

Tissue Specific Heterophile Aggregation of Protozoans Promoted Heterosis

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Research Article

Keywords: Maize, Heterosis, Transcriptome

Posted Date: April 19th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-380439/v1>

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Abstract

A plethora of studies have described heterosis or hybrid vigor; however, a global understanding of its regulation and the transmission of transcriptional levels between parents and hybrid has yet to be attained. To improve our understanding the molecular mechanisms controlling maize heterosis, we used an incomplete diallel cross design consisting of four elite maize inbred lines and six of their hybrids to measure the degree of variation in gene expression between the parents and their hybrids. We found that differentially expressed genes (DEGs) drove diversity of tissue specific heterosis and that heterophile expression was a generally complementary mechanism of gene expression in hybrids. However, the full expression of heterosis was due to the proportion of super dominant gene expression patterns that aggregate the regulatory network of dominant genes in response to adversity, and thus promotes heterosis in hybrids. Our results provide a new understanding and perspective into the regulatory mechanisms that control heterosis and represent an important step towards a more comprehensive explanation of heterosis in maize.

Full-text

Due to technical limitations, full-text HTML conversion of this manuscript could not be completed. However, the manuscript can be downloaded and accessed as a PDF.

Figures

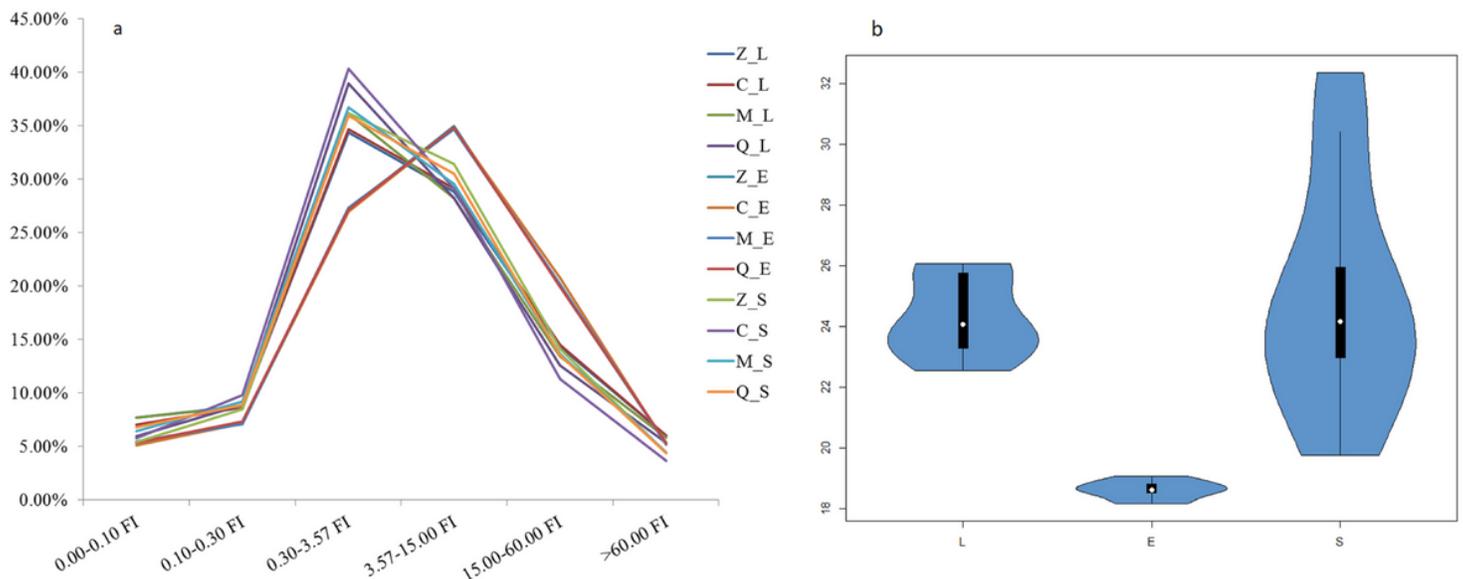


Figure 1

The interval distribution of gene expression ratios in maize inbred lines. FPKM intervals (FI) at different frequencies are shown in (a) with the intervals shown on the x axis and the gene expression ratios (GERs) on the y axis. Distinctive distributions (y axis) and probability densities (x axis) of genes expressed in

maize leaf (L), ear (E), and seed (S) tissues are shown as violin plots in (b). The distribution of expression frequencies was lowest in ears but exhibited a more variable distribution in seeds.

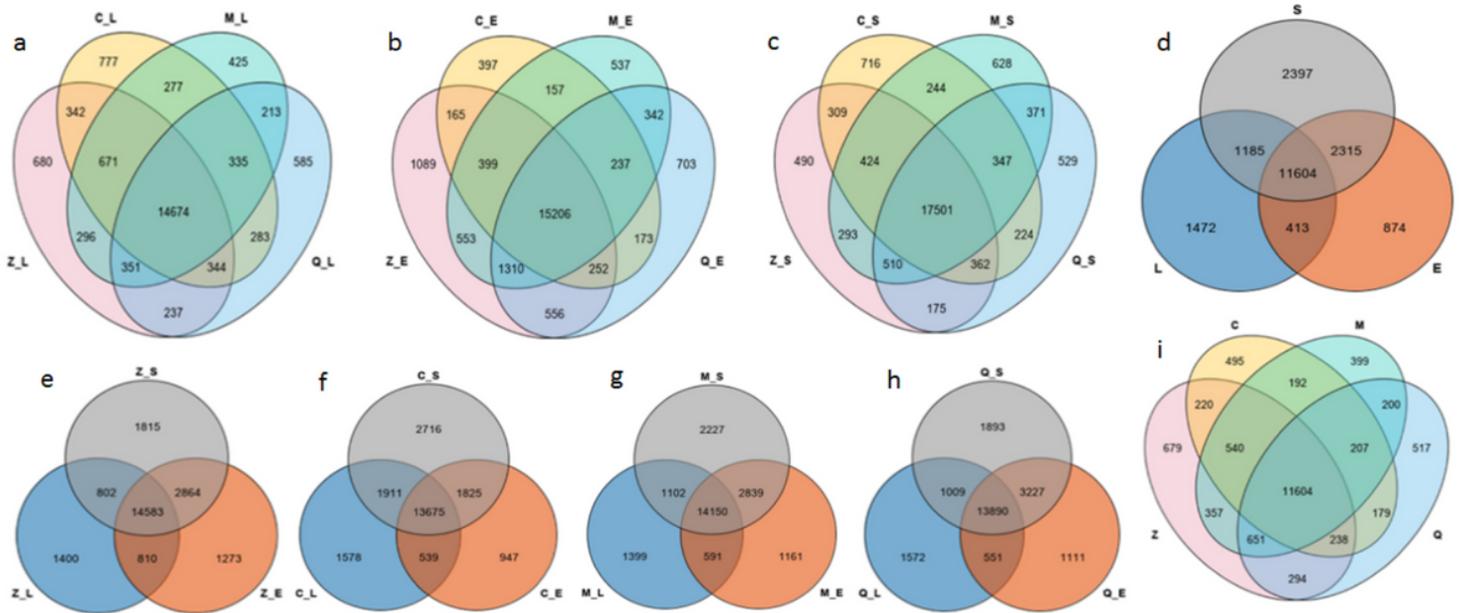


Figure 2

Distribution of DEGs in different maize inbred lines and tissues. Venn diagrams depict the distribution of DEGs in leaves (L) in (a), ears (E) in (b), and seeds (S) in (c) among the four inbred lines Z, C, M, and Q, which represent the maize inbred lines Zheng58, Chang7 2, Mo17, and Qi319, respectively. The co expressed DEGs between and among tissues are shown in (d), and the distribution of genes expressed in different tissues among the inbred lines Z, C, M, and Q are shown in panels (e), (f), (g), and (h), respectively. The distribution of DEGs in each inbred line Z, C, M, and Q is shown in (i), indicating relatively consistent quantities of co expressed DEGs across inbred genotypes.

