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# Genetic Analysis and QTL Mapping of Parthenocarpy in *Cucumis sativus* L

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**Abstract** Breeding of cucumber cultivars with high parthenocarpy rate are the prerequisite that ensuring yield and quality under undesirable environment. The mixed major gene plus polygene inheritance model was used to analyze cucumber parthenocarpy trait in the six generations, including $P_1$, $P_2$, $F_1$, $BC_1$, $BC_2$ and $F_2$, derived from a cross between the highly parthenocarpic line DDX and low parthenocarpic line ZK. The major-effect quantitative trait locus (QTL) was identified by genome-wide comparison of single nucleotide polymorphisms (SNPs) between high- and low- parthenocarpy rate $F_2$ pools, and confirmed by traditional QTL mapping with genetic map. Genetic analysis showed that the genetic model E-2, mixed two additive-dominant-epistatic major genes and additive-dominant polygenes, is the best-fitting genetic model for cucumber parthenocarpy phenotype. A major-effect QTL, namely *par2.1*, were identified by the method of Δ(SNP_index). *par2.1* was confirmed by traditional markers based QTL mapping method with least likelihood (LOD) peak score of 12.6, genetic distance of 11.5cM and accounting for 26.6% of the total phenotypic variance. *par2.1* was narrowed down to a 765kb region through comparison of markers physical locations on chromosome 2. The major-effect QTL, *par2.1* on Chr2, for parthenocarpy identified by this study was not reported previously. Our findings shed light on the genetic architecture underlying cucumber parthenocarpy trait, and lay a solid basis for innovation of cucumber parthenocarpy germplasm and breed of new cucumber varieties with high parthenocarpy.

**Keywords** Cucumber (*Cucumis sativus* L.); Parthenocarpy; Genetic analysis; QTL; *par2.1*

Cucumber (*Cucumis sativus* L.) is an important vegetable crop cultivated under facility conditions. However, low temperature and weight light activity or absence of insect vectors can easily affect normal pollination and fertilization, resulting in reduced cultivation benefits (Jat et al., 2018). Cucumber varieties with high parthenocarpy rate can obtain stable seed setting rate under the conditions of open field cloudy and rainy day, low temperature in protected field, weak light and no insect vector, and the developed seedless fruit flesh is thicker, corresponding pulp cavity is smaller, taste is better than the conventional pollinated fruit, and market recognition is high (Chen and Cao, 1994). Therefore, it is of great significance to explore the molecular mechanism of cucumber parthenocarpy, obtain the key genes controlling cucumber parthenocarpy, and create strong parthenocarpy intermediate materials for breeding new parthenocarpy varieties.

Early genetic analysis showed that cucumber parthenocarpy changed continuously in isolated populations with typical quantitative traits. Cao et al. (1997) studied the genetic effects of female flower number, fruit number and yield of parthenocarpy cucumber and found that the inheritance of these three traits all met the additivity-dominance model, and the additive variance accounted for 24.80%, 34.75% and 34.31% of the total variance, respectively. Wang et al. (2008) found that "additive-dominance" model was the most suitable model for cucumber parthenocarpy, without epistatic effect. Yan et al. (2010) found that cucumber parthenocarpy rate was controlled by two pairs of major genes and dominant polygenes. Sun et al. (2006) detected 10 QTLs, including 5 main effect QTLs, that controlled the parthenocarpy of American processed whole female cucumbers. Yan (2009) constructed an $F_2$ population with weak parthenocarpy rate inbred line "6429" and strong parthenocarpy all-female cucumber inbred line "6457" as parents, and selected an ISSR marker linked to parthenocarpy rate of cucumber by using extreme parthenocarpy pool. Wu et al. (2016) identified a dominant QTL for parthenocarpy on Chr2 chromosome. Lietzow

et al. (2016) identified four heritable parthenogenetic QTLs, located on Chr5, Chr6 and Chr7 respectively, and their contribution to the parthenogenetic phenotype was related to the development stage of cucumber plants.

In this study, the parthenocarpy rate of a large number of cucumber germplasm resources were identified to screen out a weak parthenogenetic line ZK and a strong parthenogenetic line DDX, and the segregation population obtained by hybridization and selfing was used as the material to analyze the genetic law of cucumber parthenocarpy. Single plant pooling and high-throughput sequencing technology based on the extreme parthenocarpy rate of $F_2$ large population were used to screen the dominant QTLS for parthenocarpy, and the obtained QTLS were verified by conventional mapping techniques. These results provided the basis for fine QTL mapping and marker-assisted selection breeding of cucumber parthenocarpy.

