variety)	9.07	59.76	32.62	69.99	20.96	25.09	292.09	279.48	162.84	140.22
F7	France-Peronne	302 Panel	OP Lacaune	8.48	56.66	26.52	77.82	20.20	23.37	221.86	214.10	103.26	96.94
GA209	Georgia	302 Panel	T61*NC37	5.80	61.35	13.78	72.56	22.10	26.71	292.09	278.36	148.15	125.31
GT112	Georgia	302 Panel	Multiple cross (includes Whatley, Cuban, Garrick, Creole, and 12% other)	11.22	59.51	32.41	67.22	21.63	24.64	333.00	329.68	172.70	164.63
H100	Indiana	302 Panel	N28*H91	9.92	61.42	28.77	78.21	20.48	23.92	250.37	231.04	105.84	98.68

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT
H105W	Indiana	302 Panel	33-16*A632(3)	8.77	62.39	21.87	73.13	21.82	24.73	241.19	223.53	119.57	106.45
H84	Indiana	302 Panel	[B37*GE440)Ht Ht	14.29	63.78	41.42	75.77	22.68	25.36	244.41	231.84	103.26	97.57
H91	Indiana	302 Panel	[B37*GE440)B14(4)] Ht Ht	9.80	53.67	24.65	74.45	20.77	24.37	246.50	216.18	115.53	97.89
H95	Indiana	302 Panel	Oh43*C.I.90A	8.09	62.32	22.83	67.40	20.39	24.91	258.10	251.19	126.03	113.58
H99	Indiana	302 Panel	Illinois Synthetic 60C	8.25	60.75	32.16	71.45	21.53	24.82	247.79	230.88	121.51	103.28
Hi27	Hawaii	302 Panel	[CM104(India)*MV source]BC6	9.73	63.64	25.36	69.52	21.53	24.01	285.97	265.25	163.01	134.03
Hp301	Indiana	302 Panel	Supergold	6.64	52.11	18.87	70.13	18.67	23.19	281.78	260.14	153.96	133.87
I205	Iowa	302 Panel	Iodent	10.94	60.77	50.89	75.36	22.01	25.09	249.73	234.24	113.75	102.96
IA2132	Iowa	302 Panel	[(TSR * 45) * 4329]	8.58	53.74	36.81	66.72	22.49	25.54	228.95	221.93	97.28	97.25
IA5125	Iowa	302 Panel	[(IP39*Tendermost)*IP39]	5.19	53.59	16.42	72.79	19.81	26.89	273.56	246.23	113.11	112.16
IDS28	Iowa	302 Panel	Yellow Pearl	10.08	60.93	30.26	68.59	19.72	21.93	288.87	256.46	162.84	148.78
IDS69	Iowa	302 Panel	South American Popcorn	7.13	58.35	22.91	72.43	20.39	23.92	263.58	242.87	146.37	128.17
IL677A	Illinois	302 Panel	[(Bolivia 1035*IL44b)*IL422a]	5.33	54.95	23.98	74.06	23.15	27.88	265.99	242.07	118.92	103.28
Ill.Hy	Illinois	302 Panel	Illinois High Yield	2.84	53.59	9.17	66.28	17.62	25.54	265.35	268.93	131.52	131.34
K148	Kansas	302 Panel	Yellow selection No. 1 (Pride of Saline, yellow strain)	11.22	57.56	37.51	73.47	22.39	25.45	295.47	282.84	140.72	124.05
K4	Kansas	302 Panel	Kansas Sunflower	8.04	54.30	25.19	71.01	22.68	26.08	302.88	284.44	159.62	152.42
K55	Kansas	302 Panel	Pride of Saline	6.59	54.84	22.32	72.91	19.91	26.71	264.54	239.20	137.65	116.44
K64	Kansas	302 Panel	Pride of Saline	5.40	55.14	21.34	70.63	22.10	26.17	292.89	270.37	156.87	135.46
Ki11	Thailand	302 Panel	Suwan 1(S)C4-S8-18-7	7.91	68.56	20.46	76.33	24.39	28.61	281.13	259.82	158.48	132.76
Ki14	Thailand	302 Panel	Suwan 1(S)C4-S8-19-5	6.76	58.54	23.45	70.13	22.68	26.35	287.58	277.56	162.20	146.08
Ki21	Thailand	302 Panel	Pacific 9-S8-45	9.20	57.53	28.99	70.90	22.96	27.88	294.34	282.20	187.55	163.52
Ki3	Thailand	302 Panel	Suwan 1(S)C4-S8-5-3	4.25	59.69	20.18	70.94	18.10	25.27	276.46	263.65	154.29	128.80
Ki43	Thailand	302 Panel	Suwan 3(S)C3-S7-138	9.56	64.98	26.71	75.48	21.72	25.54	295.63	263.81	163.33	130.86
KUI2007	Thailand	302 Panel	DK version of Ki3; Suwan 1(S)C4-S8-5-3	10.46	58.67	39.38	74.66	24.20	27.07	336.54	310.49	199.18	171.60
KUI2021	Thailand	302 Panel	DK version of Ki9; Suwan 1(S)C4-S8-16-7	14.00	59.28	44.86	72.12	25.06	27.07	331.71	319.92	195.46	167.48
KUI44	Thailand	302 Panel	KS 6(S)C2-S7-366	14.62	61.64	44.33	73.98	24.39	25.00	286.77	282.68	167.37	148.14
Ky21	Kentucky	302 Panel	Boone County White	13.49	60.72	38.98	71.43	25.06	26.98	297.56	284.60	159.62	147.83
Ky226	Kentucky	302 Panel	NCLauDA*Coahuila 8	11.52	64.84	39.18	71.08	21.91	25.00	295.95	282.04	165.91	151.95
Ky228	Kentucky	302 Panel	Pride of Saline	12.30	65.59	34.62	76.97	23.15	25.36	279.85	266.21	137.01	125.47