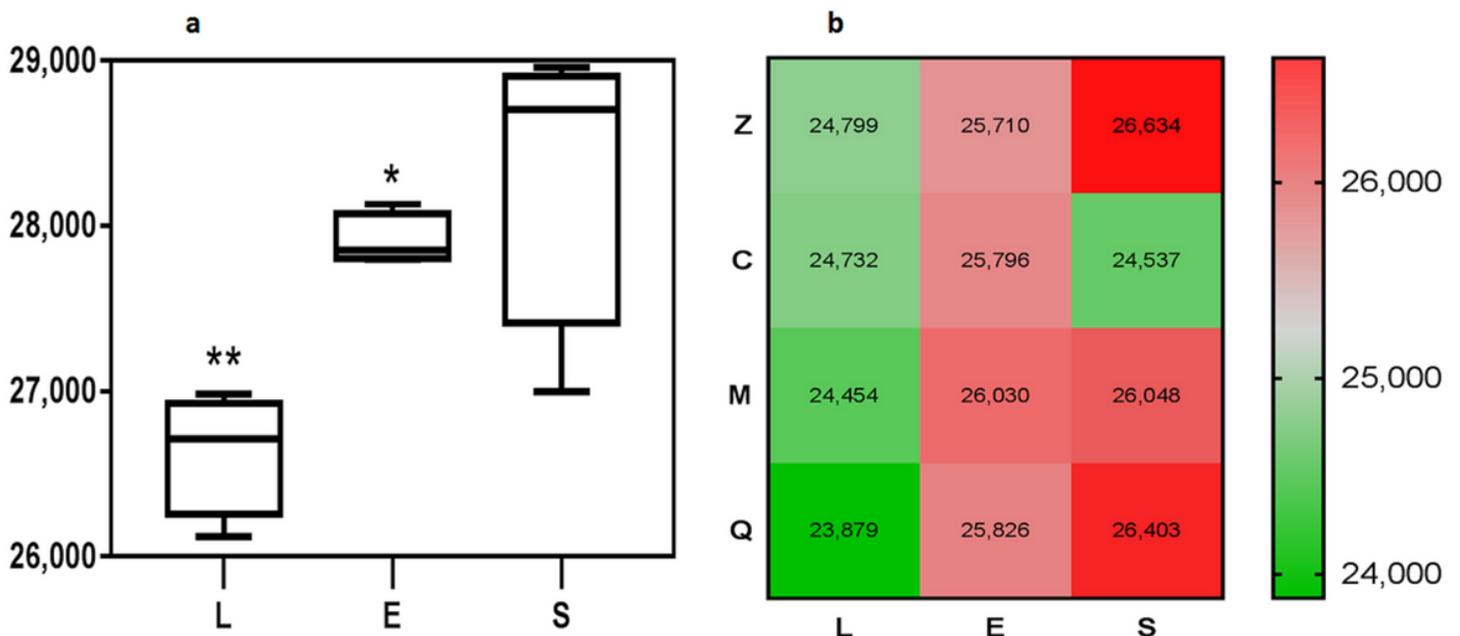


Figure 3

Tissue specific expression genes of different maize inbred lines. A box plot showing the range of gene expression in maize leaves (L), ears (E), and seeds (S) from inbred lines Z, C, M, and Q, which represent the maize inbred lines Zheng58, Chang7 2, Mo17, and Qi319, respectively, is shown in (a), indicating significant differences in the expression of different genes at * $p < 0.05$ or ** $p < 0.01$ based on ANOVA. The number of DEGs of different inbreds among tissues is show as a matrix in (b) with the orders of magnitude listed in the atlas by different colors.

