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Research Paper

Identifying quantitative trait loci for the general combining ability of yield-relevant traits in maize

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Maize is the most important staple crop worldwide. Many of its agronomic traits present with a high level of heterosis. Combining ability was proposed to exploit the rule of heterosis, and general combining ability (GCA) is a crucial measure of parental performance. In this study, a recombinant inbred line population was used to construct testcross populations by crossing with four testers based on North Carolina design II. Six yield-relevant traits were investigated as phenotypic data. GCA effects were estimated for three scenarios based on the heterotic group and the number of tester lines. These estimates were then used to identify quantitative trait loci (QTL) and dissect genetic basis of GCA. A higher heritability of GCA was obtained for each trait. Thus, testing in early generation of breeding may effectively select candidate lines with relatively superior GCA performance. The GCA QTL detected in each scenario was slightly different according to the linkage mapping. Most of the GCA-relevant loci were simultaneously detected in all three datasets. Therefore, the genetic basis of GCA was nearly constant although discrepant inbred lines were appointed as testers. In addition, favorable alleles corresponding to GCA could be pyramided via marker-assisted selection and made available for maize hybrid breeding.

Key Words: general combining ability, linkage mapping, maize, quantitative trait locus.

Introduction

Maize is a staple allogamous crop. It generally has high heterosis for yield-relevant traits. This property enables maize to contribute significantly to global food and animal feed supply and bioenergy production. Discovery of the heterosis phenomenon prompted the development of hybrid varieties (Darwin 1876, East 1908, Shull 1908). Hybrids with yield potential and pathogen and insect pest resistance superior to those of their parents can be developed by crossing two inbred lines derived from different heterotic groups. Therefore, dissection of the genetic architecture of hybrid performance is pivotal in the formulation of efficient breeding strategies.

Hybrid value is statistically decomposed into general combining ability (GCA) and specific combining ability (SCA). The former indicates the average hybrid performance of the parental line and reflects additive allelic effects in quantitative genetics, mainly including additive and epistatic gene action effects. The latter is defined as the values for certain combinations relative to the expected performance based on parental GCA effects. Its allelic effects involve only dominant and epistatic gene action (Griffing 1956a, 1956b, Sprague and Tatum 1942). Evaluation of the GCA effects of parental lines plays an important role in commercial maize breeding. High GCA effects suggest that the candidate line has high breeding value and better performance as the more favorable alleles are pyramided. Hence, GCA estimation is a key step in the assessment of the performance of parental lines. The objective is the creation of potential high-yield hybrids based on the heterotic group theory. In maize, hybrid performance is closely correlated with the GCA effects (Fischer *et al.* 2008). Nevertheless, the GCA is of genetically complex. It really requires enormous amount of labors, time and resources to evaluate the GCA effects of lines in conventional breeding program. Hence, further elucidation for the quantitative trait loci (QTL) of GCA are imperative for implementing marker-assisted selection (MAS).

Exploration of the QTL relevant to the GCA could lead to the enhancement of elite inbred line selection efficiency. In general, both association- and linkage mapping can dissect the genetic architecture of complex quantitative traits.

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In earlier studies, biparental (Liu *et al.* 2015c, Qi *et al.* 2013, Wang *et al.* 2017, Zhou *et al.* 2017, 2018), multi-parental (Giraud *et al.* 2017), and natural (Chen *et al.* 2019, Riedelsheimer *et al.* 2012) populations were used to detect the QTL related to the GCA effects. The use of only a few testers decreases the estimation accuracy of the GCA effects (Giraud *et al.* 2017). Increasing the number of testers may not necessarily improve the detection power of QTL mapping for GCA effects. On the other hand, it may have an impact on the effect and position of QTL (Li *et al.* 2013). Relatively few major QTL related to GCA effects could be identified in multiple populations. They may have been retained in the processes of crop improvement and domestication (Chen *et al.* 2019). The favorable QTL alleles of the GCA effects vary among heterotic groups. Functional loci corresponding to certain groups may be used in MAS for elite lines (Giraud *et al.* 2017). Recurrent selection can be implemented to improve the GCA effects by pyramiding favorable alleles during population improvement (Lv *et al.* 2012, Qi *et al.* 2013). Thus, integrating MAS with recurrent selection may be preferable for the accumulation of favorable genes and the selection of elite inbred lines with good performance in breeding programs. In this way, time and labor may be saved and cost-benefit balance can be achieved.

In the present study, we dissected the genetic basis of GCA in order to furnish useful suggestions to plant breeders regarding the acceleration of the breeding process and the selection of elite lines with superior GCA performance. Based on North Carolina mating design II, 194 recombinant inbred lines (RILs) were used to construct testcross populations of four elite inbred lines. The datasets in this study consist of phenotypic data for six complex traits and genotypic data from a 55K single-nucleotide polymorphism (SNP) array. The aims of this study were to (1) evaluate the GCA effects using various tester combinations; (2) explore the genetic basis of GCA and detect its associated candidate genes; and (3) present several viable proposals to plant breeders for the improvement of maize breeding efficiency.

Materials and Methods

Plant materials

A biparental population consisting of 194 recombinant inbred lines was derived by crossing Zheng58 and HD568 (Liu *et al.* 2018, 2019). According to the North Carolina mating design II, the testers Zheng58, HD568, B73, and Mo17 were used to construct testcross populations by crossing with RILs for the estimation of GCA effects. These testers are elite Chinese inbred lines belonging to the Reid, Sipingtou, Reid, and Lancaster subgroups, respectively (Liu *et al.* 2015b, Wang *et al.* 2017). Zheng58 and B73 are typical inbred lines originating from the Iowa Stiff Stalk Synthetic (SS) heterotic group (Liu *et al.* 2015a, Zhang *et al.* 2016).

Experimental management and trait measurement

The testcross populations were grown in Henan Province (35.3° N, 113.9° E), China in 2015 and 2016 and in Jilin Province (43.5° N, 124.8° E), China in 2016. The field scheme had a completely randomized design and was performed in two replicates. Two-row plots were planted and harvested as grain trials. Six yield-relevant traits were investigated per location and included plant height (PH, cm), ear height (EH, cm), ear length (EL, mm), ear diameter (ED, mm), row number (RN), and hundred-kernel weight (HKW, g). The phenotypic value of HKW was adjusted to 140 g kg^{-1} grain moisture.

