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Tomato yellow leaf curl virus alters the host preferences of its vector *Bemisia tabaci*

SUBJECT AREAS:

VIRAL TRANSMISSION

ENTOMOLOGY

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VIRUS-HOST INTERACTIONS

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Bemisia tabaci, the whitefly vector of *Tomato yellow leaf curl virus* (TYLCV), seriously reduces tomato production and quality. Here, we report the first evidence that infection by TYLCV alters the host preferences of invasive *B. tabaci* B (Middle East-Minor Asia 1) and Q (Mediterranean genetic group), in which TYLCV-free *B. tabaci* Q preferred to settle on TYLCV-infected tomato plants over healthy ones. TYLCV-free *B. tabaci* B, however, preferred healthy tomato plants to TYLCV-infected plants. In contrast, TYLCV-infected *B. tabaci*, either B or Q, did not exhibit a preference between TYLCV-infected and TYLCV-free tomato plants. Based on gas chromatography-mass spectrometry (GCMS) analysis of plant terpene volatiles, significantly more β -myrcene, thymene, β -phellandrene, caryophyllene, (+)-4-carene, and α -humulene were released from the TYLCV-free tomato plants than from the TYLCV-infected ones. The results indicate TYLCV can alter the host preferences of its vector *Bemisia tabaci* B and Q.

B *emisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) originated in the tropics and subtropics¹ and has rapidly spread as a consequence of the international trade in flowers and other nursery stock. Because of its wide host range, rapid propagation, and superior ability to transmit virus, *B. tabaci* has become one of the most important pests in field crops worldwide². *B. tabaci* is a complex of numerous genetically distinct populations, previously referred to as biotypes and now recognized as cryptic species²⁻⁴. There are about 24 cryptic species of *B. tabaci*, including the two most widely distributed and invasive biotypes, B and Q, hereafter referred to as B and Q whiteflies⁵. *B. tabaci* is the only known vector of *Tomato yellow leaf curl virus* (TYLCV), which seriously reduces tomato production and quality. TYLCV is a single-stranded DNA (ssDNA) plant virus in the genus begomovirus, family Geminiviridae, that originated in the Middle East^{6,7}. Begomoviruses are transmitted by *B. tabaci* in a circulative manner and persist in the whitefly vector⁸⁻¹¹.

Plant-pathogen-vector systems are characterized by complex direct and indirect interactions^{12,13}. Virus-induced plant reactions can influence the behavior, physiology, and dynamics of insect vectors in plant populations, sometimes causing behavioral changes in the vectors that favor virus transmission¹⁴. For example, a recent paper by Stafford et al. (2011)¹⁵ demonstrated that plant-infecting viruses can directly alter vector feeding behavior. The authors found that *Tomato spotted wilt virus* infected male thrips spent more time feeding than that of non-infected thrips. However, modification of virus “behavior” within the host plant in response to attack by herbivorous insect vectors has been addressed only very recently¹⁶.

B. tabaci B was introduced into China in the mid-1990’s¹⁷, but the first incidence of TYLCV was not recorded until 2006 in Shanghai¹⁸, following the introduction and spread of the Q whitefly in 2003¹⁹. The virus has since spread throughout most of China²⁰, and the pattern of its spread has followed that of *B. tabaci* Q²¹. Researchers have hypothesized that the spread of TYLCV is closely related with the establishment and spread of *B. tabaci* Q^{20,22,23}. Our recent study showed that TYLCV is benefit *B. tabaci* Q, but harm *B. tabaci* B²². In addition, TYLCV infected weed (*Datura stramonium*) also affects the host preference and performance of *B. tabaci* Q²³. The results indicated that *B. tabaci* Q preferentially settled and oviposited on TYLCV-infected plants rather than on healthy plants. In addition, *B. tabaci* Q performed better on TYLCV-infected plants than on healthy plants²³.

Prior studies¹⁸⁻²¹ suggest a closer mutualistic relationship that TYLCV spreads following *B. tabaci* Q, rather than B. In the present study, we compared the host preference of B and Q whiteflies for TYLCV-infected and healthy (i.e., virus-free) tomato plants. We also compared the volatile compounds released by healthy and



Figure 1 | Symptoms of (A) healthy and (B) TYLCV-infected tomato plants. Photographs by Yong Fang.

TYLCV-infected tomato plants to explain the alteration in the host-selection behavior of *B. tabaci*. This information increases our understanding of TYLCV spread and outbreaks.