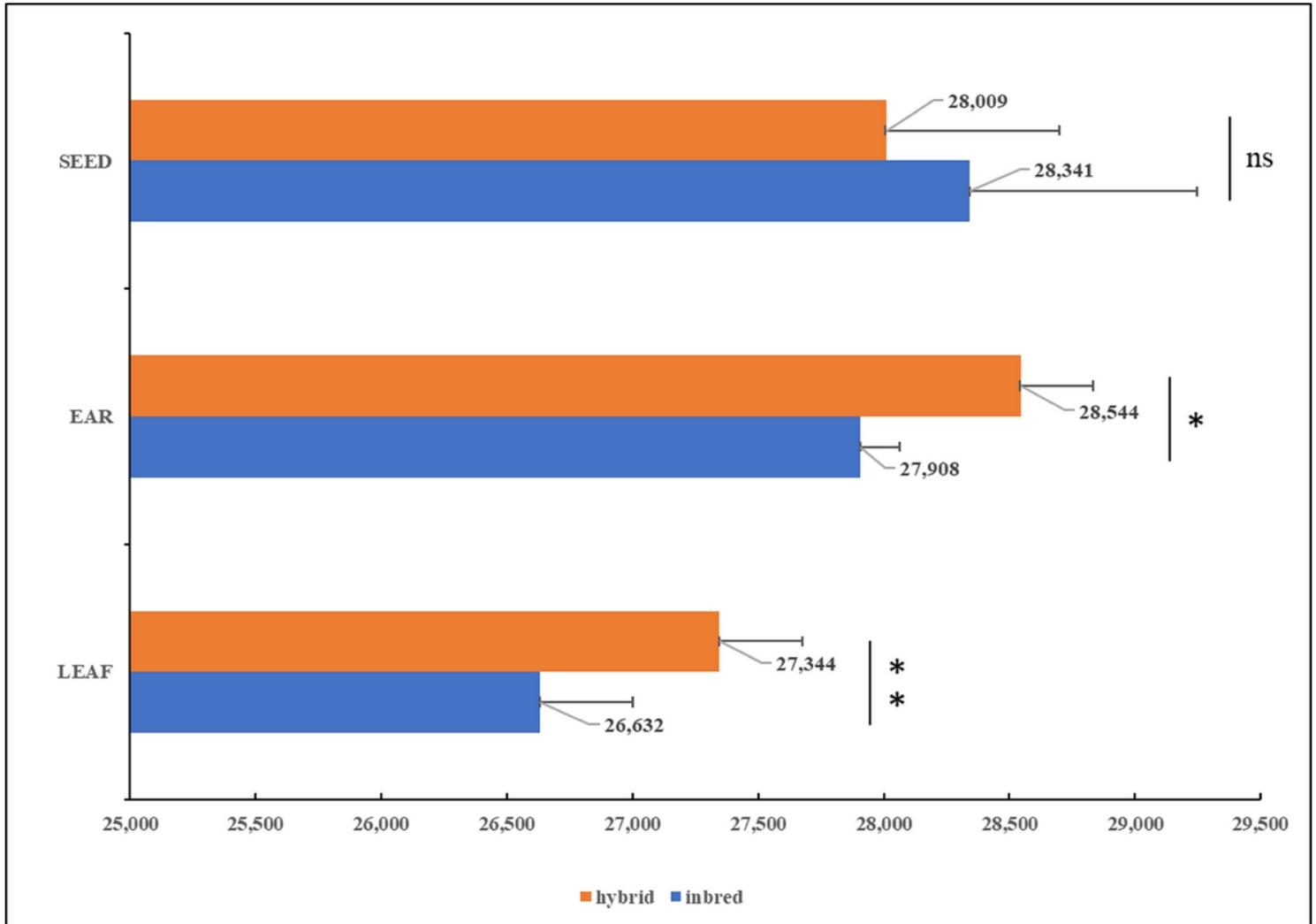


Figure 4

Characteristics of gene expression in leaf, ear, and seed tissues in a partial diallel of maize inbreds and hybrids. Comparison of expressed gene numbers for hybrids and inbred across tissues. The inbred parental lines include the maize inbreds Zheng58, Chang7 2, Mo17, and Qi319. The hybrids include Zheng58 × Chang7 2, Zheng58 × Mo17, Zheng58 × Qi319, Chang7 2 × Mo17, Chang7 2 × Qi319, and Mo17 × Qi319. The number of samples plotted in each box is shown above the box. Two tailed t tests were performed to identify significant differences between in inbred parents and hybrids in the number of genes expressed in each tissue (*, $p < 0.05$, **, $p < 0.01$, ns, not significant).

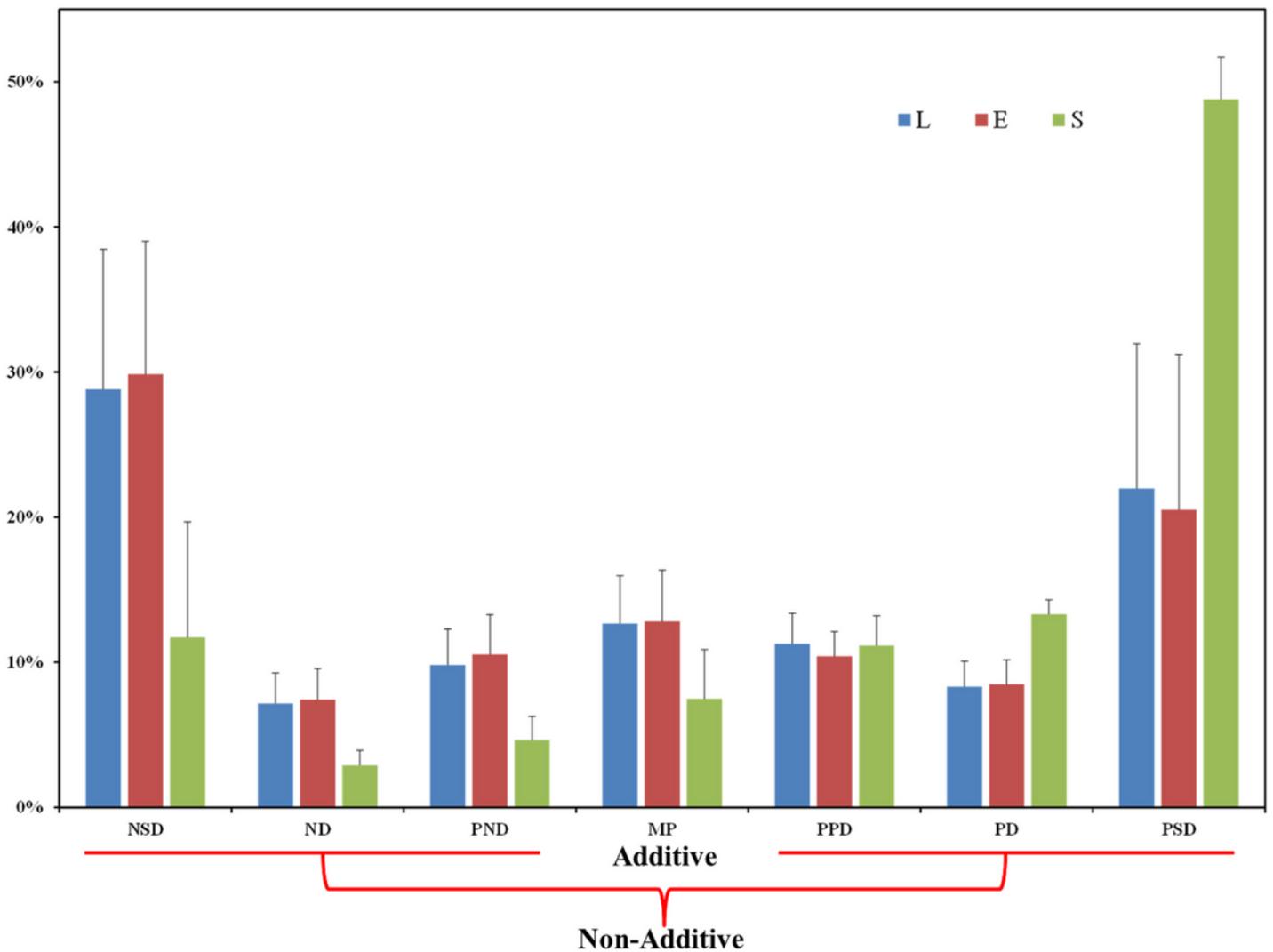


Figure 5

Potential gene expression patterns in hybrids. The gene expression levels in hybrid relative to inbreds are often expressed at the NSD or PSD level, representing the two transgressive expression patterns, with the Blue, red and green bars represent the DEGs in leaves (L), ears (E), and seeds (S), respectively. Additive and non additive gene expression patterns are indicated in the figure. The differences in expression of the hybrids are shown on the x axis while the gene expression ratio (GER) for each pattern (additive or non additive) of gene expression is shown on the y axis. The abbreviations used are defined hereunder: negative super dominance (NSD), negative dominance (ND), partial negative dominance (PND), mid parent (MP), partial positive dominance (PPD), positive dominance (PD) positive super dominance and (PSD).