Estimating GCA effects and heritability

The phenotypic values of the testcrosses in multiple environments were used to estimate the variance components. The total variance of the hybrid values was decomposed into the variances in the general and specific combining abilities (GCA and SCA) following a linear mixed model (Giraud *et al.* 2017, Zhou *et al.* 2018):

$$y_{ijkl} = \mu + e_l + r_{k(l)} + g_i' + g_j'' + s_{ij} + (g'e)_{il} + (g''e)_{jl} + (se)_{ijl} + \varepsilon_{ijkl},$$

where y_{ijkl} is the phenotypic value of the testcross between the i^{th} individual and the j^{th} tester in the l^{th} environment with the k^{th} replicate, the l^{th} environment refers to one of the three environments, μ is the overall mean, e_l is the fixed effect of the l^{th} environment, $r_{k(l)}$ is the fixed effect of the k^{th} replicate within the l^{th} environment, g_i' is the GCA effect of the i^{th} individual, g_j'' is the GCA effect of j^{th} tester, s_{ij} is the SCA effect of the testcross between the i^{th} individual and the j^{th} tester, $(g'e)_{il}$ is the GCA-by-environment interaction effect between the i^{th} individual and the l^{th} environment, $(g''e)_{jl}$ is the GCA-by-environment interaction effect between the j^{th} tester and the l^{th} environment, $(se)_{ijl}$ is the SCA-by-environment interaction between the l^{th} environment and the testcross composed by crossing the i^{th} individual and the j^{th} tester, and ε_{ijkl} is the residual effect. All variance components were estimated by the restricted maximum likelihood method using the *lme4* v. 1.1-21 package in R (Bates *et al.* 2015). A model comparison with the likelihood ratio test was performed to test the significance of the variance component estimates (Stram and Lee 1994). To evaluate the gene effects in the inheritance of a target trait in the testcross population, the ratio of the variances between GCA and SCA was calculated. Heritability of GCA values was estimated as follows (Riedelsheimer *et al.* 2012):

$$h^2_{GCA} = \sigma^2_{GCA_L} / \left(\sigma^2_{GCA_L} + \sigma^2_{SCA}/t + \sigma^2_{GCA_L \times E}/e + \sigma^2_{SCA \times E}/te + \sigma^2_{\varepsilon}/ter\right),$$

where $\sigma^2_{GCA_L}$ is the GCA variance of the lines, $\sigma^2_{GCA_L \times E}$ is the interaction variance between the GCA of the lines and the environment, σ^2_{SCA}, $\sigma^2_{SCA \times E}$, and σ^2_{ε} are the SCA,

SCA-by-environment interaction, and residual variance components, respectively, and *t*, *e*, and *r* are the numbers of testers, environments, and replicates, respectively. Based on the information of the heterotic group of testers mentioned in the section of *Plant materials*, the phenotypic data of the testcrosses were analyzed in three scenarios to compare the GCA effects and detect the difference of genetic basis when the testers were derived from distinct heterotic groups. Furthermore, the implication of results can be used to provide several suggestions for practical breeding programs. In the first case, the GCA effects were evaluated for the dataset derived from the testcross population using the inbred lines Zheng58 and B73 as testers. For the second dataset, HD568 and Mo17 were chosen as the testers. In the third scenario, all testers were used to estimate the GCA effects of the RILs. The abovementioned datasets were simply named Z58&B73, HD568&Mo17, and ALL, respectively.

Clustering tree construction and correlation analysis

To construct the clustering tree, the GCA effects of the yield-relevant traits were standardized with zero mean and unit variance. The Euclidean distances among the GCA effects of the six agronomic traits were calculated using the standardized values. The clustering tree was plotted with the *hclust* function in the *stats* v. 3.6.0 package of R. The process of clustering tree construction was based on Pan *et al.* (2017). The GCA effects of each trait estimated in ALL dataset were used to construct the clustering tree. The correlation coefficients (*r*) and the *P*-values of the significance tests were calculated with the *cor* and *cor.test* functions in the *stats* v. 3.6.0 package in R, respectively.

Bin map construction and QTL mapping

The RILs were genotyped by the maize 55K SNP array (Xu *et al.* 2017). Qualified markers with missing rates <0.10 and heterozygous allele rates <0.05 were retained and then assessed with a chi-square test to screen out markers with segregation distortion ($P < 0.05$). The bin markers were aligned and determined by the sliding-window approach described in previous studies (Huang *et al.* 2009, Liu *et al.* 2019, Zhou *et al.* 2016). The genetic map was plotted by the Kosambi mapping method and with the *mstmap* function in the *ASMap* v. 1.0-4 package of R (Taylor and Butler 2017). QTL mapping of the GCA effects was performed by the composite interval mapping method and with the *R/qtl* v. 1.44-9 package in R (Arends *et al.* 2010). Using 1,000 permutation tests and setting $P < 0.05$, a logarithm of the odds (LOD) values ranged from 3.37 to 3.58 for different situations were designated as threshold to identify QTL for the GCA effects. A drop of 1.5 from the peak LOD value was defined as the confidence interval for one QTL. The genomic locations consisting of multiple QTL with overlapped confidence intervals were detected in this study, which might be recognized as essential genomic regions affecting GCA effects in maize. Candidate genes within the confidence intervals were detected and queried in the maize genetics and genomics database (MaizeGDB; https://www.maizegdb.org/).