Results

Symptoms and viral load in TYLCV-infected and healthy tomato plants. Compared to the leaves of healthy tomato plants (Fig. 1A), the leaves of TYLCV-infected plants curl upward and are yellow and stunted (Fig. 1B). The viral load was significantly higher in the

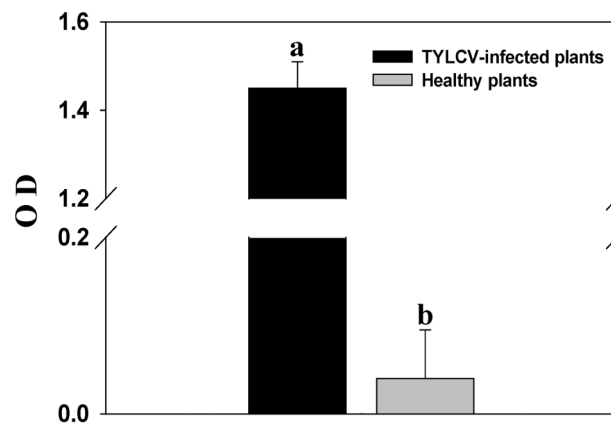


Figure 2 | Viral load in healthy and TYLCV-infected tomato plants.

TYLCV-infected plants than in the healthy plants ($F_{1, 22} = 45367.531$, $p < 0.0001$, Fig. 2).

Host selection. TYLCV-free B whiteflies (reared on virus-free plants) preferred to settle on TYLCV-free tomato plants over TYLCV-infected tomato plants (Fig. 3A) ($F_{1, 56} = 50.060$, $p < 0.0001$), whereas TYLCV-free Q whiteflies displayed the opposite behavior, settling in significantly greater proportions on TYLCV-infected plants than on TYLCV-free plants (Fig. 3C) ($F_{1, 56} = 40.856$, $p < 0.0001$). In contrast, the TYLCV-infected whiteflies of both *B. tabaci*

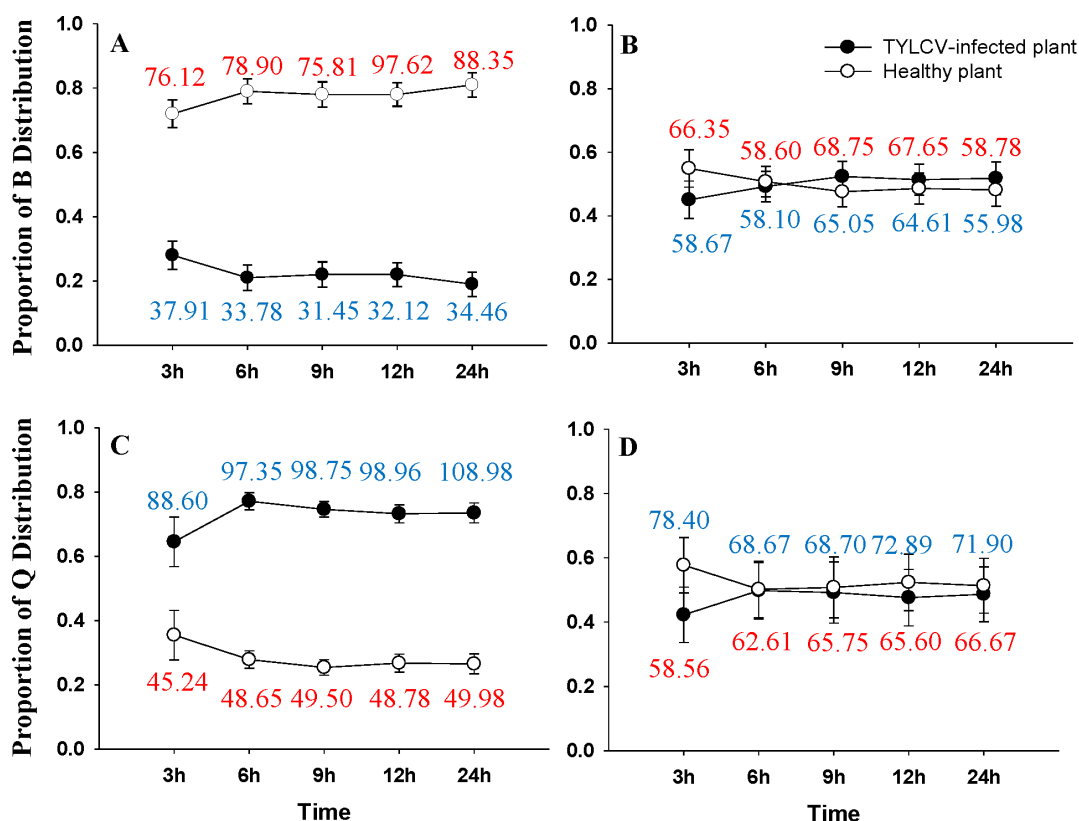


Figure 3 | Proportion of *B. tabaci* B and Q individuals that settled on healthy vs. TYLCV-infected tomato plants in a choice test. *B. tabaci* B and Q settling on TYLCV-free (open circles) versus TYLCV-infected tomato plants (closed circles) in two choice laboratory bioassays: (A) noninfected *B. tabaci* B; (B) TYLCV-infected *B. tabaci* B; (C) noninfected *B. tabaci* Q; and (D) TYLCV-infected *B. tabaci* Q. The numbers of adult whiteflies are also shown in the figure: the red number indicates the number of whiteflies on the healthy plant, and the blue number indicates the number of whiteflies on the TYLCV-infected plant.