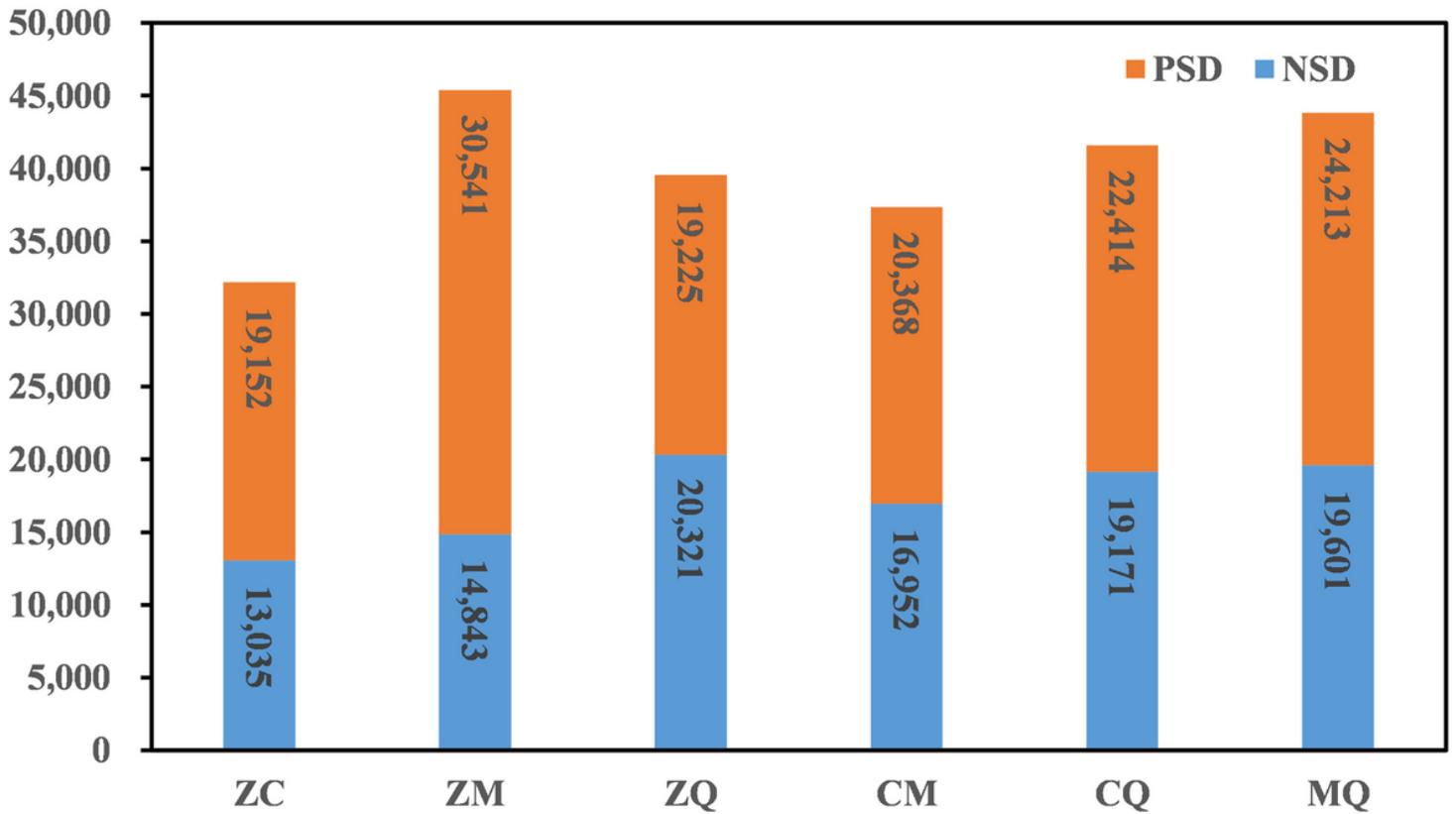


Figure 6

Numbers of transgressively expressed genes in each hybrid. The number of DEGs represented by each box is shown inside the box. The different hybrids are shown on the x-axis, and the total number of DEGs is shown on the y-axis with orange and blue representing the genes in Positive Super-dominance (PSD) and Negative Super-dominance (NSD) expression patterns, respectively. The hybrids include Zheng58 × Chang7-2 (ZC), Zheng58 × Mo17 (ZM), Zheng58 × Qi319 (ZQ), Chang7-2 × Mo17 (CM), Chang7-2 × Qi319 (CQ), and Mo17 × Qi319 (MQ).