## 1 Result and Analysis

### 1.1 Parthenocarpy rate distribution

The average parthenocarpy rate of strong parthenocarpic line DDX (P1) was 72.6%, while the low parthenocarpic line ZK (P2) was only 19.8% (Figure 1). The parthenocarpy rate of $F_1$ (DDX×ZK) was 33.2%, which was slightly lower than the mean of the parents, and close to the low parthenocarpic line ZK. The parthenocarpy rate of $BC_1$ was 70.1%, close to DDX, while that of $BC_2$ was 42.9%, higher than that of $F_1$. The average parthenocarpy rate of 166 $F_2$ plants was 46.8%, and the distribution of individual plants in the $F_2$ population was continuously biased normal (Table 1; Figure 2). The results showed that the parthenocarpy rate of this population was in line with quantitative genetic characteristics.

Figure 1 Development of unpollinated ovaries between DDX and ZK

Table 1 Frequency distribution and basic statistics of parthenocarpy rate in the six generations

| Progeny | The frequency distribution of parthenocarpy rate (%) | | | | | | | | | | Mean value (%) | Numbers |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0~10 | 10~20 | 20~30 | 30~40 | 40~50 | 50~60 | 60~70 | 70~80 | 80~90 | 90~100 | | |
| $P_1$ | - | - | - | 1 | 2 | 4 | 3 | 3 | 1 | 6 | 72.6 | 20 |
| $P_2$ | 3 | 7 | 7 | 3 | - | - | - | - | - | - | 19.8 | 20 |
| $F_1$ | 4 | 5 | 6 | 4 | 7 | 5 | - | - | - | - | 33.2 | 20 |
| $BC_1$ | 1 | - | 1 | 5 | 4 | 8 | 14 | 11 | 21 | 8 | 70.1 | 73 |
| $BC_2$ | 8 | 1 | 6 | 6 | 16 | 5 | 5 | 4 | 2 | - | 42.9 | 53 |
| $F_2$ | 25 | 13 | 13 | 24 | 31 | 17 | 13 | 11 | 9 | 10 | 46.8 | 166 |

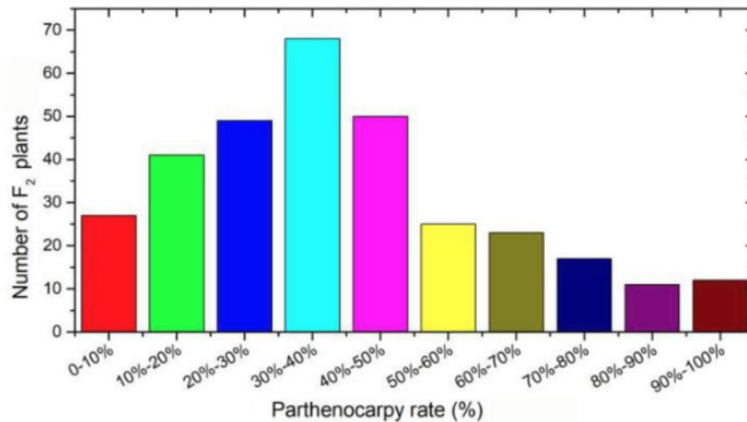

Figure 2 Frequency distribution of the parthenocarpy rate among the 323 $F_2$ plants

## 1.2 Genetic model of cucumber parthenocarpy rate

According to the calculation of AIC (Akaike information criterion) values and MLV (Max-likelihood value) of 23 models in Table 2, E-0 and E-1 model have the lowest AIC values of -411.44 and -413.44 respectively, which are determined to be the 2 optimal models. The suitability tests of E-0 and E-1 models were carried out respectively. Among them, 4 and 3 statistics of E-0 and E-1 model reached the significant level respectively. Therefore, the optimal inheritance of cucumber parthenocarpy fits the E-1 (2 pairs of additive dominant epistatic major genes and additive dominant polygenes) model.