Results

Correlation analysis and construction of the hierarchical clustering tree

Here, the distribution and range of yield-relevant traits in each population were illustrated in **Supplemental Fig. 1**, and then the correlation coefficients between RILs and hybrids within each testcross population in multiple environments were calculated, showing a relatively higher correlation at significant level in most situations (**Supplemental Table 1**). Furthermore, the GCA effects of each RIL were estimated for three scenarios in which different testers were selected to construct testcross populations. The aim was to assess the effects of various tester combinations. A correlation analysis was performed to evaluate the relationships of the GCA effects derived from the different datasets. The GCA effects estimated for the Z58&B73 and HD568&Mo17 datasets were closely correlated with those obtained for the ALL dataset. In all cases, *P*-values were remarkably lower than 0.01 (**Supplemental Fig. 2**). The correlation coefficients for the GCA values estimated for these three datasets were in the range of 0.88–0.96 for the six agronomic traits. Maximum *r* was estimated for RN after comparing the GCA effects between the Z58&B73 and ALL datasets. In addition, *r* was relatively high for the association of the GCA effects between the Z58&B73 and HD568&Mo17 datasets and was in the range of 0.59–0.78. The lower *r* limit of 0.59 was determined for EL and ED (**Supplemental Fig. 2**). The correlation coefficients of the GCA effects between all pairs of traits were evaluated in each dataset. The GCA effects of PH were positively correlated with those of EH ($P < 0.01$). The *r* values for the GCA of ED and RN in the three datasets were positive and significant ($P < 0.01$). The *r* was in the range of 0.72–0.84 for the association between PH and EH and 0.61–0.72 for the correlation between ED and RN (**Supplemental Fig. 3**). However, the GCA of RN was negatively and significantly correlated with the estimated GCA for HKW ($P < 0.01$), and the *r* ranged from –0.38 to –0.54 for the three datasets (**Supplemental Fig. 3**). The GCA estimate of EL was positively correlated with those for PH and EH. However, the *r* was relatively low. The hierarchical clustering analysis classified the GCA effects of the six yield-relevant traits into three groups. PH and EH were included in one group, RN, ED, and HKW appeared in a second, and EL was classified in its own group (**Fig. 1**).

Analysis of variance (ANOVA) and comparison of GCA effects among various datasets

ANOVA was performed using different datasets. The total hybrid variance was decomposed into seven variance components. Significant GCA variances of the RILs were verified at $P < 0.01$ for all six traits in all three datasets and

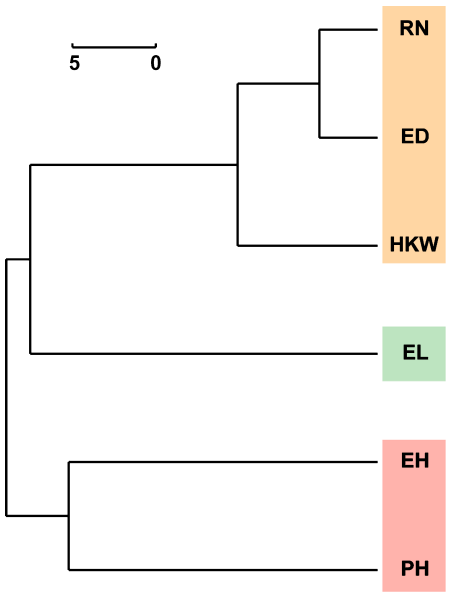

Fig. 1. Hierarchical clustering of GCA effects of six yield-relevant traits. Scale: Euclidean distance estimated on the basis of standardized GCA effects data for yield-relevant traits.

was based on the likelihood ratio test. However, *P*-value of GCA variance of the testers in the different datasets were greater than 0.05 when the hybrid values for ED were analyzed. The significance test of the interaction between the combining ability and environments in ALL dataset indicated that *P*-values were basically less than 0.01, except SCA-by-environment interaction in ED (**Table 1**). For the variance components of the GCA and SCA effects, ratios larger than one were obtained for all traits in all datasets except EL in Z58&B73 dataset. The ratio ranged from 0.83 in EL to 34.15 in RN. Comparatively low ratios were calculated for ED relative to other traits in the three datasets (**Table 1**). The heritability of GCA ranged from 0.64 for EL in the HD568&Mo17 dataset to 0.87 for EH in the Z58&B73 dataset. Compared to the other yield-relevant traits, h^2_{GCA} for EL was low in all three datasets (**Table 1**). On the other hand, the distribution plot of the GCA effects in the RIL population was drawn based on the results obtained from all three datasets (**Fig. 2A**, **2B**). The GCA estimates for the RILs mostly gathered around 0, especially for the PH in the HD568&Mo17 dataset. Only a few RILs had larger values associated with positive or negative GCA effects (**Fig. 2A**). Moreover, parallel distribution of the GCA effects was detected for HKW in the different datasets (**Fig. 2B**). Most RILs had concordant GCA effects between the Z58&B73 and HD568&Mo17 datasets. This finding was consistent with the results in the correlation analysis (**Fig. 2C**, **2D**). Highly significant linear relationship of GCA effects between these two datasets was shown for PH and HKW in both plots (**Fig. 2C**, **2D**).

Bin marker assignment and linkage map construction

The maize 55K SNP array was used to identify the genotypes of all lines. Then 15,474 SNP markers with heterozygous allele rates <0.05 and missing rates <0.10 were retained. A total of 12,318 SNPs in these markers conformed to a chi-square test without segregation distortion. The sliding-window approach determined and assigned 2,081 bins that were diversely distributed on chromosomes 1–10 (**Supplemental Table 2**, **Fig. 3A**). The average physical distance between adjacent bin markers in each chromosome ranged from 0.80 Mb to 1.73 Mb (**Supplemental Table 2**). The overall length of the physical map was 2,036.5 Mb and the average genomic physical distance between adjacent bins was 0.98 Mb. The maximum and minimum physical bin lengths were 53.72 Mb and 5.09 Kb and were identified on chromosomes 10 and 7, respectively (**Supplemental Table 2**). Twenty bin markers with physical lengths >10 Mb that can be recognized as linkage blocks were located mainly at the centromeric or pericentromeric regions of each chromosome. Few bins were situated in the regions covered by low-density SNPs (**Supplemental Table 3**). All bin markers were used to construct the linkage map in the *ASMap* package of R. The length of the genetic map was 1,526.7 cM (**Supplemental Table 4**, **Fig. 3B**). The average genetic distance between adjacent bins was 0.7 cM and the maximum genetic length was 5.3 cM. The unit length in the genetic map was equivalent to 1.33 Mb in the physical map in the present study (**Supplemental Table 4**). To compare the orders of the bin markers between the physical and linkage maps, a collinearity plot was drawn using marker location data. The plot illustrated excellent collinearity between the bin markers and the reference maize B73 genome (**Supplemental Fig. 4**).