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT
L317	Iowa	302 Panel	Lancaster surecrop (from Noah Hershey)	20.82	64.05	44.90	75.80	22.68	24.19	305.78	291.63	157.68	147.83
L578	Louisiana	302 Panel	Unknown	8.05	56.89	27.87	69.63	21.53	24.64	319.95	292.11	175.92	147.19
M162W	South Africa	302 Panel	K64R**2 x B1138T	6.47	56.04	18.32	68.50	22.39	27.07	295.31	283.32	174.96	146.08
M37W	South Africa	302 Panel	21A**2 x Jellicorse	8.32	59.58	17.06	71.41	23.82	28.34	298.05	288.75	158.65	141.96
Mo.G	Missouri	302 Panel	Mastadon variety from Pennsylvania	15.29	63.13	39.54	69.25	25.16	25.99	292.57	272.61	163.65	153.37
Mo17	Missouri	302 Panel	C.I.187-2*C103	2.30	57.94	9.82	76.23	17.73	27.38	250.63	239.12	110.86	109.59
Mo18W	Missouri	302 Panel	Wf9*Mo22(2)	9.07	64.81	24.47	74.11	23.06	25.90	289.03	276.92	157.35	135.78
Mo1W	Missouri	302 Panel	[Mo22*Wf9(2)]	8.03	61.75	22.68	76.45	21.25	25.09	267.43	248.47	116.28	107.56
Mo24W	Missouri	302 Panel	(K10*K49/Ziler Hi-cob) (pipe corn)	6.52	51.29	17.10	66.78	21.72	27.61	291.77	294.03	150.57	139.74
Mo44	Missouri	302 Panel	Mo22*Pioneer Mexican Synthetic 17	3.25	63.21	11.41	71.11	17.62	25.90	284.19	277.40	147.67	134.67
Mo45	Missouri	302 Panel	Race Negro de Tierra Caliente (Guatemala)	12.95	65.70	44.41	77.98	22.01	23.73	277.11	269.25	150.41	138.31
Mo46	Missouri	302 Panel	Race Cravo Paulista (Brazil)	3.03	63.52	8.55	76.08	16.86	26.62	233.14	260.94	108.26	111.20
Mo47	Missouri	302 Panel	Race Candela (Ecuador)	12.78	64.09	32.07	76.83	23.06	26.08	228.79	209.78	90.34	82.99
Mp339	Mississippi	302 Panel	T61*Hill Yellow Dent	12.69	59.85	30.14	80.20	22.96	25.81	302.07	288.11	154.45	140.06
MS1334	Michigan	302 Panel	[(Golden glow * Maize Amargo)*Golden Glow]	6.37	60.06	14.04	77.16	20.10	24.01	246.02	234.72	106.00	93.77
MS153	Michigan	302 Panel	Iowa stiff stalk synthetic	12.36	56.63	37.49	72.57	21.91	24.37	244.73	228.33	123.44	116.44
MS71	Michigan	302 Panel	A619*R168	6.97	60.19	13.47	71.53	20.96	25.54	250.21	230.40	113.92	104.55
Mt42	Minnesota	302 Panel	Minnesota No.13 (Owen's)	10.40	56.32	29.75	77.29	23.06	25.09	225.24	216.66	101.64	97.41
N192	Nebraska	302 Panel	CM105*B73	7.84	56.42	33.15	71.46	21.72	25.18	219.28	197.15	102.61	81.56
N28Ht	Nebraska	302 Panel	N28= BSSS	8.91	60.50	31.74	77.25	22.01	25.54	256.01	238.88	126.67	108.03
N6	Nebraska	302 Panel	Hays Golden	6.97	61.95	23.57	68.05	23.34	27.07	272.44	238.24	123.12	107.08
N7A	Nebraska	302 Panel	Oh07*Stiff stalk Synthetic	8.29	58.32	27.93	70.41	20.77	25.18	246.99	220.65	124.73	94.72
NC222	North Carolina	302 Panel	Jarvis Golden Prolific	13.75	60.77	34.26	71.34	22.77	24.55	306.91	285.08	156.55	139.11
NC230	North Carolina	302 Panel	K55*Yellow line or inbred	7.27	54.70	21.31	74.31	21.25	25.00	266.96	248.31	140.56	119.13
NC232	North Carolina	302 Panel	[(T204*Low Ear outcross) T204 (2)]	6.19	59.98	20.89	68.03	21.05	26.71	283.39	270.69	148.96	125.16
NC250	North Carolina	302 Panel	[(Nigeria Composite ARb*B37)B37)	7.90	68.20	25.18	72.88	22.39	26.62	254.72	243.67	125.06	112.79
NC258	North Carolina	302 Panel	TZ(2)*[(NC248*246)*C103]	16.51	61.20	47.65	73.03	21.72	24.10	291.77	276.12	142.50	127.53
NC260	North Carolina	302 Panel	[(Mo44*Mo17)Mo44(3)]	4.78	57.49	12.88	74.29	19.43	25.36	284.68	268.93	139.91	118.81
NC262	North Carolina	302 Panel	TZ (TZ=McNair 14*18)	11.92	60.53	39.19	74.36	22.77	26.62	271.31	232.80	128.13	96.46

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT
NC264	North Carolina	302 Panel	[(SC76*Gaspe)Gaspe]SC76(3)	10.71	61.33	29.13	70.65	21.34	24.64	276.14	246.55	138.30	122.94
NC268	North Carolina	302 Panel	(B73*NC250) B73	5.96	53.70	18.16	70.88	19.24	24.64	248.44	237.76	125.38	105.02
NC290A	North Carolina	302 Panel	McNair inbred lines 14*18 (largely of C103 origin); sister line of NC290	7.56	65.40	27.40	68.90	22.10	25.45	288.70	268.13	142.66	121.83
NC292	North Carolina	302 Panel	[(B73*NC250) B73 (3)]	8.02	63.51	27.12	68.87	20.10	23.28	227.66	202.43	112.95	94.08
NC294	North Carolina	302 Panel	[(B73*NC250) B73]	6.72	60.97	23.46	72.05	22.87	25.99	250.69	252.62	121.51	119.77
NC298	North Carolina	302 Panel	PioneerX105A * H-5 * Agroceres155	4.77	69.17	19.84	75.13	21.34	25.18	282.75	268.45	156.87	135.46
NC304	North Carolina	302 Panel	(H5*PioneerX105A)*H101	4.32	67.07	16.72	73.12	19.34	26.89	275.34	280.28	144.44	127.06
NC306	North Carolina	302 Panel	(B73*NC250)*B73	6.53	63.65	21.67	73.78	21.15	24.37	249.73	240.63	122.15	114.06
NC308	North Carolina	302 Panel	(B73*NC250)*B73	8.88	64.38	27.60	68.33	21.25	25.00	246.02	226.09	114.56	95.99
NC310	North Carolina	302 Panel	improved B73-type derived from NC250*B73^3	7.39	61.34	24.38	69.16	20.10	22.83	238.29	223.37	121.18	106.77
NC312	North Carolina	302 Panel	(B73*NC250)*B73	9.15	67.22	20.87	72.25	18.96	24.01	247.63	239.04	121.02	111.20
NC314	North Carolina	302 Panel	B73*NC250	4.91	61.96	19.30	71.31	20.01	25.81	248.11	224.49	116.82	95.35
NC316	North Carolina	302 Panel	(B73Ht1rhm1*NC250)B73Ht1rhm1^3	7.14	62.63	25.95	69.65	20.96	23.92	252.79	235.84	128.77	111.36
NC318	North Carolina	302 Panel	[(SC76*B52)SC76(3)]	11.22	63.30	33.46	77.57	21.05	24.55	280.81	261.58	150.57	132.13
NC320	North Carolina	302 Panel	[(SC76*B52)SC76(3)]	10.25	64.47	28.38	74.84	20.86	24.64	295.79	277.56	159.62	134.67
NC322	North Carolina	302 Panel	[(SC76*B52)SC76(3)]; sister line to NC318	10.38	65.82	39.53	73.39	21.72	23.92	281.94	271.97	146.37	138.79
NC324	North Carolina	302 Panel	B73*NC250	3.43	50.52	13.55	63.88	21.05	24.46	239.74	235.04	101.16	103.75
NC326	North Carolina	302 Panel	[(B73*NC250)*B73(3)]	7.92	59.72	31.30	73.83	19.81	23.01	226.21	205.47	117.31	92.50
NC328	North Carolina	302 Panel	[(B73*NC250)*B73(3)]	10.04	62.25	33.84	73.60	20.48	24.19	235.07	213.30	120.37	94.56
NC33	North Carolina	302 Panel	Weekley's Improved	7.90	62.66	23.84	73.19	22.20	26.17	317.70	317.37	177.22	160.19
NC330	North Carolina	302 Panel	[(B73*NC250)*B73(4)]	8.51	57.41	28.62	65.65	20.86	23.28	228.46	211.06	116.98	104.55
NC332	North Carolina	302 Panel	(SC76*B52); sister line of NC334	11.57	61.60	32.63	71.41	21.72	25.18	285.00	263.01	150.41	136.41
NC334	North Carolina	302 Panel	(SC76*B52); sister line of NC332	10.45	62.67	31.32	77.66	21.82	24.64	273.73	252.30	136.04	126.42
NC338	North Carolina	302 Panel	[PioneerX105A*H5] * [Pioneer304B*Agroceres504]	4.86	58.84	22.05	73.27	20.20	26.17	307.71	286.03	185.78	141.48
NC342	North Carolina	302 Panel	McNair inbreds 14*18(of Coker 811Ax C103 origin)	19.84	60.80	39.86	74.63	22.77	26.35	279.52	263.33	145.73	127.53
NC344	North Carolina	302 Panel	TZ(2)*[(NC248*246)*C103]; Sister line of NC258	11.66	58.79	38.01	69.82	21.44	25.36	291.44	274.20	137.49	124.20
NC348	North Carolina	302 Panel	PioneerX105A * H-5 * Agroceres155	4.17	70.55	18.40	75.26	18.19	25.99	283.39	276.12	160.75	146.87
NC350	North Carolina	302 Panel	(H5*PioneerX105A)*H101	12.52	64.79	35.80	75.01	24.20	26.89	302.40	282.84	157.84	139.11
NC356	North Carolina	302 Panel	TROPHY SYN	6.38	56.74	22.63	70.27	20.58	25.45	278.88	249.43	153.16	119.45