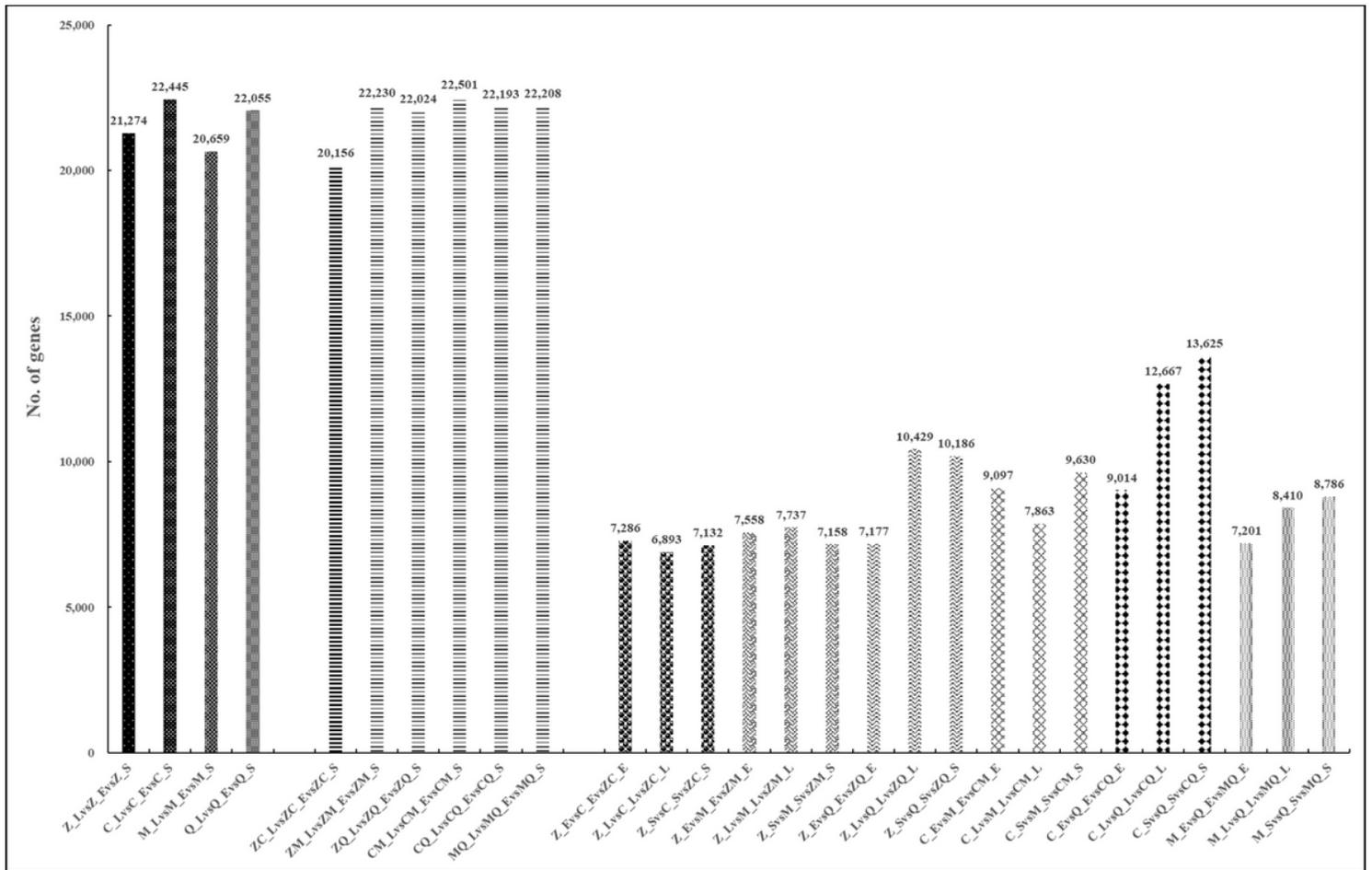


Figure 7

Numbers of significant DEGs. Histogram depicting the numbers of statistically significant DEGs in each genotype (inbreds and hybrids) and tissue (leaves (L), ears (E), and seeds (S)). The columns in the histogram are divided into three sections divided by wide gaps. The left hand section depicts the number of DEGs in L, E, and S tissues of maize inbred lines Z, C, M, and Q, which represent Zheng58, Chang7 2, Mo17, and Qi319. The central section depicts the number of DEGs in L, E, and S tissues of the hybrids, which include Zheng58 × Chang7 2 (ZC), Zheng58 × Mo17 (ZM), Zheng58 × Qi319 (ZQ), Chang7 2 × Mo17 (CM), Chang7 2 × Qi319 (CQ), and Mo17 × Qi319 (MQ). The righthand section depicts the number of DEGs in L, E, and S tissues of triplets consisting of hybrids and their parental inbred lines. The different inbred and hybrid genotypes are shown on the x axis, and the number of significant DEGS expressed by the different genotypes are shown on the y axis.

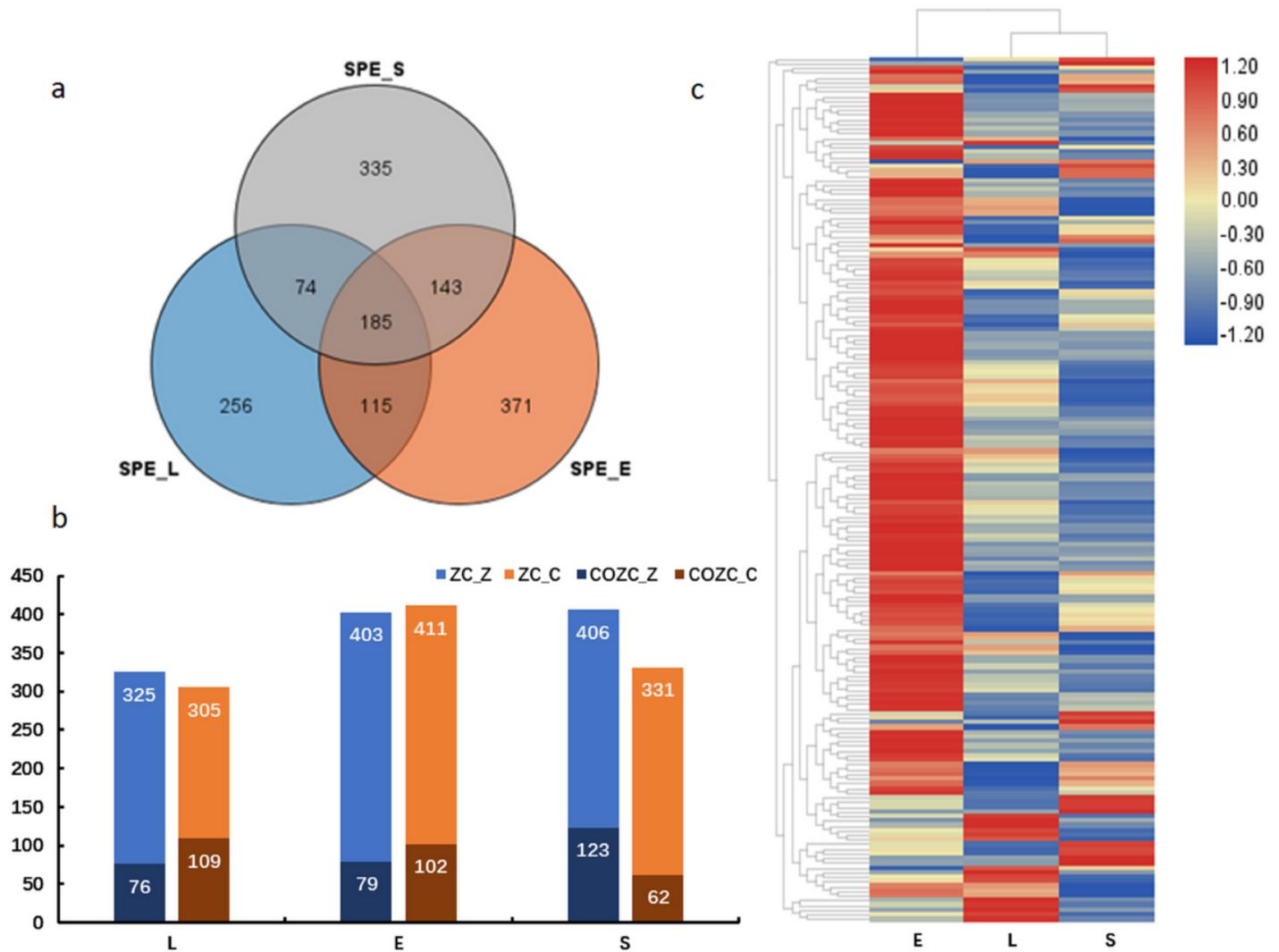


Figure 8

Distribution of DEGs under the SPE model in different tissues of the ZC hybrid. SPE gene distribution in different tissues (leaves (L), ears (E), and seeds (S)) (a), in which the difference of heterophile expressed distribution (COZC represents the SPE genes co expressed in different tissues of the ZC hybrid, the short line is followed by the directional biased parental inbred line). Co expressed SPE DEGs were expressed more consistently different tissues with numbers on the bars distinguish types of genes (b). Transcript abundances in different tissues of hybrid lines are log base 2 transformed. In (c), relatively higher transcript expression is indicated in red, relatively lower transcript expression is indicated in blue, and no expression is shown in yellow.