QTL mapping of the GCA effects of yield-relevant traits

Forty-one QTL related to the GCA effects were detected in the ALL dataset and there were 5–9 QTL per agronomic trait (**Fig. 4**, **Supplemental Table 5**). The phenotypic variances explained (PVE) by the QTL were in the range of 3.12–16.54%. The QTL *qPH*$_A$*8*, *qEH*$_A$*1-3*, *qEL*$_A$*4*, and *qRN*$_A$*3* explained over 10% of the phenotypic variation in the GCA effects of the target traits (**Supplemental Table 5**). For the Z58&B73 dataset, 34 QTL were associated with GCA estimates of yield-relevant traits and there were 4–7 QTL per trait (**Fig. 4**, **Supplemental Table 6**). These QTL individually explained from 2.64% to 17.34% of the phenotypic variation of the GCA effects in each trait. The PVEs of the QTL *qPH*$_Z$*1-3*, *qEH*$_Z$*1-3*, *qED*$_Z$*2*, *qRN*$_Z$*4*, and *qHKW*$_Z$*7* were all greater than 10% (**Supplemental Table 6**). In the HD568&Mo17 dataset, 33 QTL were identified for the GCA effects and there were 3–7 QTL per trait (**Fig. 4**, **Supplemental Table 7**). The PVE of the QTL were in the range of 2.19–15.99% and four QTL individually accounted for over 10% of the phenotypic variation in the GCA effects (**Supplemental Table 7**). There were 28 genomic locations consisting of overlapped confidence intervals between multiple QTL that were detected among

Table 1. Variance of each component and heritability of GCA for yield-relevant traits

Comb. of testers[a]	Source[b]	PH[c]	EH	EL	ED	RN	HKW
Zheng58&B73	$\sigma^2_{GCA_L}$	110.06**	48.44**	44.36**	1.36**	0.45**	1.98**
	$\sigma^2_{GCA_T}$	1281.88**	424.97**	<0.01	1.6	2.35	12.04**
	σ^2_{SCA}	64.98**	16.11**	53.31**	1.04**	0.14**	1.20**
	$\sigma^2_{GCA_L \times E}$	3.79	3.53**	7.98**	<0.01	0.02	0.06
	$\sigma^2_{GCA_T \times E}$	8.17**	0.16	14.6**	1.02**	0.33**	0.04*
	$\sigma^2_{SCA \times E}$	11.55**	4.09*	12.2**	0.15	0.09**	1.11**
	σ^2_{ε}	51.99	33.88	66.73	4.97	0.61	2.31
	$\sigma^2_{GCA} / \sigma^2_{SCA}$	21.42	29.39	0.83	2.83	19.67	11.65
	h^2_{GCA}	0.84	0.87	0.69	0.74	0.86	0.80
HD568&Mo17	$\sigma^2_{GCA_L}$	52.53**	29.10**	49.47**	1.22**	0.28**	2.56**
	$\sigma^2_{GCA_T}$	1012.72**	154.55**	912.73**	<0.01	2.55	3.85*
	σ^2_{SCA}	51.78**	15.95**	69.04**	0.76**	0.08**	1.40**
	$\sigma^2_{GCA_L \times E}$	4.8	<0.01	12.88**	0.35*	0.10**	0.1
	$\sigma^2_{GCA_T \times E}$	8.54**	2.73**	5.09**	1.90**	0.40**	0.35**
	$\sigma^2_{SCA \times E}$	22.44**	14.17**	15.83**	0.06	<0.01	1.28**
	σ^2_{ε}	60.2	33.93	105.49	5.27	0.68	3.51
	$\sigma^2_{GCA} / \sigma^2_{SCA}$	20.57	11.52	13.94	1.6	34.15	4.56
	h^2_{GCA}	0.74	0.82	0.64	0.70	0.78	0.80
All testers	$\sigma^2_{GCA_L}$	79.02**	37.40**	49.00**	1.29**	0.38**	2.21**
	$\sigma^2_{GCA_T}$	842.68**	206.57**	342.73**	0.39	1.66**	5.40**
	σ^2_{SCA}	61.5**	17.75**	59.29**	0.93**	0.11**	1.35**
	$\sigma^2_{GCA_L \times E}$	5.56**	2.94**	10.22**	0.21**	0.05**	0.13*
	$\sigma^2_{GCA_T \times E}$	9.88**	2.40**	8.95**	1.23**	0.25**	0.23**
	$\sigma^2_{SCA \times E}$	14.77**	7.04**	13.93**	0.05	0.05**	1.14**
	σ^2_{ε}	56.62	34.92	85.26	5.13	0.64	2.88
	$\sigma^2_{GCA} / \sigma^2_{SCA}$	14.99	13.74	6.61	1.81	18.52	5.63
	h^2_{GCA}	0.79	0.83	0.68	0.71	0.84	0.79

[a] The datasets based on different combination of testers were used to perform analysis of variance. Zheng58&B73: the inbred lines Zheng58 and B73 were assigned as testers; HD568&Mo17: the inbred lines HD568 and Mo17 were assigned as testers; All testers: total of 4 inbred lines were used as testers.

[b] Variance components. $\sigma^2_{GCA_L}$: general combining ability variance of lines; $\sigma^2_{GCA_T}$: general combining ability variance of testers; σ^2_{SCA}: specific combining ability variance; $\sigma^2_{GCA_L \times E}$: general combining ability of lines by environment interaction variance; $\sigma^2_{GCA_T \times E}$: general combining ability of testers by environment interaction variance; $\sigma^2_{SCA \times E}$: specific combining ability by environment interaction variance; σ^2_{ε}: residual variance; $\sigma^2_{GCA} / \sigma^2_{SCA}$: the ratio between variance of general combining ability and specific combining ability; h^2_{GCA}: heritability of general combing ability.

[c] PH: plant height; EH: ear height; EL: ear length; ED: ear diameter; RN: row number; HKW: hundred-kernel weight. Significance levels: * $P < 0.05$; ** $P < 0.01$.

the yield-relevant traits in at least one of the three datasets, which were denoted as LOC1-LOC28 in order of their positions on the genome (**Table 2**). Ten of these genomic locations were simultaneously identified in all three datasets (**Table 2**). QTL mapping disclosed that 86 QTL in all GCA-relevant loci formed these genomic locations (**Table 2**, **Supplemental Tables 5–7**). In addition, LOC4, whose confidence intervals encompassed *qEH$_A$1-2*, *qEH$_Z$1-2*, and *qPH$_Z$1-2*, were located on chromosome 1 and the PVEs of these QTL were all greater than 10%. For the QTL hotspots LOC19 and LOC27, six QTL were identified in each overlapped genomic region (**Table 2**). The favorable alleles corresponding to LOC19 were entirely derived from the male parent (**Table 2**, **Fig. 4**). According to the maize genetics and genomics database (https://www.maizegdb.org/), the candidate genes, such as GRMAM2G403620, GRMZM2G082087, and GRMZM2G001541, were detected within the genomic region of LOC5, 15, and 17 that contained multiple GCA-relevant QTL. These predicted candidate genes were potentially related to the GCA effects of PH, EL, and RN, respectively.