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT
NC358	North Carolina	302 Panel	TROPHY SYN	12.42	56.07	36.50	71.03	22.96	24.73	283.55	274.68	135.72	127.69
NC360	North Carolina	302 Panel	Agroceres155*PioneerX105A/NC262	10.04	60.59	26.07	70.06	24.01	26.44	286.93	268.61	129.42	114.37
NC362	North Carolina	302 Panel	Agroceres155*PioneerX105A/NC262	11.25	57.20	33.78	72.53	22.96	25.54	308.52	286.99	163.81	136.09
NC364	North Carolina	302 Panel	Agroceres155*PioneerX105A/NC262	6.85	56.88	22.23	69.40	21.44	26.35	282.10	255.02	139.91	113.11
NC366	North Carolina	302 Panel	FLA Syn	14.47	64.51	46.23	75.73	22.39	25.45	296.92	284.12	152.83	130.55
NC368	North Carolina	302 Panel	[B73*NC250]/[(B73*NC250)*B73]	7.25	62.83	24.75	66.27	20.29	25.54	256.49	223.53	121.83	98.36
NC370	North Carolina	302 Panel	[(SC76*B52)SC76(3)]	7.88	61.06	30.66	72.96	21.15	24.37	294.66	280.60	164.46	141.48
NC372	North Carolina	302 Panel	[(B73*Pa91)*B73]	8.05	57.36	30.82	68.52	21.25	23.28	238.61	217.77	119.24	104.55
ND246	North Dakota	302 Panel	W755*W771	7.89	65.04	19.88	80.30	21.34	23.82	221.22	223.69	95.51	100.58
Oh40B	Ohio	302 Panel	Eight line composite of Lancaster Surecrop lines	6.77	60.81	17.38	72.40	19.24	24.91	251.66	239.84	111.17	105.34
Oh43	Ohio	302 Panel	Oh40B*W8	8.67	59.08	24.46	63.18	22.49	26.08	271.95	243.67	130.23	105.18
Oh43E	Ohio	302 Panel	ERF/Oh43; ERF=LeamingxReid + other Pioneer inbreds	7.04	61.59	27.88	70.23	20.86	24.55	236.52	217.93	97.44	89.49
Oh603	Ohio	302 Panel	« Syn of Va58, OhS3267, H95, Va26, Coas. Trop. FL. »	9.13	54.92	23.71	66.62	22.87	26.22	280.65	257.90	133.94	116.28
Oh7b	Ohio	302 Panel	[(Oh07*38-11)Oh07]	6.63	56.58	24.73	71.07	22.39	25.99	274.53	264.93	132.97	126.90
Os420	Iowa	302 Panel	Osterland yellow dent	7.19	54.31	21.03	71.76	23.25	26.89	274.05	266.21	124.90	121.19
P39	Indiana	302 Panel	Purdue Bantam	6.65	49.16	17.38	67.47	19.43	24.64	235.55	237.28	102.13	97.10
Pa762	Pennsylvania	302 Panel	Oh43*Pa70L	10.38	59.10	23.58	62.68	22.10	26.53	257.13	247.67	117.79	115.96
Pa875	Pennsylvania	302 Panel	Wf9 Synthetic (original)	9.40	63.00	27.52	66.24	21.82	24.64	296.92	277.88	153.32	135.30
Pa880	Pennsylvania	302 Panel	Wf9 Synthetic C3	7.94	59.52	20.01	66.68	21.91	27.07	287.09	275.96	142.98	127.85
Pa91	Pennsylvania	302 Panel	(Wf9*Oh43)S4*[(38-11*L317)38-11]S4	10.57	62.96	30.19	72.59	22.96	26.53	286.77	278.36	142.17	135.30
R168	Illinois	302 Panel	Illinois Synthetic 60C	12.39	63.65	30.44	72.66	20.96	24.46	251.82	234.72	129.09	115.01
R177	Illinois	302 Panel	Germplasm 230B(Snelling Corn Borer Synthetic)	9.00	65.82	38.04	80.44	21.72	25.54	278.72	240.79	115.21	93.29
R229	Illinois	302 Panel	[(479*B73)B73(2)]S6; 479 is a Brazilian inbred of Tuxpeño type	6.98	64.34	29.21	69.36	20.20	24.19	241.67	217.77	129.74	109.14
R4	Illinois	302 Panel	Funk Yellow dent	7.36	54.72	18.43	69.69	20.67	23.28	281.30	268.13	131.03	120.08
SC357	South Carolina	302 Panel	[(Whately yellow * Tennessee Redcob) Young]	15.03	61.48	38.66	67.97	22.68	24.82	292.41	283.48	143.95	123.73
SC55	South Carolina	302 Panel	[(L501*L503)*(L548*L569)]	11.67	61.76	36.15	73.04	21.44	25.00	322.85	313.69	184.81	166.21
SD40	South Dakota	302 Panel	Pioneer hybrid 3709	9.58	64.00	21.67	71.69	21.91	25.81	229.75	228.33	99.38	97.41
SD44	South Dakota	302 Panel	SDp309*SD30	7.36	62.06	21.35	72.75	22.29	24.64	258.42	249.11	113.27	108.03
Sg1533	Indiana	302 Panel	Super gold	7.86	52.23	24.92	64.42	20.96	23.01	299.82	279.96	180.61	156.54