Table 2 Estimation of max-likelihood value (MLV) and Akaike information criterion (AIC) value of the different inheritance models

| Model | Implication of model | MLV | AIC value |
|---|---|---|---|
| A-1 | 1 MG-AD | 186.35 | -364.69 |
| A-2 | 1 MG-A | 182.79 | -359.58 |
| A-3 | 1 MG-EAD | 83.32 | -160.65 |
| A-4 | 1 MG-AEND | 44.96 | -83.92 |
| B-1 | 2 MG-ADI | 213.03 | -406.05 |
| B-2 | 2 MG-AD | 194.18 | -376.36 |
| B-3 | 2 MG-A | 169.01 | -330.01 |
| B-4 | 2 MG-EA | 178.76 | -351.52 |
| B-5 | 2 MG-AED | 99.78 | -191.56 |
| B-6 | 2 MG-EEAD | 100.11 | -194.23 |
| C-0 | PG-ADI | 201.99 | -383.98 |
| C-1 | PG-AD | 189.95 | -365.91 |
| D-0 | MX1-AD-ADI | 201.98 | -379.97 |
| D-1 | MX1-AD-AD | 219.39 | -402.78 |
| D-2 | MX1-A-AD | 213.57 | -397.13 |
| D-3 | MX1-EAD-AD | 201.99 | -387.97 |
| D-4 | MX1-AEND-AD | 205.74 | -395.49 |
| E-0 | MX2-ADI-ADI | 214.72 | -411.44 |
| E-1 | MX2-ADI-AD | 214.72 | -413.44 |
| E-2 | MX2-AD-AD | 198.74 | -375.48 |
| E-3 | MX2-A-AD | 197.17 | 376.35 |
| E-4 | MX2-EA-AD | 190.19 | -364.39 |
| E-5 | MX2-AED-AD | 197.67 | -377.35 |

Note: MG: Major gene model; MX: Mixed major gene and polygene model; PG: Polygene model; A: Additive effect; D: Dominant effect; I: Interaction; N: Negative; E: Equal

### 1.3 Genetic parameter estimation under optimal genetic model

The $1^{st}$ order genetic parameters and $2^{nd}$ order genetic parameters are estimated according to the parameters. The first-order genetic parameters of E1 model were calculated (Table 3). The additive effect values of the two pairs of main genes and polygenes were both positive, and the dominant effect values of polygenes were also positive, indicating that the inheritance of cucumber parthenocarpy rate was mainly controlled by the additive effect of main genes and the additive-dominant effect of polygenes (Table 3). The $2^{nd}$ order genetic parameter calculation of E1 model showed that the heritability of the main gene of cucumber parthenocarpy rate was 22.6%, 93.9% and 88.52% in $BC_1$, $BC_2$ and $F_2$ generations, respectively, and the heritability of the main gene of $BC_2$ was higher. The heritability of polygene in $BC_1$, $BC_2$ and $F_2$ generations was 43.65%, 0.91% and 3.26%, respectively. Environment and other factors had a certain influence on the parthenocarpy, which was 33.73%, 5.16% and 8.22%, respectively. The results indicated that in the breeding of cucumber parthenocarpy, it was better to select characters in the early generations.

Table 3 Estimation of genetic parameters of parthenocarpy by E-1 model

| $1^{st}$ order parameter | Estimated value | $2^{nd}$ order parameter | Estimated value | | |
|---|---|---|---|---|---|
| | | | $BC_1$ | $BC_2$ | $F_2$ |
| m | 0.30408 | $\sigma_p^2$ | 0.01757 | 0.11496 | 0.07215 |
| da | 0.18968 | $\sigma_e^2$ | 0.00767 | 0.00105 | 0.00236 |
| db | 0.18968 | $\sigma_{mg}^2$ | 0.00397 | 0.10798 | 0.06387 |
| ha | 0.24579 | $\sigma_{pg}^2$ | 0.00767 | 0.00105 | 0.00236 |
| hb | 0.30256 | $h_{mg}^2$ (%) | 22.62 | 93.93 | 88.52 |
| ha/da | 1.29581 | $h_{pg}^2$ (%) | 43.65 | 0.91 | 3.26 |
| hb/db | 1.59511 | 1- $h_{mg}^2$ (%) - $h_{pg}^2$ (%) | 33.73 | 5.16 | 8.22 |