Contribution of pyramiding favorable alleles

The GCA effects of HKW were used to represent and depict the contribution of accumulating favorable alleles. Nine QTL were identified for the GCA effects of HKW when four inbred lines were used as testers to construct the testcross populations. Seven favorable alleles were derived from the female parent of Zheng58 while the others originated with the male parent of HD568 (**Supplemental Table 5**). Bins with peak LOD in the confidence interval of each QTL were selected to represent those alleles. The genetic effects of these QTL ranged from –0.38 to 0.38 and accounted for 3.55–8.08% of the phenotypic variation in

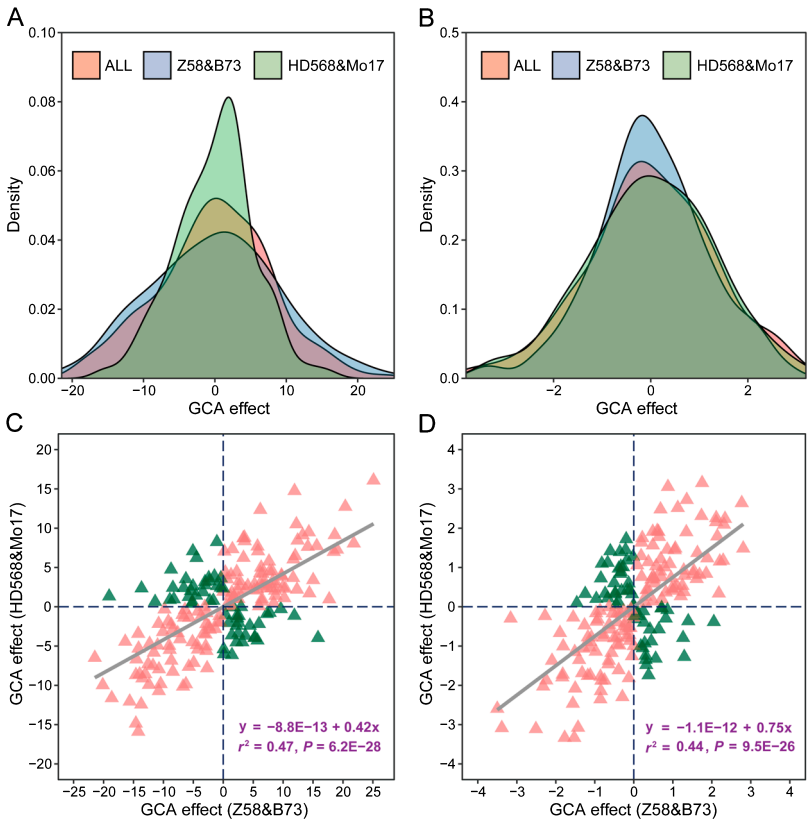

Fig. 2. Comparison of GCA effects estimated in different datasets. (A) and (B) Distribution of GCA effects of plant height and hundred-kernel weight estimated in each dataset. (C) and (D) Comparison of GCA effects of plant height and hundred-kernel weight calculated in Z58&B73 and HD568&Mo17 datasets. ALL: four inbred lines used as testers; Z58&B73: inbred lines Zheng58 and B73 assigned as testers; HD568&Mo17: inbred lines HD568 and Mo17 assigned as testers.

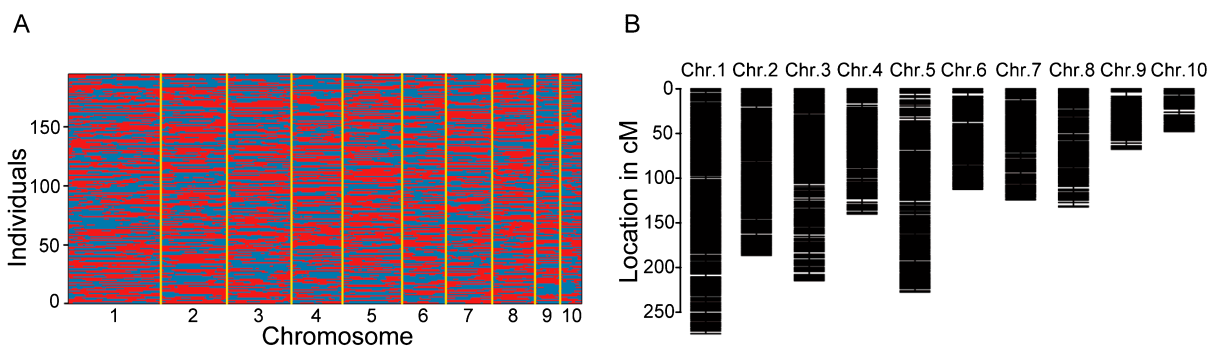

Fig. 3. Recombination bin map and genetic map of RIL population. (A) Recombination bin map of RIL population. Red: Zheng58 genotype; blue: HD568 genotype. (B) Genetic map of RIL population. Chr.: chromosome.

the GCA effects of HKW (**Supplemental Table 5**, **Supplemental Fig. 5**). Two RILs containing nine and zero favorable alleles, respectively, showed the highest (2.39) and lowest (–3.59) average GCA effects of HKW, respectively. In addition, the amount of difference between various aggregates of favorable alleles increased ranging from 0.4 to 5.98 as the accumulation of favorable alleles. However, only one RIL in 194 lines had nine favorable alleles with positive effects. Moreover, the average GCA effects decreased as the number reduction of favorable alleles. Most of the lines in the RIL population had 3–6 favorable alleles and their corresponding average GCA effects ranged from –0.81 to 1.07 (**Table 3**).