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT
SG18	Indiana	302 Panel	Super gold	7.47	51.28	20.82	68.10	19.91	23.01	285.16	271.17	147.99	145.13
T232	Tennessee	302 Panel	Jellicorse*Teko yellow	11.42	63.07	44.39	76.34	23.53	25.09	290.96	280.60	146.37	142.28
T234	Tennessee	302 Panel	[T111*RB.L*III.A)]T111(4)	13.36	59.80	34.61	72.66	24.58	26.44	277.91	259.98	137.01	119.29
T8	Tennessee	302 Panel	Jarvis Golden Prolific	24.32	61.60	46.28	69.86	23.44	25.27	285.64	261.90	147.50	131.81
Tx303	Texas	302 Panel	Yellow Surcropper	6.58	65.09	19.23	75.85	21.82	26.53	315.28	300.74	184.48	158.29
Tx601	Texas	302 Panel	Yellow Tuxpan	17.53	61.01	45.18	71.22	25.92	27.52	348.78	334.31	194.82	181.75
Tzi10	Nigeria	302 Panel	Tlaltizapan 7844 x TZSR	10.26	54.31	36.56	68.29	24.20	26.89	309.16	305.38	189.17	173.03
Tzi11	Nigeria	302 Panel	Mo17 x RppSR	6.22	64.40	28.76	72.17	23.25	25.99	290.96	288.43	148.15	134.67
Tzi16	Nigeria	302 Panel	PI 540747 = N28/RPPTZSR-Y	7.18	59.69	27.47	70.55	22.96	27.07	318.66	302.82	181.25	145.92
Tzi18	Nigeria	302 Panel	Sete Lagoas 7728 x TZSR	7.52	60.51	20.53	69.97	20.96	27.07	289.51	271.49	170.60	141.33
Tzi25	Nigeria	302 Panel	[(B73*RPPSR-TZ)*B73(2)]	15.66	64.17	45.72	71.41	23.92	25.81	310.29	296.91	189.81	171.45
Tzi8	Nigeria	302 Panel	TZB x TZSR	2.39	65.70	5.76	74.74	16.74	26.91	266.56	294.53	168.50	161.50
Tzi9	Nigeria	302 Panel	SIDS7734/TZSR	14.04	65.49	33.80	73.21	22.68	24.91	318.34	299.14	180.45	158.61
U267Y	South Africa	302 Panel	WF9r*Mex.155^3	5.57	58.09	17.50	76.00	21.15	26.71	276.62	260.14	137.49	118.34
Va102	Virginia	302 Panel	Va59*Va60	7.03	57.44	26.04	72.08	22.01	25.27	263.09	236.80	136.20	108.83
Va14	Virginia	302 Panel	[(VaCBS selection*Va17)Va17]	15.51	59.78	41.64	71.29	23.25	26.26	281.62	258.54	125.87	112.31
Va17	Virginia	302 Panel	Wf9*T8	16.42	67.27	49.53	82.24	24.68	25.54	266.64	240.47	121.18	104.55
Va22	Virginia	302 Panel	Va17*C103 backcross	21.26	58.19	46.71	72.74	23.92	26.35	275.98	255.02	136.68	125.79
Va26	Virginia	302 Panel	Oh43*K155	7.27	55.62	20.61	75.55	20.86	25.90	260.84	246.87	115.21	100.58
Va35	Virginia	302 Panel	[(C103*T8)T8]	18.62	61.41	41.19	72.50	23.82	26.26	270.99	246.55	126.35	110.89
Va59	Virginia	302 Panel	[(C103*T8(2))*(K4*C103(2))]	9.98	64.26	33.11	73.68	22.20	25.63	265.67	240.31	127.16	107.88
Va85	Virginia	302 Panel	Virginia Long Ear Synthetic	7.97	54.30	23.53	67.81	22.10	27.16	276.46	261.26	144.27	127.22
Va99	Virginia	302 Panel	Oh07B*Pa91	8.10	63.49	31.44	76.12	23.25	26.17	260.03	251.82	131.36	117.70
VaW6	Virginia	302 Panel	unknown	2.74	63.00	9.06	75.66	16.29	25.00	219.44	241.91	100.19	109.30
W117HT	Wisconsin	302 Panel	W117=643*Minnesota No.13	8.94	57.68	32.83	77.54	21.82	25.09	224.44	220.81	102.45	97.10
W153R	Wisconsin	302 Panel	[(la153*W8)la153]	16.23	65.49	53.63	73.54	23.53	25.00	241.19	226.09	115.37	97.89
W182B	Wisconsin	302 Panel	WD*W22	9.12	55.18	27.21	70.58	23.06	25.63	264.06	254.54	115.69	111.20
W22	Wisconsin	302 Panel	III.B10*W25	7.78	59.82	31.99	75.36	23.09	26.86	286.31	266.05	148.65	129.10
W401	Wisconsin	302 Panel	[(33*Wisconsin No.25)*67C]	16.10	63.81	50.00	75.81	23.44	25.18	237.48	227.37	102.77	102.33

Inbred	State/Country	Panel Type	Pedigree	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT
W64A	Wisconsin	302 Panel	Wf9*CI.187-2	8.66	59.77	24.68	73.94	21.63	25.18	236.52	220.33	115.85	106.13
Wf9	Indiana	302 Panel	Reid yellow dent (Indiana station strain)	7.66	61.20	22.09	75.95	22.39	26.98	266.64	253.90	125.70	119.45

Supplemental Table 4. Trait correlations of various traits using mean values of Maize Diversity Lines (MDL) X *Oy1-N1989/oy1*:B73 F_1 test cross populations.