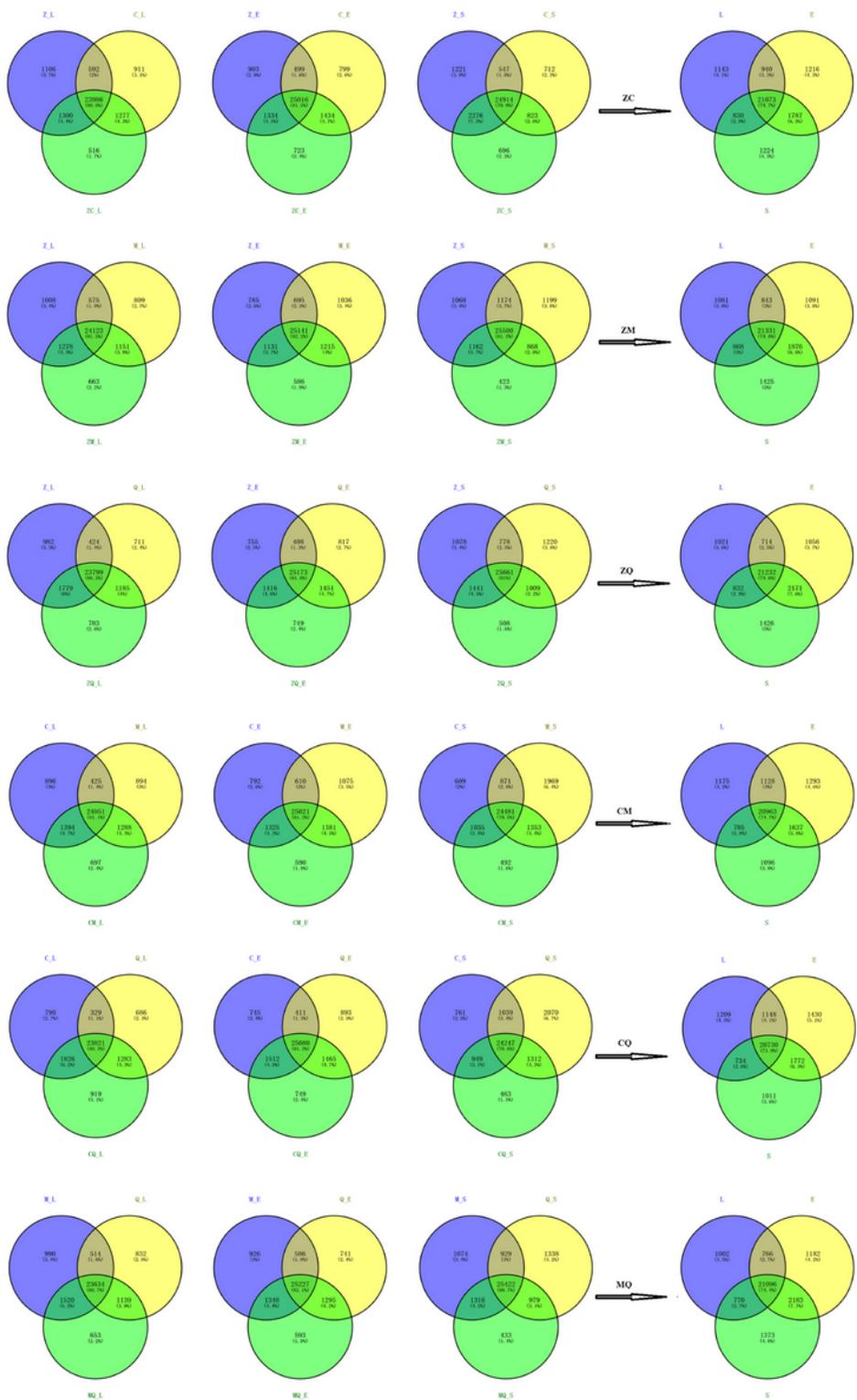


Figure 9

Number of expressed genes in triplets consisting of hybrids and their parental inbred lines. The coexpressed genes among different tissues (leaves (L), ears (E), and seeds (S)) in the six triplets were shown in the last column with Venn diagram, which were derived from coexpressed genes from different tissues in a triplet.