Note: m: Population mean; da: Additive effect of the first major gene; db: Additive effect of the second major gene; ha: Dominant effect of the first major gene; hb: Dominant effect of the second major gene; ha/da: Degree of dominance of the first major gene; hb/db: Degree of dominance of the second major gene; $\sigma_p^2$: Phenotypic variance; $\sigma_e^2$: Environmental variance; $\sigma_{mg}^2$: Major gene variance; $\sigma_{pg}^2$: Polygene variance; $h_{mg}^2$: Heritability of major gene; $h_{pg}^2$: Heritability of polygene

### 1.4 Identification major-effect QTL for parthenocarpy based on SNP_index

Illumina HiSeq sequencing instrument was used for whole gene resequencing of ZK, DDX, H_pool (Strong parthenocarpy Pool), and L_pool (Low parthenocarpy pool), obtaining 126 Gbp data with Q30 of more than 87.9% and an average sequencing depth of 46X (Table 4). High quality reads were compared to cucumber 9930_V2 reference genome for marker screening. Low quality sequencing markers were removed, and polymorphic SNP markers containing parental loci (heterozygous) were selected to obtain 779 215 SNP markers for association analysis of SNP_index. After SNP_index association and fitting regression analysis, the region above 99% quantile threshold (above the white line) was selected as the main QTL locus for parthenocarpy. Finally, only one region (15 589 893~17 206 312 bp) was obtained on Chr2 with the physical distance of ~1.62 Mb. This QTL was named as *par2.1* (Figure 3).

Table 4 Summary of sequencing data

| Sample | Clean_Reads | Q20 (%) | Q30 (%) | Sequencing depth | GC content (%) |
|---|---|---|---|---|---|
| ZK | 51457328 | 94.43 | 90.09 | 33 | 37.03 |
| DDX | 55249477 | 93.23 | 87.9 | 36 | 35.86 |
| L_pool | 93914419 | 93.41 | 88.21 | 64 | 36.03 |
| H_pool | 78432324 | 93.83 | 88.97 | 51 | 36.33 |

### 1.5 Validation of the major-effect QTL*par2.1* of cucumber parthenocarpy

In order to verify the accuracy of SNP_index based on localization results, seven polymorphic InDel and three polymorphic SNP markers were developed in this region. The DNA genotypes of 239 $F_2$ plants were identified by using the 10 markers mentioned above. The linkage group of *parth2.1* region was constructed with Joinmap4.0. The

total genetic distance was 29.7 cM, and the average genetic distance between markers was 2.97 cM. Combined with the parthenocarpy rate of each $F_2$ plant, a QTL was detected by R/QTL composite interval mapping between InDel44 and InDel01, with a peak LOD of 12.6, a genetic distance of 11.5 cM, a phenotypic contribution rate of 26.6% (Figure 4), and a physical distance of 1.22 Mb (Chr2: 15 123 339~16 345 864 bp). The results showed that the mapping results besed on SNP_index (Chr2: 15 589 893~17 206 312 bp) were consistent with the traditional QTL results, and the major-effect QTL*parth2.1* should be located on ~756 KB of Chr2 (Chr2: 15 589 893 bp~16 345 864 bp).

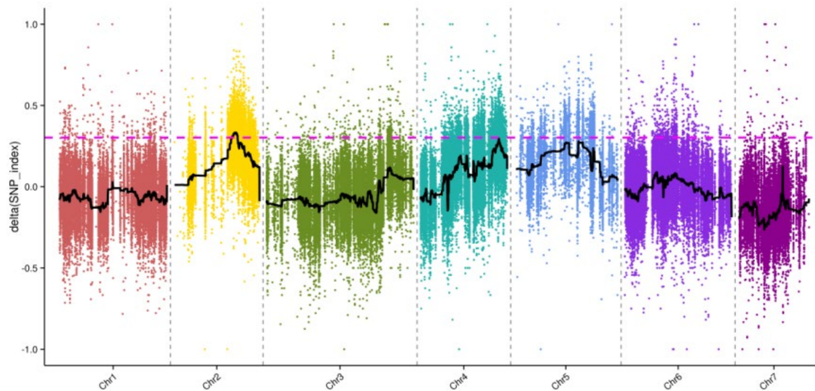


Figure 3 Identification major-effect QTL for parthenocarpy with Δ(SNP_index) method