	MT_CCMI	WT_CCMI	MT_CCMII	WT_CCMII	MT_SW	WT_SW	MT_FlHT	WT_FlHT	MT_EaHT	WT_EaHT	MT_Ea2Fl	WT_Ea2Fl
MT_CCMI		0.1755	0.8542	0.1287	0.6364	-0.1238	0.2345	0.1243	0.1301	0.0968	0.2637	0.1217
WT_CCMI	0.0011		0.1713	0.3288	0.0708	0.0517	0.159	0.1545	0.155	0.1317	0.0404	0.1303
MT_CCMII	<.0001	0.0015		0.1714	0.628	-0.1632	0.185	0.0612	0.1027	0.0398	0.2079	0.0745
WT_CCMII	0.0174	<.0001	0.0015		0.0783	0.1097	-0.0888	-0.0472	-0.1231	-0.0868	0.0531	0.0472
MT_SW	<.0001	0.1921	<.0001	0.1488		0.2807	0.3391	0.2036	0.194	0.1473	0.3692	0.2206
WT_SW	0.0222	0.3413	0.0025	0.043	<.0001		0.3171	0.3685	0.252	0.270	0.199	0.3928
MT_FlHT	<.0001	0.0032	0.0006	0.1015	<.0001	<.0001		0.9169	0.8982	0.8479	0.4129	0.6476
WT_FlHT	0.0217	0.0042	0.2599	0.3846	0.0002	<.0001	<.0001		0.8811	0.9254	0.2593	0.7061
MT_EaHT	0.0162	0.0041	0.0582	0.023	0.0003	<.0001	<.0001	<.0001		0.9353	-0.0296	0.3974
WT_EaHT	0.0742	0.015	0.4635	0.1097	0.0064	<.0001	<.0001	<.0001	<.0001		-0.0096	0.3851
MT_Ea2Fl	<.0001	0.4571	0.0001	0.3283	<.0001	0.0002	<.0001	<.0001	0.5862	0.8595		0.6491
WT_Ea2Fl	0.0247	0.0161	0.1699	0.3854	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	

Lower half contains correlation p-values and upper half contains Pearson correlation coefficient for each pairwise trait comparison. Self-comparisons (diagonal) are left blank.

Supplemental Table 5. Broad sense heritability and variance estimates of traits measured in MDL x *Oy1-N1989/oy1*:B73 F_1 test cross populations.

Trait	Heritability	LSD	Variance
MT_CCMI	0.95	3.22	18.77
WT_CCMI	0.59	14.56	80.64
Ratio_CCMI	0.92	0.06	0.01
MT_CCMII	0.96	7.36	126.66
WT_CCMII	0.63	11.74	57.20
Ratio_CCMII	0.94	0.12	0.02
MT_SW	0.86	2.73	6.50
WT_SW	0.81	2.15	3.22
Ratio_SW	0.83	0.11	0.01
MT_FlHT	0.97	18.00	844.73
WT_FlHT	0.96	20.76	986.88
Ratio_FlHT	0.68	0.10	0.00
MT_EaHT	0.97	15.87	726.33
WT_EaHT	0.95	17.47	598.19
Ratio_EaHT	0.48	0.20	0.01
MT_Ea2Fl	0.88	14.92	230.83
WT_Ea2Fl	0.88	14.59	186.17
Ratio_Ea2Fl	0.68	0.16	0.01

Figures

Figure 1. Plant growth and pigmentation defects differ in severity for *Oy1-N1989/oy1* in B73 and B73/Mo17 hybrid backgrounds. Representative wildtype (*oy1/oy1*) and mutant (*Oy1-N1989/oy1*) siblings from (A) *Oy1-N1989/oy1*:B73 x B73 and (B) *Oy1-N1989/oy1:*B73 x Mo17 F_1 crosses. Measuring stick in the two figures is 243 cm. (C) Non-destructive chlorophyll measurement in mutant and wildtype siblings at 3 weeks (CCMI) and 6 weeks (CCMII) after planting; data in CCM (chlorophyll content meter) units, data for each class of genotype is derived from 39 experimental replications. Asterisk indicates statistical significance at $p<0.001$ determined using student's t-test.

Figure 2. Crossing scheme to map *Oy1-N1989* enhancer/suppressor loci using RIL (IBM) and DH (Syn10) populations of B73 x Mo17. Red, blue and white colors indicate B73, Mo17, and missing genotypes. The heterozygous tester (*Oy1-N1989/oy1*:B73) shows chromosome 10 with a black spot indicating *Oy1-N1989* mutant allele. F_1 progenies depicted here show state of chromosome 10 for each F_1 test cross showing segregation of wildtype and mutant (with the black spot) siblings.

Figure 3. (A) Distribution of the CCMII of the mutants (MT_CCMII) in Syn10-DH x *Oy1-N1989/oy1*:B73 F_1 population. (B) Distribution of the MT_CCMII in IBM-RILs x *Oy1-N1989/oy1*:B73 F_1 population. (C) Genome wide QTL plot of MT_CCMII in

Syn10-DH x *Oy1-N1989/oy1*:B73 F_1 population. X-axis indicates the chromosome number and Y-axis indicates the logarithm of odds (LOD) to the base 10 of tested markers. Black horizontal bar indicates permutation testing based threshold to declare statistical significance of the QTL based on permutation testing. (D) Close up view of the major QTL *vey1* on chromosome 10. X-axis indicates the centiMorgan (cM) position of the molecular markers.

Figure 4. Recombinants detected in F_1 crosses of *Oy1-N1989/oy1*:B73 with Syn10-DH, BC_1F_1, and IBM-RIL populations. Number at a given marker and population intersection indicates the total number of recombinants between the respective marker genotype and phenotype; hyphen denotes no genotyping. dCAPS marker at *oy1* is highlighted in bold.

Figure 5. Manhattan plot of CCM traits (A) Top 500 SNPs associated with each trait plotted at the genome-wide level. Horizontal red bar indicates genome-wide bonferroni threshold level. (B) Zoomed-in view of the *vey1* region along with the gene models from B73. X-axis indicates the physical position (B73 RefGen v2) of the markers.

Figure 6. Single locus test of *oy1* showing interaction between *Oy1-N1989* and *oy1-yg* allele in a cross (B73 x *oy1-yg/oy1-yg*) x *Oy1-N1989/oy1*:B73. White-fill arrows indicate *Oy1-N1989/oy1* plants, whereas yellow-fill arrows indicate *Oy1-N1989/oy1-yg* plants.

Supplemental Tables

Supplemental Table 1. Primary trait mean values of the wild-type (WT) and mutant (MT) siblings of F_1 test crosses of *Oy1-N1989/oy1*:B73 with respective IBM-RILs.

Supplemental Table 2. Primary trait mean values of the wildtype (WT) and mutant (MT) siblings of F_1 test crosses of *Oy1-N1989/oy1*:B73 with respective Syn10-DH line.

Supplemental Table 3. Primary trait BLUP value of the wild-type (WT) and mutant (MT) siblings of F_1 test crosses of *Oy1-N1989/oy1*:B73 with respective maize inbred line from maize diversity lines (MDL). Information on the inbred lines from maize association panel (referred to as 302 panel) was adapted from Flint-Garcia *et al*. 2005.

Supplemental Table 4. Trait correlations of various traits using mean values of Maize Diversity Lines (MDL) X *Oy1-N1989/oy1*:B73 F_1 test cross populations.

Supplemental Table 5. Broad sense heritability and variance estimates of traits measured in MDL x *Oy1-N1989/oy1*:B73 F_1 test cross populations.

Supplemental Figures

Supplemental Figure 1. Linear regression of the chlorophyll pigment measurements using non-destructive CCM-200 plus meter (CCM reading in CCM units) and absolute chlorophyll pigment quantification using spectrophotometric method from the same leaf. Absolute amount of chlorophyll a, chlorophyll b, and total chlorophyll was quantified using spectrophotometer; units are mg/g fresh weight. Linear fit of CCM readings with (a) Chlorophyll a, (b) Chlorophyll b, (c) Total chlorophyll, (d) Chlorophyll a/b ratio (chl a/b ratio).