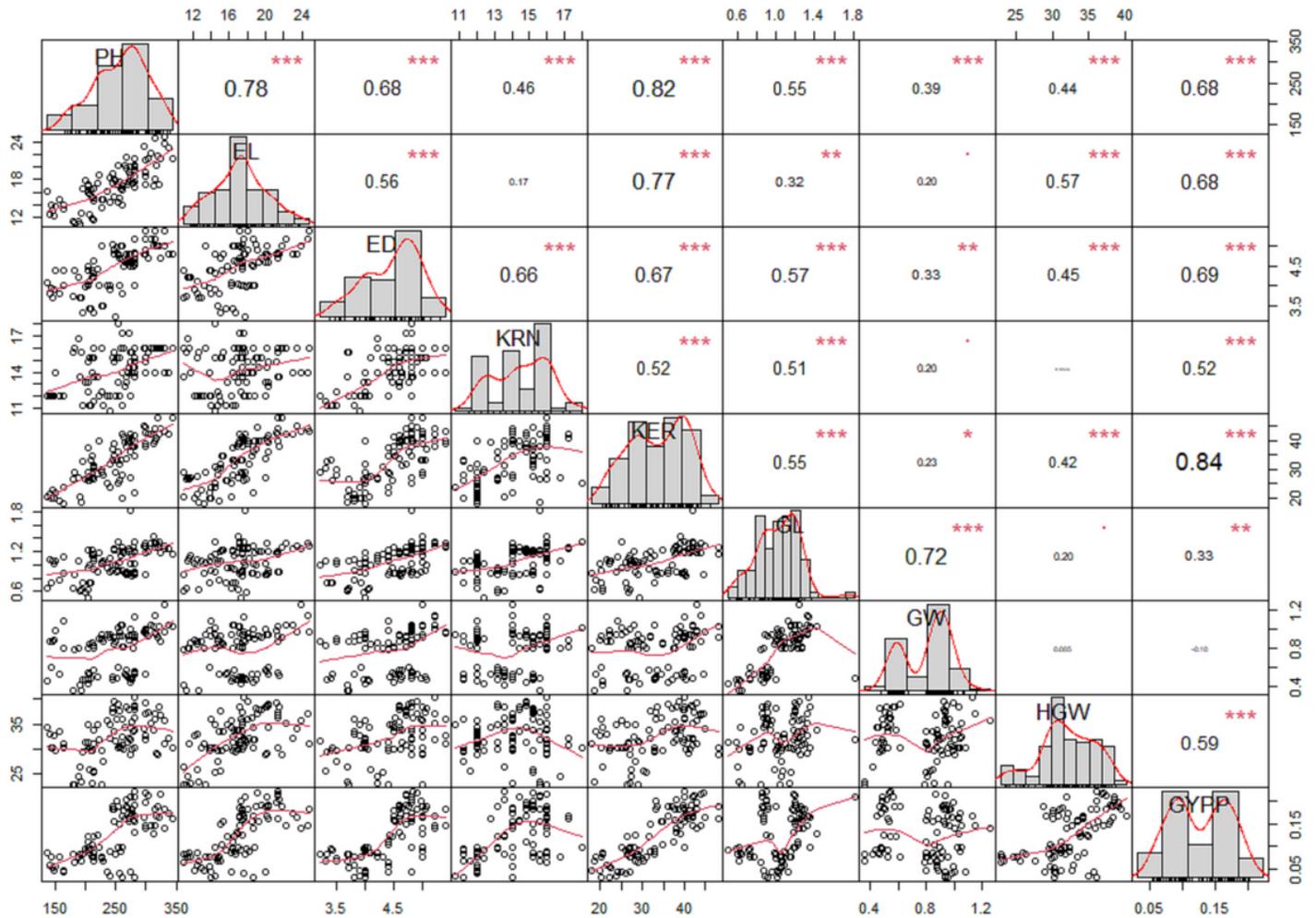


Figure 10

Pairwise correlations among the nine traits based on the best linear unbiased estimations (BLUEs) of the six hybrids and their parental inbred lines. The three biological replicates of [[how many]] different genotypes correspond to the hollow dots at the bottom left of the figure, and the best fit lines for each trait are shown with dashed red lines. The diagonals show the frequency distribution of each trait with histograms. The numbers in the top right figure with one or more red stars represent the significant Pearson correlation coefficients; *, **, and *** represent significant at $p < 0.05$, 0.01 , and 0.001 , respectively. The size of each number is correlated to the value of each Pearson coefficient. PH, plant height (cm); EL, ear length (cm); ED, ear diameter (cm); KRN, kernel row number; KER, kernels per ear row; GL, grain length (mm); GW, grain width (mm); HGW, hundred grain weight (g); GYPP, grain yield per plant (g).

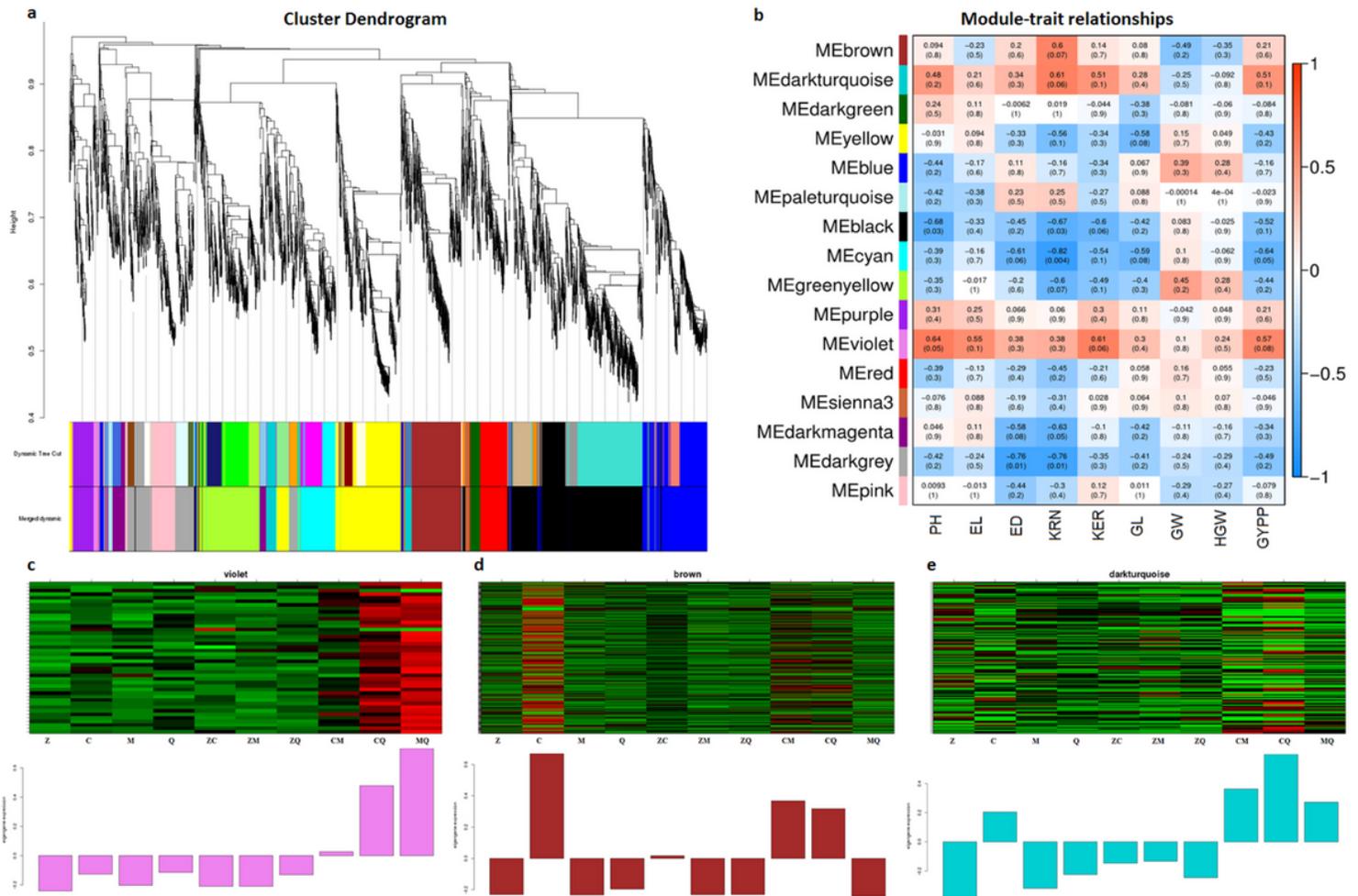


Figure 11

WGCNA network of heterosis related traits. Cluster dendrograms showing the co expression modules defined by WGCNA labeled in various colors (a). Matrix of the module trait relationships (MTRs) and corresponding p values between the detected modules on the y-axis and heterosis-related traits (PH, EL, ED, KRN, KER, GL, GW, HGW and GYPP) on the x-axis (b). The MTRs are colored in red for a strong positive correlation or blue for a strong negative correlation. In panels c, d, e: WGCNA modules with module eigengene value (y-axis) across genotypes (x-axis) by different colors of violet, brown, and dark turquoise associated with yield heterosis representing one or more trait of PH, KRN and HGW.