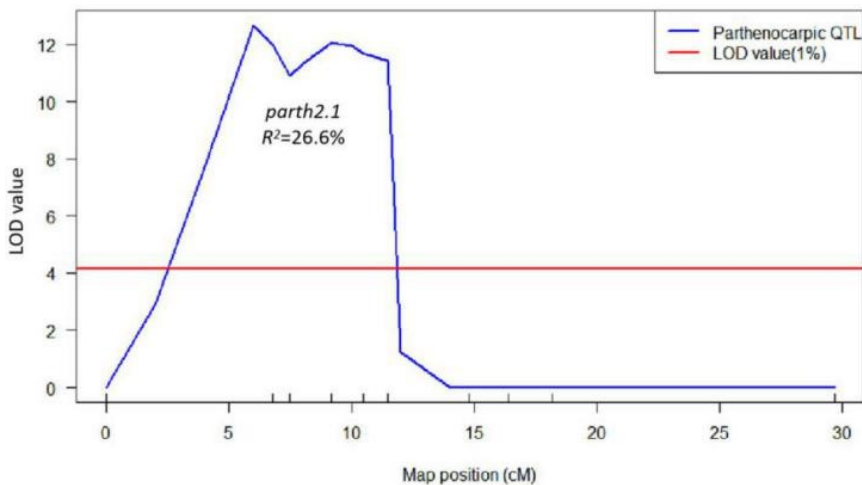


Figure 4 QTL mapping of parthenocarpy on cucumber chromosome

## 2 Discussion

In this study, the genetic model of two additive-dominant epistatic main genes+additive-dominant polygenes (E-1) was obtained for the first time through generation joint analysis, which was the same as the research results of Yan et al. (2010) on the genetic rules of cucumber parthenocarpy in monoecious cucumber plants. The quantitative traits controlled by both main genes and multiple genes were further identified. Due to the high heritability of the main genes, breeding and improvement of cucumber parthenocarpy is suitable for the early generations. In addition, the parthenocarpy genes in the strong parthenocarpic line DDX used in this study have additive effect, which is more suitable for the current situation of cucumber breeding based on heterosis utilization, and it is easy to achieve the purpose of artificial control of the strong parthenocarpy rate of $F_1$ hybrid.

Sun et al. (2006) carried out the QTL mapping of cucumber parthenocarpy earlier. By crossing 126 $F_{2:3}$ families of cucumber germplasm 2A and Gy8, 10 main QTLs with phenotypic contribution ranged from 16.5% to 22.5% were identified. However, RAPD and SCAR markers were mainly used in this study, and the specific physical location

of SCAR markers in cucumber reference genome could not be accurately estimated. Lietzow et al. (2016) used the same parents to construct a genetic map containing 192 SSR molecular markers, 7 linkage groups with a total length of 571.7 cM, and located 7 QTLs related to parthenocarpy. QTLs on Chr5 (*parth5.1*), Chr6 (*parth6.1*, *parth6.2*), Chr7 (*parth7.1*) can be detected repeatedly. Wu et al. (2016) identified seven QTLs for parthenocarpy in 145 $F_{2:3}$ populations derived from a cross between an all-female cucumber parthenocarpy inbred line EC1 and a non-parthenocarpy inbred line 8419 s-1, and only the major QTL *parth2.1* between SSR00684-SSR22083 (Physical location: Chr2: 3 255 765~6 234 833 bp) on Chr2 was detected in different seasons. Mixed analysis of isolated populations is one of the effective methods for gene mapping. As the cost of sequencing technology decreases, the combination of extreme single plant pool method and whole genome sequencing technology is currently a common method to quickly obtain the main effect QTL (Lu et al., 2014; Xu et al., 2018). In this study, a major QTL locus *par2.1* was obtained on Chr2 by using extreme $F_2$-based mixed plant sequencing and SNP_index method, and its physical location was between 15 589 893~17 206 312 bp of Chr2 (Figure 3). The accuracy of *par2.1* was further confirmed by constructing linkage map of Chr2 region and QTL mapping (Figure 4), and it was shortened to 756 kb (Chr2: 15 589 89~16 345 864 bp). The mapping results in this study did not coincide with the QTL loci reported by Wu et al. (2016) and Lietzow et al. (2016), indicating that *par2.1* in DDX is a new QTL locus for controlling parthenocarpy. Genetic effect analysis shows that the DDX parthenocarpy by two pairs of main effect genes and micro polygenic control together, and this study only appraisal to a primary effect QTL, may be due to this study sequencing of two mixing pool by 50 each extreme parthenocarpy phenotype of per plant, *par2.1* effect obscures the other lower effect the main effect of QTL and micro site identification, QTLs controlling parthenocarpy should be explored comprehensively by constructing genetic maps covering the whole genome of chromosomes. In addition, by comparing the physical locations, it was found that *par2.1* was at the end of Chr2, indicating a high probability of recombination and fine localization could be achieved by further screening the recombination individual plants.