Supplemental Figure 2. CCM quantification of the mutants (*Oy1-N1989/oy1*) in B73, Mo17xB73, and Mo17 (BC_6 generation) genetic background at 30 days after planting. Statistical significance indicated by an asterisk was determined using ANOVA followed by Tukey's HSD posthoc test at $p<0.01$.

Supplemental Figure 3. Pairwise scatter plot of primary trait measurements in IBM-RIL x *Oy1-N1989/oy1*:B73 F_1 test cross populations.
Supplemental Figure 4. Pairwise scatter plot of primary trait measurements in Syn10-DH x *Oy1-N1989/oy1*:B73 F_1 test cross populations.
Supplemental Figure 5. CCMII distribution in the wildtype and mutant siblings of (A) IBM-RIL x *Oy1-N1989/oy1*:B73 F_1 populations, (B) Syn10-DH x *Oy1-N1989/oy1*:B73 F_1 populations.
Supplemental Figure 6. Cartoon of BM-NILs (on Y-axis) with the genotypes (B73, Mo17, Heterozygous, and missing colored as blue, golden, grey and white respectively) at given SNPs (X-axis of the left figure; physical position from B73 RefGen v2) and position of *oy1* locus (between the two SNPs that are highlighted by a black arrow). Mean (five replications) of primary traits and their ratios (mutant/wildtype) of respective NIL F_1 test crosses and the parental F_1 (B73 and Mo17) test crosses with *Oy1-N1989/oy1:B73* is shown on the right in a tabular format.
Supplemental Figure 7. CCMI and CCMII distribution in the wild-type and mutant siblings of maize diversity lines (MDL) x *Oy1-N1989/oy1*:B73 F_1 test cross populations.

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Figure 1. Plant growth and pigmentation defects differ in severity for *Oy1-N1989/oy1* in B73 and B73/Mo17 hybrid backgrounds. Representative wildtype (*oy1/oy1*) and mutant (*Oy1-N1989/oy1*) siblings from (A) *Oy1-N1989/oy1*:B73 x B73 and (B) *Oy1-N1989/oy1*:B73 x Mo17 F_1 crosses. Measuring stick in the two figures is 243 cm. (C) Non-destructive chlorophyll measurement in mutant and wildtype siblings at 3 weeks (CCMI) and 6 weeks (CCMII) after planting; data in CCM (chlorophyll content meter) units, data for each class of genotype is derived from 39 experimental replications. Asterisk indicates statistical significance at $p<0.001$ determined using student's t-test.

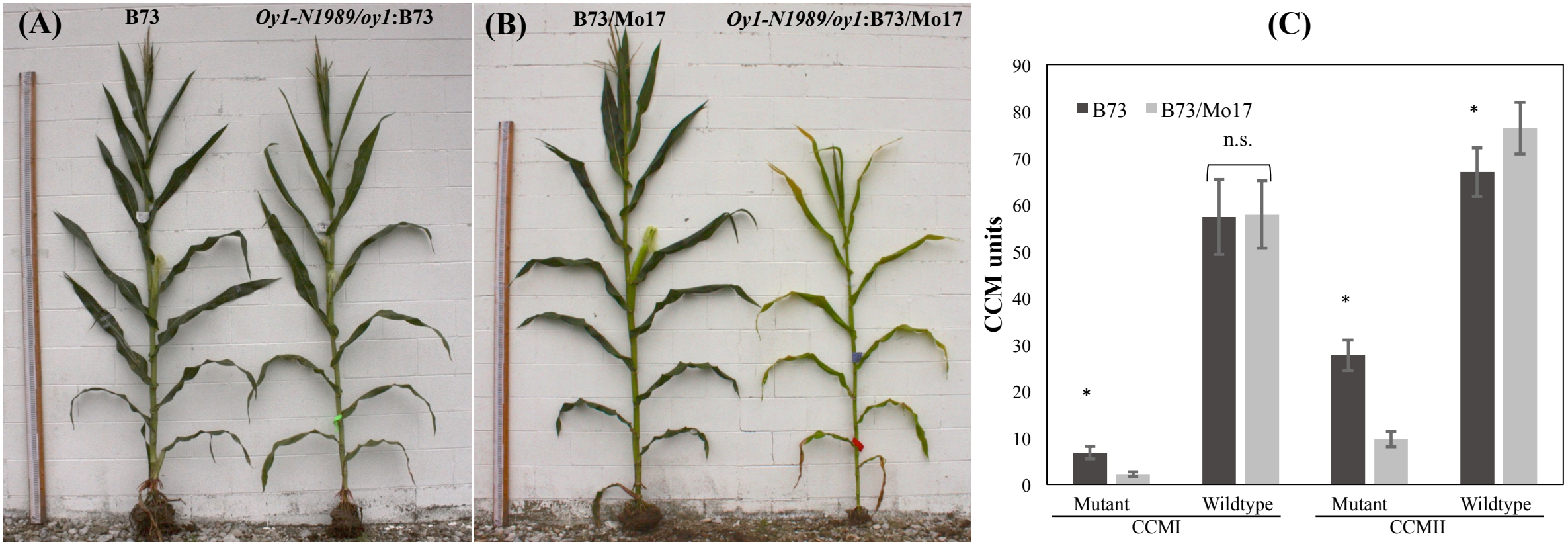


Figure 2. Crossing scheme to map *Oy1-N1989* enhancer/suppressor loci using RIL (IBM) and DH (Syn10) populations of B73 x Mo17. Red, blue and white colors indicate B73, Mo17, and missing genotypes. The heterozygous tester (*Oy1-N1989/oy1*:B73) shows chromosome 10 with a black spot indicating *Oy1-N1989* mutant allele. F_1 progenies depicted here show state of chromosome 10 for each F_1 test cross showing segregation of wildtype and mutant (with the black spot) siblings.