Discussion

Modern maize breeding generally involves the selection of commercially available inbred lines and the development of potentially valuable hybrid combinations. In the first stage, the evaluation of testcross hybrids was used to assess the

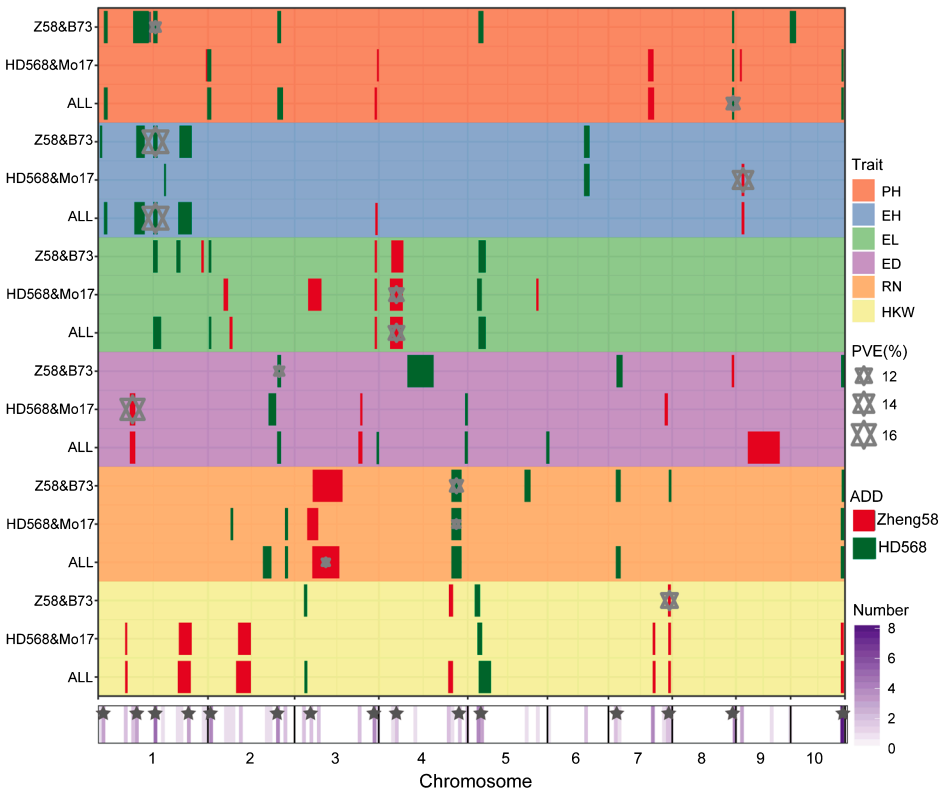

Fig. 4. QTL distribution of GCA of yield-relevant traits identified in each dataset. PH: plant height; EH: ear height; EL: ear length; ED: ear diameter; RN: row number; HKW: hundred-kernel weight. Hexagram size is commensurate with phenotypic variance explained by individual QTL (PVE). QTL with PVE >10 are shown. Boxes represent QTL position and confidence interval. Box width refers to confidence interval length in genomic regions. ADD: additive effect value. X-axis denotes genetic positions across maize genome (Mb). Heatmap under x-axis shows density of GCA-relevant QTL across genome. The asterisks denote the genomic locations that consist of at least three GCA related QTL. Z58&B73: inbred lines Zheng58 and B73 assigned as testers; HD568&Mo17: inbred lines HD568 and Mo17 assigned as testers; ALL: four inbred lines used as testers.

performance of new inbred lines in each heterotic group, aiming at estimating the GCA effects of candidate lines as it is vital to the selection of parental lines. Elite lines with high GCA estimates may increase the likelihood of generating superior commercial hybrids by crossing with excellent inbred lines derived from complementary heterotic groups. Hence, dissection of the genetic basis of the GCA effects greatly contributes to the improvement of parental lines and the development of superior hybrid combinations.

The GCA effects of each RIL were estimated using the phenotypic data of testcross populations constructed on the basis of different tester groups. There were significantly strong linear correlations between the GCA estimates based on two testers and those obtained using four testers (**Supplemental Fig. 2**). However, a previous study reported that the accuracy of the estimation of the GCA effects could be diminished by the use of only one or two lines from the complementary group as testers (Giraud *et al.* 2017). In contrast, the present study revealed that the GCA effects may be estimated with reasonable accuracy by using only two tester lines compared to using four testers (**Supplemental Fig. 2**). As for the different conclusion between the previous and present studies, it may be attributed to the different program of genetic mating design. The former study adopted the incomplete factorial design to produce experimental hybrids. However, the NC II design was implemented in the present study. Therefore, testcross trials on two tester lines may be practical for breeding programs constrained by limited budgets. In addition, the difference of GCA values of several individuals between datasets with two testers was obtained in this study (**Fig. 2C**, **2D**). This phenomenon was likely attributed to at least two factors. The first is that the comparatively large standard error of GCA effects of each RIL was likely obtained when the estimation based on only two hybrids derived from two testers. Secondly, these testers were derived from different heterotic groups and possessed distinctly heritable alleles that regulated and controlled a series of good characters. Consequently, the testcross hybrids with distinct performance were created by these testers (Liu *et al.* 2015a, 2015b, Wang *et al.* 2017, Zhang *et al.* 2016), and then GCA was defined as the average performance of a parent in hybrid combinations (Sprague and Tatum 1942), which would be varied by the hybrid performance (Lv *et al.* 2012). The output of the clustering analysis of the GCA effects between yield-related traits was consistent with the results of the

Table 2. Summary of genomic locations consisting of multiple QTL with overlapped genomic region