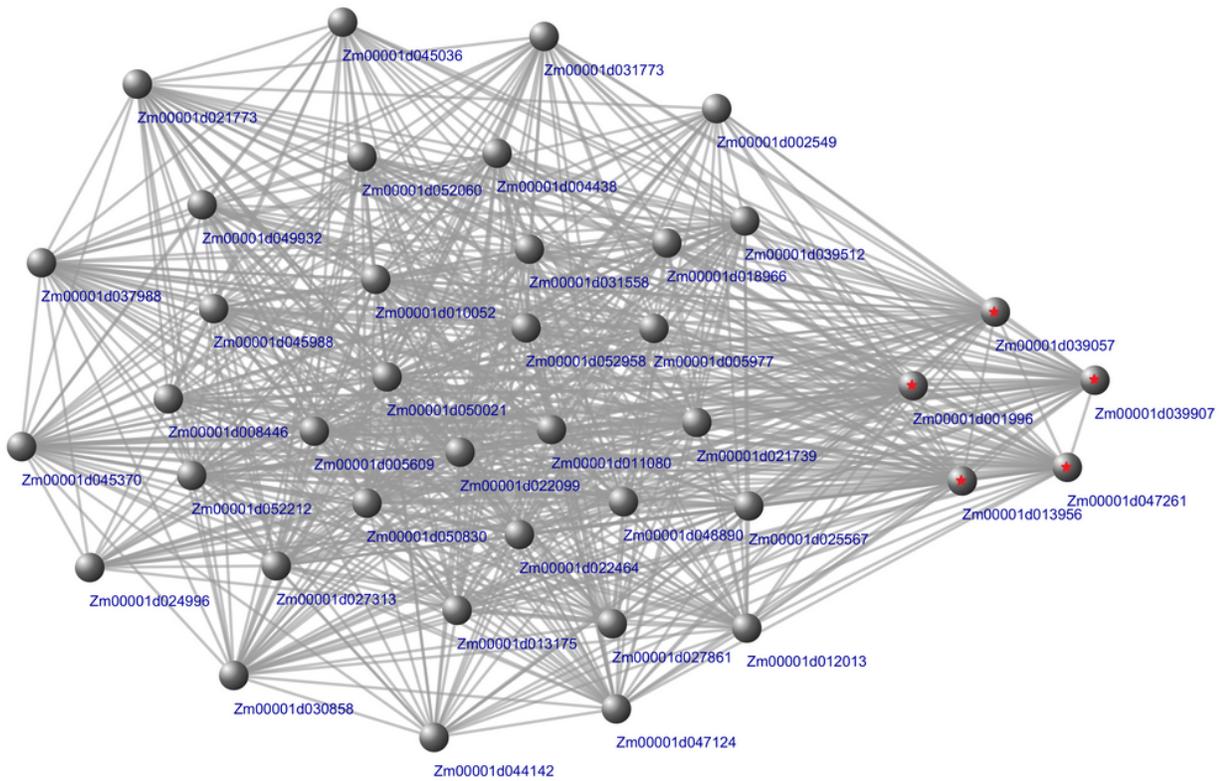


Figure 12

Co expression network of violet module. The top five hub genes are noted with red stars in the module eigengenes. The grey spheres represent the eigengenes for different network modules, and the lines connecting them represent relationships between genes without any differences in relationship strength.

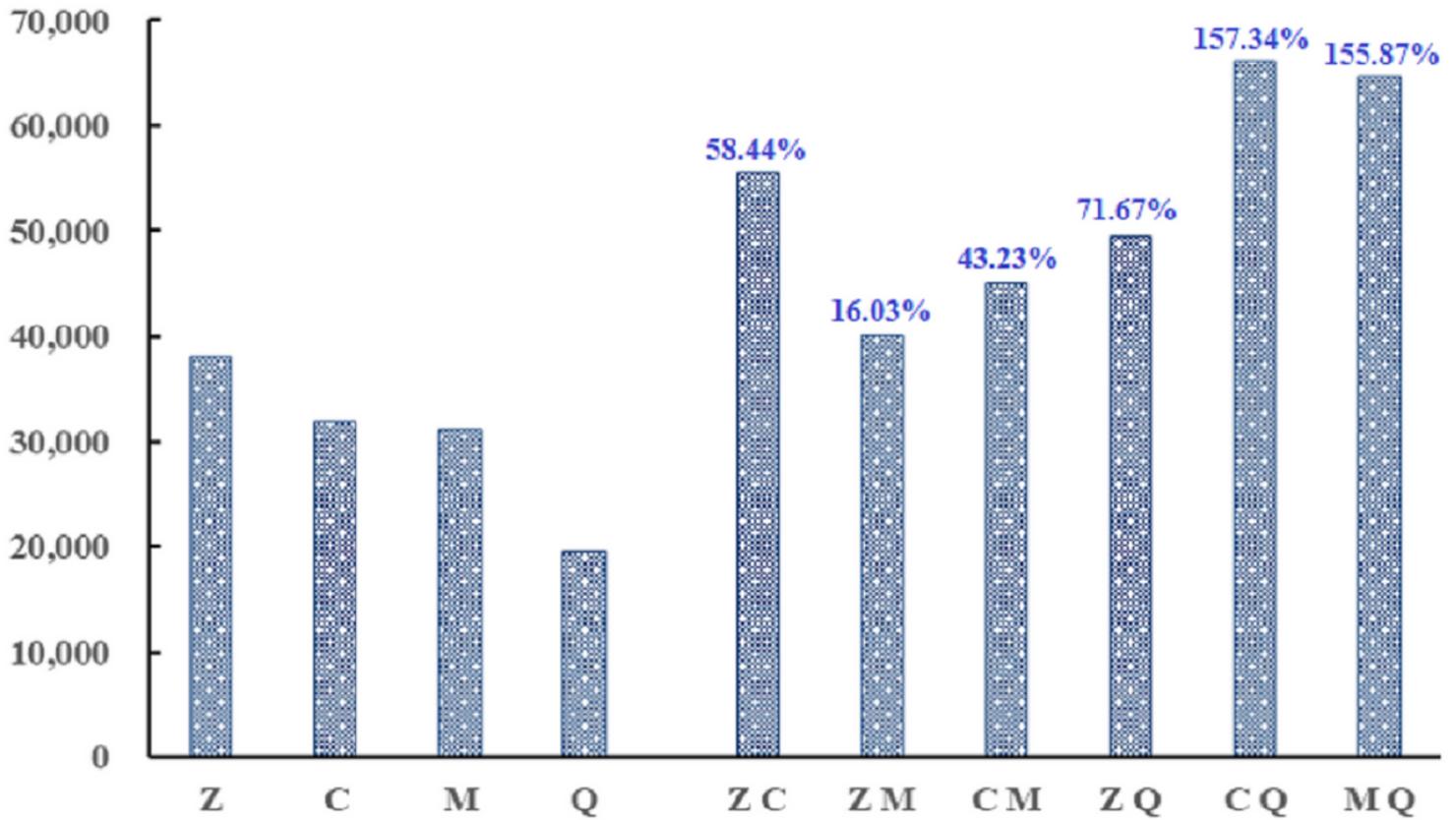


Figure 13

Leaf areas of maize hybrids and their parental inbred lines. Leaf area was measured in four elite inbred maize lines and six of their hybrids from an incomplete diallel cross (NCII). The total area of ear leaves and their upper and lower leaves (TELs) in cm² was used as an index representing photosynthetic leaf area, and the data represent the parental values and the midparent heterosis values of the hybrids. Z, C, M, and Q represent the four elite inbred lines Zheng58, Chang7 2, Mo17, and Qi319, respectively; and ZC, ZM, ZQ, CM, CQ, and MQ represent the hybrids Zheng58 × Chang7 2, Zheng58 × Mo17, Zheng58 × Qi319, Chang7 2 × Mo17, Chang7 2 × Qi319, and Mo17 × Qi319, respectively.

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