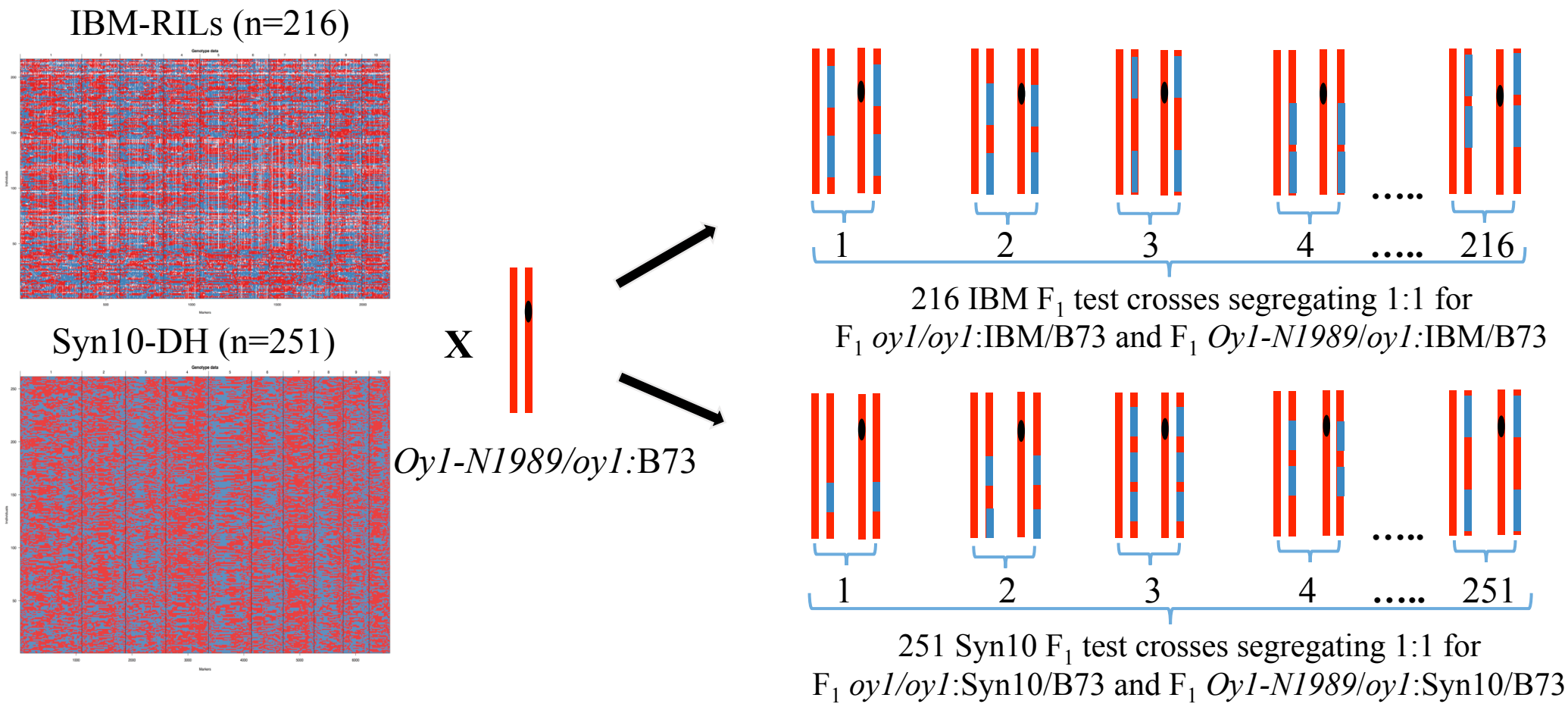


Figure 3. (A) Distribution of the CCMII of the mutants (MT_CCMII) in Syn10-DH x *Oy1-N1989/oy1*:B73 F_1 population. (B) Distribution of the MT_CCMII in IBM-RILs x *Oy1-N1989/oy1*:B73 F_1 population. (C) Genome wide QTL plot of MT_CCMII in Syn10-DH x *Oy1-N1989/oy1*:B73 F_1 population. X-axis indicates the chromosome number and Y-axis indicates the logarithm of odds (LOD) to the base 10 of tested markers. Black horizontal bar indicates permutation testing based threshold to declare statistical significance of the QTL based on permutation testing. (D) Close up view of the major QTL *vey1* on chromosome 10. X-axis indicates the centiMorgan (cM) position of the molecular markers.

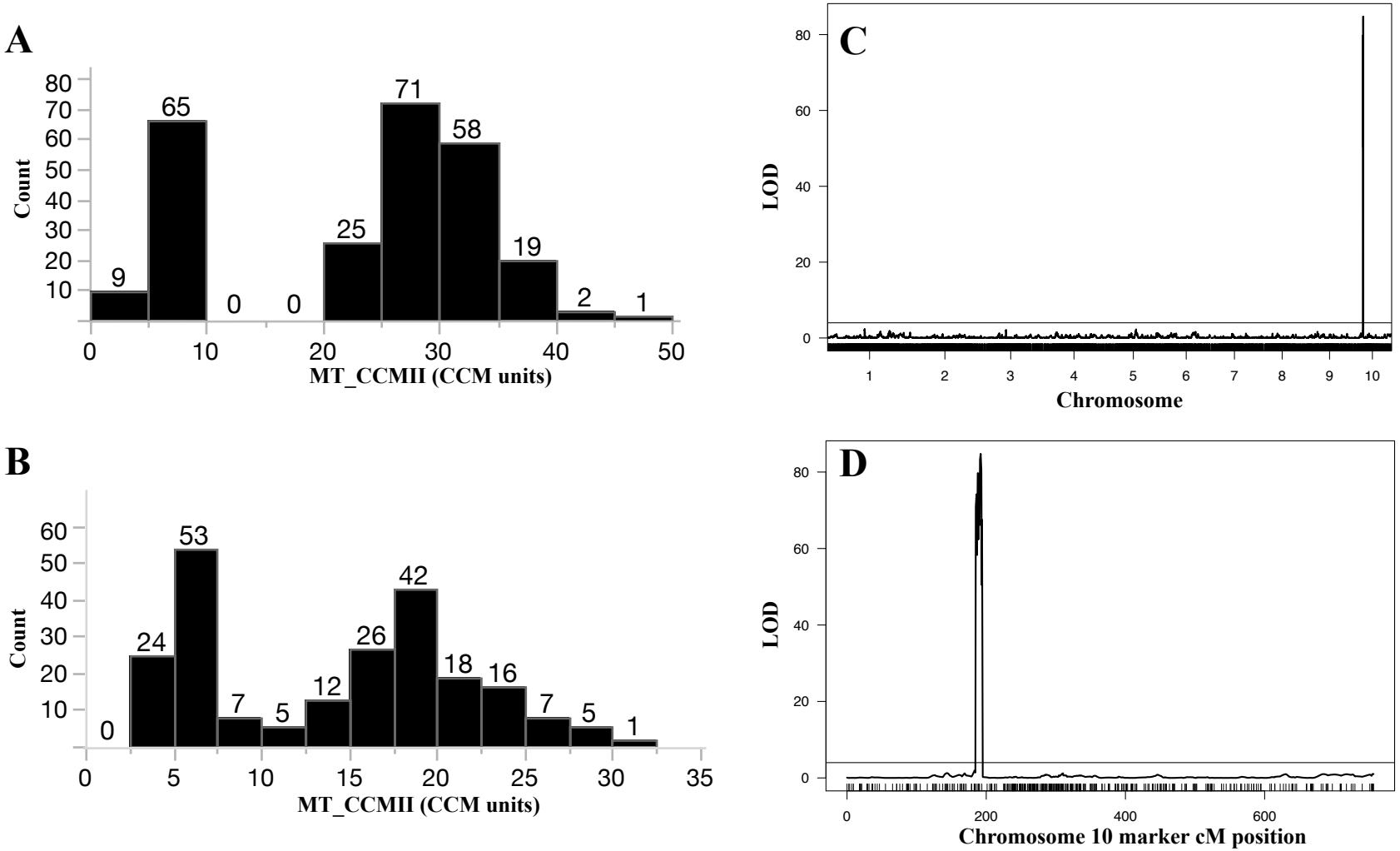
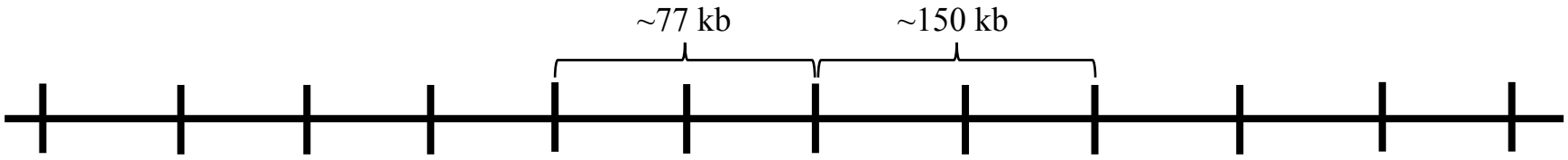
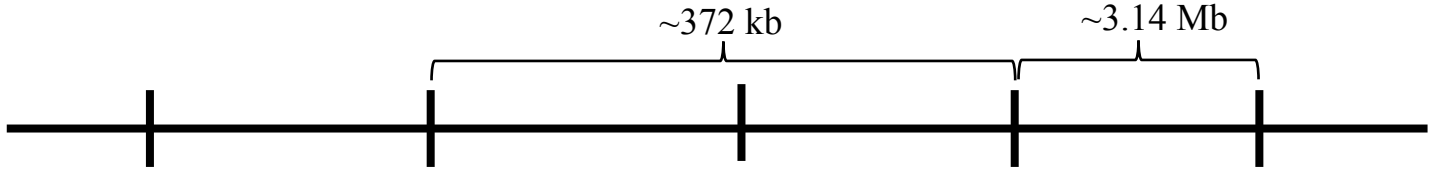