Location[a]	Chr.[b]	Interval[c] (Mb)	Physical length[d] (Mb)	No. of QTL	Integrated QTL[e]
LOC1	1	17.66–23.23	5.57	3	*qPH$_A$1*, *qPH$_Z$1-1*, *qEH$_A$1-1*
LOC2	1	74.73–77.15	2.42	2	*qHKW$_A$1-1*, *qHKW$_H$1-1*
LOC3	1	87.45–97.82	10.37	2	*qED$_A$1*, *qED$_H$1*
LOC4	1	104.81–123.22	18.41	3	*qEH$_A$1-2*, *qEH$_Z$1-2*, *qPH$_Z$1-2*
LOC5	1	150.78–157.91	7.13	5	*qEL$_Z$1-1*, *qEH$_A$1-3*, *qEL$_A$1*, *qPH$_Z$1-3*, *qEH$_Z$1-3*
LOC6	1	221.24–247.55	26.31	4	*qHKW$_A$1-2*, *qEH$_A$1-4*, *qHKW$_H$1-2*, *qEH$_Z$1-4*
LOC7	2	4.88–6.48	1.60	4	*qPH$_A$2-1*, *qPH$_H$2*, *qEL$_Z$2*, *qEL$_A$2-1*
LOC8	2	83.17–113.39	30.22	2	*qHKW$_A$2*, *qHKW$_H$2*
LOC9	2	189.22–194.63	5.41	4	*qED$_A$2*, *qED$_Z$2*, *qPH$_A$2-2*, *qPH$_Z$2*
LOC10	2	209.5–213.10	3.60	2	*qRN$_H$2-2*, *qRN$_A$2-2*
LOC11	3	28.65–31.34	2.69	2	*qHKW$_Z$3*, *qHKW$_A$3*
LOC12	3	50.75–61.24	10.49	4	*qRN$_H$3*, *qEL$_H$3-1*, *qRN$_A$3*, *qRN$_Z$3*
LOC13	3	179.01–180.32	1.31	2	*qED$_A$3*, *qED$_H$3*
LOC14	3	218.01–219.85	1.84	4	*qPH$_A$3*, *qEH$_A$3*, *qEL$_H$3-2*, *qEL$_A$3*, *qEL$_Z$3*
LOC15	4	35.76–62.54	26.78	3	*qEL$_H$4*, *qEL$_A$4*, *qEL$_Z$4*
LOC16	4	190.86–197.67	6.81	2	*qHKW$_A$4*, *qHKW$_Z$4*
LOC17	4	197.67–219.99	22.32	3	*qRN$_Z$4*, *qRN$_H$4*, *qRN$_A$4*
LOC18	4	234.86–237.69	2.83	2	*qED$_A$4*, *qED$_H$4*
LOC19	5	31.66–46.08	14.42	6	*qEL$_H$5-1*, *qHKW$_H$5*, *qPH$_Z$5*, *qEL$_A$5*, *qEL$_Z$5*, *qHKW$_A$5*
LOC20	6	100.69–111.25	10.56	2	*qEH$_Z$6*, *qEH$_H$6*
LOC21	7	23.69–30.58	6.89	3	*qRN$_A$7*, *qRN$_Z$7-1*, *qED$_Z$7*
LOC22	7	108.84–119.15	10.31	2	*qPH$_A$7*, *qPH$_H$7*
LOC23	7	121.35–123.7	2.35	2	*qHKW$_A$7-1*, *qHKW$_H$7-1*
LOC24	7	164.75–165.99	1.24	4	*qHKW$_Z$7*, *qHKW$_A$7-2*, *qHKW$_H$7-2*, *qRN$_Z$7-2*
LOC25	8	163.51–164.76	1.25	4	*qED$_Z$8*, *qPH$_A$8*, *qPH$_Z$8*, *qPH$_H$8*
LOC26	9	17.64–20.47	2.83	2	*qEH$_A$9*, *qEH$_H$9*
LOC27	10	140.00–140.97	0.97	6	*qRN$_A$10*, *qHKW$_A$10*, *qRN$_H$10*, *qHKW$_H$10*, *qED$_Z$10*, *qRN$_Z$10*
LOC28	10	143.7–144.75	1.05	2	*qPH$_A$10*, *qPH$_H$10*

[a] The name of genomic locations consisting of multiple QTL with overlapped genomic region.
[b] Chr.: the chromosome number.
[c] Interval: physical range of flanking markers.
[d] Physical length: physical distance between flanking markers.
[e] The name of each QTL consists of information regarding the abbreviation of trait, combination of testers (A: all testers; Z: Zheng58 and B73 were assigned as testers; H: HD568 and Mo17 were assigned as testers), and the chromosome number.

correlation analysis of GCA estimates among agronomic traits (**Fig. 1**, **Supplemental Fig. 3**). Thus, the same or associated genetic factors regulated the GCA effects of these traits. On the other hand, the GCA values for RN had a significant negative relationship with those for HKW (**Supplemental Fig. 3**). Balancing the genetic improvement of correlated target traits is essential for the selection of candidate lines with superior comprehensive performance in practical breeding programs. For this reason, the genetic architecture of the GCA effects requires further investigation so that breeding efficiency may be enhanced.

Previous research illustrated that GCA directly reflects breeding value of a parent line which include gene actions with additive, dominance, and epistatic effects (Reif *et al.* 2007, Wassimi *et al.* 1986). GCA variance comprises the variance components of additive and additive-by-additive interactions (Griffing 1956a, 1956b, Verhoeven *et al.* 2006). The GCA effect is heritable and may be transmitted from early to later generations (Bernardo 1991, Jenkins 1935, Lonnquist 1950). In the present study, the heritability of the GCA effects of each yield-relevant trait was comparatively high (**Table 1**). It can illustrate that the additive genetic effects held a large proportion of whole variance in comparison with the non-heritable components, which could be a stably heritable portion from early to advanced generations. Therefore, selection for the GCA effects of yield-related traits can be performed early in line development and this strategy may be used to exclude lines with low GCA effects from the breeding population. In this manner, early generation selection can effectively save more labor and time than selection process performed in later generations. However, the ratios of the variance of GCA and SCA for each agronomic trait were calculated according to the ANOVA which generally serves to identify optimal breeding strategies for hybrid selection (**Table 1**). If the magnitude of the SCA is markedly higher than those

Table 3. Favorable alleles identified for GCA of hundred-kernel weight using Zheng58, B73, HD568, and Mo17 as testers

Type	No. of alleles[a]		No. of lines[b]	Ave. GCA effects[c]	Combined group[d]	Ave. GCA effects[e]
	Positive	Negative				
1	9	0	1	2.39	13	2.09[a]
2	8	1	3	1.99		
3	7	2	9	2.09		
4	6	3	32	1.07	32	1.07[b]
5	5	4	52	0.35	52	0.35[c]
6	4	5	39	–0.15	39	–0.15[c]
7	3	6	34	–0.81	34	–0.81[d]
8	2	7	16	–1.48	16	–1.48[d]
9	1	8	7	–2.64	8	–2.76[e]
10	0	9	1	–3.59		

[a] The number of favorable alleles with positive effect.
[b] The number of lines with different genotype.
[c] The average effects of general combining ability for the individuals that contain different numbers of favorable alleles.
[d] Constructing the groups to perform the multiple comparisons. The datasets of type 1 to 3 were integrated into one group as these sets had a few individuals respectively. Similarly, the datasets of type 9 and 10 were combined into a group.
[e] The average effects of general combining ability for different groups. The different letters denote significant difference based on multiple comparison with method of Tukey test at significance level of 0.01.