## 3 Materials and Methods

### 3.1 Experimental material

All female strong parthenocarpy cucumber inbred line DDX and all female low parthenocarpy cucumber inbred line ZK were used as parents.

### 3.2 Statistics of parthenocarpy rate in the field

Field trials were conducted from March to July 2014. 20 DDX, 20 ZK, 20 $F_1$ (DDX×ZK), 73 $BC_1$ ($F_1$×DDX), 53 $BC_2$ ($F_1$×ZK) and 330 $F_2$ ($F_1$⊗) were sown in the same greenhouse in the experimental farm of College of Horticulture and Plant Protection, Yangzhou University, and the plant spacing was 40 cm. Each cucumber plant was numbered, and the female flowers to open the next day were clamped. After a week, the number of fruit that normally developed was recorded. To calculate the parthenocarpy rate of the fruits on the main stem of each plant from 1 to 20 nodes, the specific calculation method is as follows:

Parthenocarpy rate=Number of normally developed fruits per plant/Total number of fruits of single flower x 100%

### 3.3 Genetic analysis

Genetic effects were analyzed by referring to genetic model analysis of plant quantitative traits proposed by Gai and Wang (1998). Firstly, the optimal candidate model was selected according to the AIC minimum value, and then the suitability test of the candidate model was carried out. Finally, the distribution parameters of each component of the optimal model were calculated by the ordinary least squares.

### 3.4 Sequencing of extreme single plant mixed pool and identification of associated regions

Based on the statistical results of 330 $F_2$ parthenocarpy in spring 2014, 50 low and 50 strong parthenocarpy $F_2$ plants (with parthenocarpy rate less than 13%) and 50 strong parthenogenesis $F_2$ plants (with parthenocarpy rate greater than 70%) were selected, and DNA was extracted by CTAB method. Nanodrop one™ was used to determine the concentration, and the same amount of DNA was mixed into L_pool (Low parthenocarpy pool) and H_pool (Strong

parthenocarpy pool) respectively. According to Illumina standard library construction method, the resequencing libraries of DDX, ZK, L_pool and H_pool were constructed respectively. The qualified libraries were sequenced by Illumina HiSeq$^{TM}$ 2500. The original reads obtained by sequencing were filtered and used for subsequent association analysis (Zhu and Chen, 2015). SAMtools (Wysoker et al., 2009) and GATK (Mckenna et al., 2010) software kit was used to compare Clean Reads with cucumber 9930_v2 reference gene (http://cucurbitgenomics.org) to realize SNP (Single nucleotide polymorphism) detection. SNP genotype frequency differences between mixed pools were used to screen for candidate regions of the genome associated with phenotypes (Ma et al., 2018). With Δ(SNP_index) threshold determination method and fitting regression analysis (Hill et al., 2013), the region above threshold was determined as the QTL interval. The stronger the correlation between SNP and trait, the closer Δ(SNP_index) was to 1.

### 3.5 Construction of genetic linkage map and QTL analysis

The polymorphic SNP and InDel markers used in this study were derived from resequencing. A genetic linkage map of 239 $F_2$ plants was used to map QTLs based on the average parthenocarpy rate of $F_2$ plants. The genetic distance between markers was calculated by Joinmap4.0, and QTL was identified by composite interval mapping in R/qtl (Arends et al., 2010).

## Authors' contributions

CXH was the designer and principal of the project, guiding the experimental design. YYL, HM and HMX were the executors of this study. XXW completed the paper writing and experimental data analysis; QXH and XQ participated in the writing and revision of the paper. All authors read and approved the final manuscript.

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