Figure 4. Recombinants detected in F_1 crosses of *Oy1-N1989/oy1*:B73 with Syn10-DH, BC_1F_1, and IBM-RIL populations. Number at a given marker and population intersection indicates the total number of recombinants between the respective marker genotype and phenotype; hyphen denotes no genotyping. dCAPS marker at *oy1* is highlighted in bold.



Marker name (position in Mb)	Chr10.82.5 (8.15)	Chr10.84.5 (8.35)	Chr10.88.5 (8.75)	Chr10.90.5 (8.95)	*ftcl1* (9.14)	Chr10.93 (9.175)	***oy1* (9.22)**	*gfa2* (9.36)	Chr10.94.5 (9.375)	Chr10.95.5 (9.5)	Chr10.96.5 (9.6)	Chr10.98 (9.725)
Syn10-DH (n=241)	11	11	6	2	3	0	0	0	1	7	23	32
BC_1F_1 (n=576)	-	-	-	-	3	-	0	0	-	-	-	-



Marker name (cM position)	umc2034 (94 cM)	phi059 (104.4 cM)	isu085b (105.6 cM)	***oy1***	umc2069 (116.6 cM)
Physical position (Mb)	6.37	8.85	9.13	9.22	12.36
IBM-RILs (n=176)	22	1	0	-	27

Figure 5. Manhattan plot of CCM traits (A) Top 500 SNPs associated with each trait plotted at the genome-wide level. Horizontal red bar indicates genome-wide bonferroni threshold level. (B) Zoomed-in view of the *vey1* region along with the gene models from B73. X-axis indicates the physical position (B73 RefGen v2) of the markers.

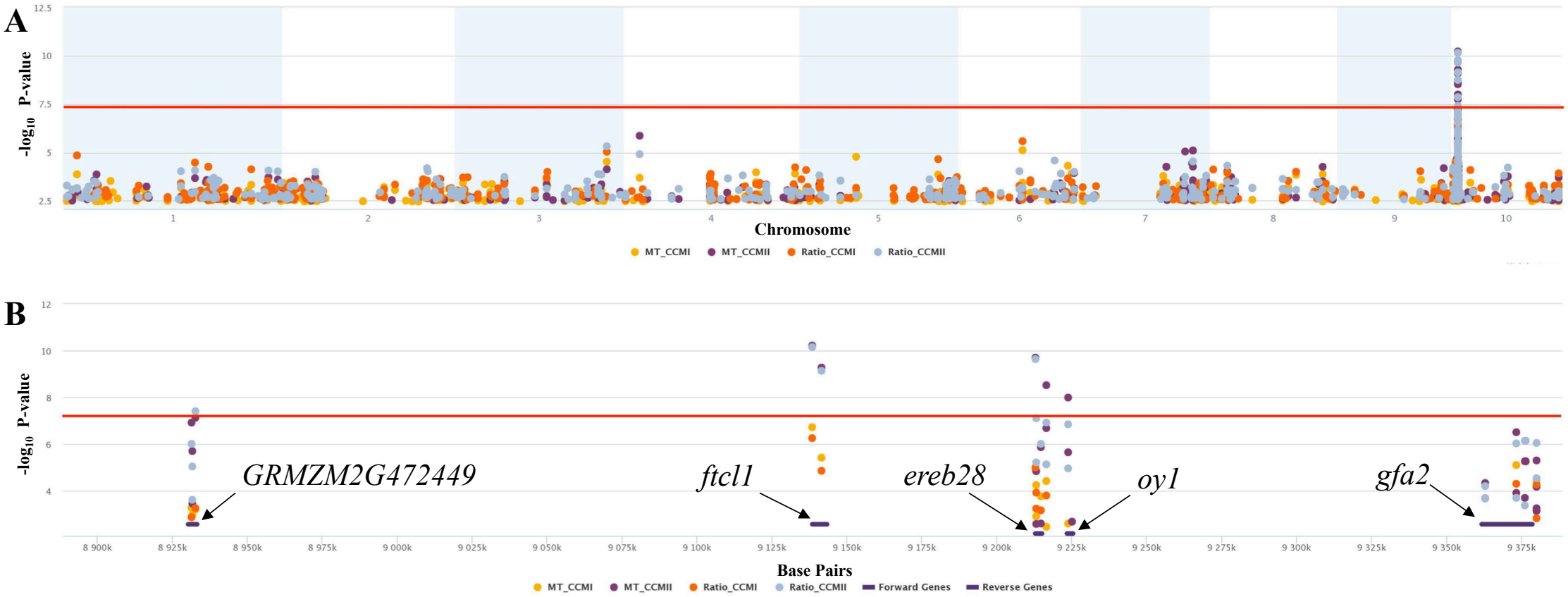


Figure 6. Single locus test of *oy1* showing interaction between *Oy1-N1989* and *oy1-yg* allele in a cross (B73 x *oy1-yg/oy1-yg*) x *Oy1-N1989/oy1*:B73. White-fill arrows indicate *Oy1-N1989/oy1* plants, whereas yellow-fill arrows indicate *Oy1-N1989/oy1-yg* plants.