of the GCA effects, then more resources are required to identify the best hybrid combinations, and the tester selection is crucial in the GCA evaluation of new inbred lines (Giraud *et al.* 2017). High ratios were obtained for almost every trait in the various datasets except for EL in the Z58&B73 dataset as the GCA variance of testers was very low. Large ratios imply that additive gene effects predominate whereas smaller ratios show that dominance and epistatic gene action effects prevail (Bhullar *et al.* 1979, Griffing 1956b). Several studies provided evidence illustrating that SCA effects usually explained lower than 20% of the phenotypic hybrid variation for the target traits. In practice, it may even be less than 10% (Parisseaux and Bernardo 2004, Schrag *et al.* 2006, 2009, 2010, Technow *et al.* 2014, Zhou *et al.* 2018). In this case, hybrid performance can be predicted on the basis of the GCA effects of both parents (Christie and Shattuck 2010, Gowda *et al.* 2012, Reif *et al.* 2007). This strategy could be useful in the selection of potential combinations for hybrid breeding. Earlier studies disclosed that the GCA effects vary among testers (Li *et al.* 2013, Lv *et al.* 2012). Nevertheless, the results of the present study indicated that inbred lines with comparatively higher GCA estimates may be selected according to the testcross regardless of the heterotic groups to which the testers belong.

For the linkage map constructed with the *ASMap* v. 1.0-4 package in R, the bin markers were evenly distributed on the genetic map (**Fig. 3**). Moreover, the scatterplot illustrated excellent collinearity between the physical and linkage maps in terms of the bin order (**Supplemental Fig. 4**). Therefore, this linkage map is suitable for QTL mapping of RIL populations. The positions and effects of the QTL for the GCA effects of yield-relevant traits differed among the three datasets as different inbred lines were used as testers in each case (**Fig. 4**, **Supplemental Tables 5–7**). However, several genomic locations consisting of overlapped confidence intervals between multiple QTL were identified among the three datasets (**Table 2**). Certain GCA-relevant loci were detected and may be fixed in this population regardless of the testers selected to estimate the GCA effects. In addition, previous study already illustrated that group-specific GCA QTL were already fixed in the discrepant heterotic group (Giraud *et al.* 2014, 2017), which could support the abovementioned point. The QTL for the GCA effects of PH, EH, and RN in the present study had been previously identified elsewhere (Qi *et al.* 2013, Zhou *et al.* 2018). It can imply that certain GCA QTL detected in multiple populations may be fixed during crop improvement and domestication (Chen *et al.* 2019, Liu *et al.* 2015c). Fixed and stable GCA QTL may be used in the development of markers to perform MAS for the selection of inbred lines with high GCA. This approach can accelerate the maize breeding process.

According to the MaizeGDB database, several candidate genes for the GCA effects of yield-relevant traits were detected in the present study. The candidate gene with gene model identification GRMAM2G403620 (*rs2*) located in the genomic region of LOC5 and was correlated with the GCA effects of PH, EH, and EL. This gene is expressed in the lateral primordia and encodes the Myb-domain protein (Timmermans *et al.* 1999). Its mutation results in the ectopic expression of the *knox* genes in the floral and leaf primordia and several defective phenotypes including leaf twisting, dwarfism, and aberrant vascular patterns (Schneeberger *et al.* 1998). Two candidate genes related to the GCA effects of EL and RN were detected within the LOC15 and LOC17, respectively. The gene model identification of the first candidate was GRMZM2G082087 (*opr8*). This gene is associated with jasmonic acid (JA) biosynthesis in maize. JA is a phytohormone that regulates plant adaptation to abiotic and biotic stress. It has biological activity in several events including reproductive development, root growth, and leaf senescence (Huang *et al.* 2017, Yan *et al.* 2012, 2014). The other candidate gene regulates RN and has the gene model identification GRMZM2G001541 (*KRN4*). This gene controls the expression level of *Unbranched3* (*UB3*) which is the SBP-box gene that regulates quantitative variation in RN (Liu *et al.* 2015d). *UB3* also participates in cytokinin biosynthesis and signaling. Mutation in *UB3* results in elevated cytokinin levels and increased row numbers (Du *et al.* 2017). In conclusion, QTL related to GCA effects may be closely correlated with genes regulating various traits *per se*. Further, improvement of these traits *per se* may enhance the GCA effects.

Integrating recurrent selection with MAS in GCA improvement may be preferable for maize breeding programs (Chen *et al.* 2019, Giraud *et al.* 2017, Lv *et al.* 2012, Qi *et al.* 2013). This approach can rapidly pyramid favorable alleles in fewer selection cycles, thereby saving labor, time, and costs. Development of various sequencing techniques has dramatically lowered genotyping costs. As a result, genomic selection (GS) that shortens cycle time and accelerates breeding may be implemented in modern maize breeding (Beyene *et al.* 2015, Crossa *et al.* 2014, Desta and Ortiz 2014, Guo *et al.* 2019, Jonas and de Koning 2013, Voss-Fels *et al.* 2019, Xu *et al.* 2020, Zhang *et al.* 2015). The use of GS to select lines with high GCA effects and predict hybrid values is a promising and powerful complementary strategy. Nevertheless, multiparental populations can still be used to elucidate the genetic basis of GCA. There are at least three points to illustrate its advantage: the first is that QTL detection in multiparental populations is more powerful and more effective than QTL detection using biparental populations (Bardol *et al.* 2013, Blanc *et al.* 2006, Foiada *et al.* 2015, Kump *et al.* 2011); the second point is that GCA and SCA components of hybrid values can be estimated without bias using multiparental lines that are developed without selection from the original populations and represent the gamut of genetic diversity for each population; the last is that multiparental populations can be designed to approximate or simulate the populations routinely constructed by breeders (Giraud *et al.* 2017). Finally, future research should aim to further elucidate the genetic basis of GCA and integrate multiple novel techniques with a view towards expediting the maize breeding process and developing the next generation of superior maize hybrids.

Author Contribution Statement

First, C. Huang and H. Wang proposed the original idea and supervised the research project. Second, experimental materials were provided by the lab of C. Huang. Phenotypic and genotypic data were investigated by X. Liu, and completed with the assistance of X. Hu, K. Li, Z. Liu, Y. Wu, and G. Feng. Third, the analyses of data were performed by X. Liu and H. Wang. Then, X. Hu, K. Li, Z. Liu, Y. Wu, and G. Feng provided some valuable suggestions. This paper was written by X. Liu and H. Wang with support from C. Huang. All authors discussed the results and contributed to the final manuscript.

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