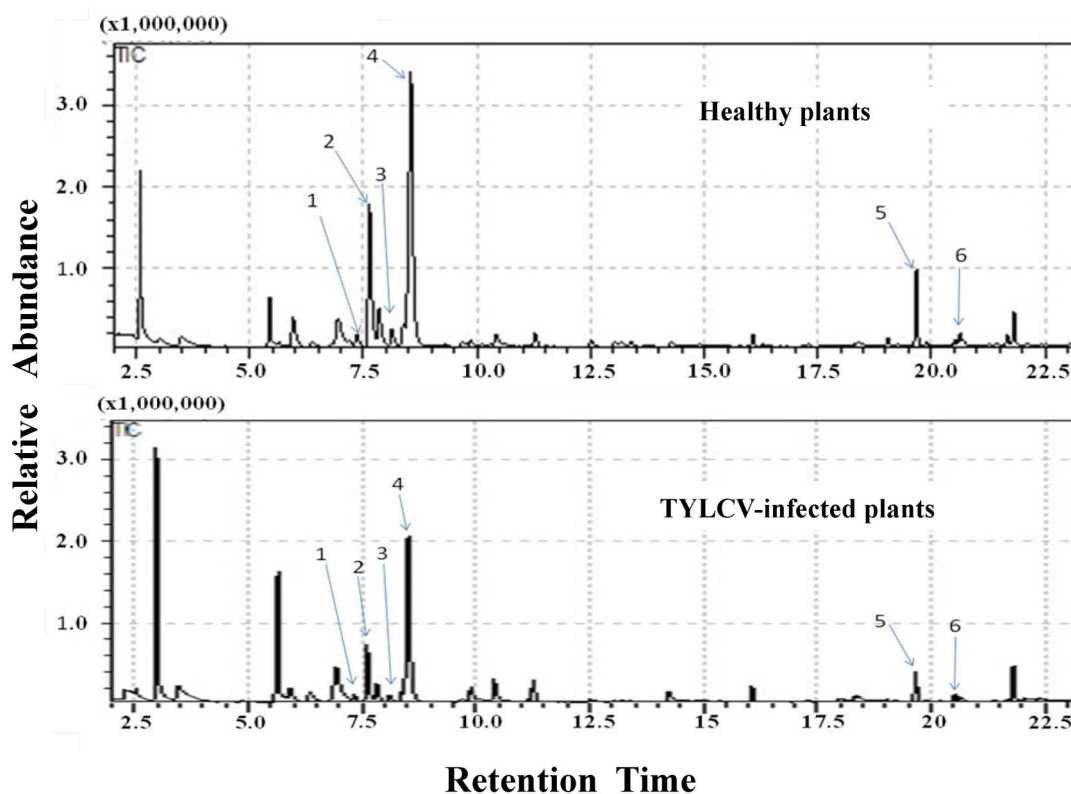


Figure 4 | Total ion chromatograms of volatile compounds released by the healthy tomato plants and the TYLCV-infected tomato plants. The identified compounds which have significant difference between the healthy tomato plants and the TYLCV-infected tomato plants: 1 = β -Myrcene, 2 = (+)-4-Carene, 3 = Thymene, 4 = β -Phellandrene, 5 = β -Caryophyllene, 6 = α -Humulene.

B and Q showed no preference between the TYLCV-free and the TYLCV-infected tomato plants (Fig. 3B, D) ($F_{1, 56} = 0.0001$, $p = 1.000$ and $F_{1, 56} = 0.0001$, $p = 1.000$, respectively).

Volatiles released by TYLCV-infected and non-infected tomato plants. GC-MS chromatograms of volatiles from the TYLCV-free and the TYLCV-infected tomato plants exhibited significant qualitative and/or quantitative differences in chemical composition (Fig. 4, Table 1). TYLCV-free tomato plants emitted significantly more β -Myrcene, Thymene, β -Phellandrene, Caryophyllene, and α -Humulene than did TYLCV-infected tomato plants. Furthermore, (+)-4-carene was detected only from TYLCV-free tomato plants (Fig. 4, Table 1).

Discussion

We have demonstrated that the host-preference of *B. tabaci* is shaped by: TYLCV infected and non-infected plants; TYLCV infected and

non-infected *B. tabaci* B and Q insects. TYLCV-free *B. tabaci* B were attracted to TYLCV-free tomato plants, whereas TYLCV-free *B. tabaci* Q were attracted to TYLCV-infected tomato plants. In addition, TYLCV-infected *B. tabaci* B and Q showed no preference between TYLCV-free and TYLCV-infected tomato plants. The host preferences we observed together with our recent studies^{20,22-24} to some extent explain why the spread of TYLCV in China appears to have been closely associated with the spread of *B. tabaci* Q rather than B.

The relationship of plant, pathogen, and vector insect includes direct and indirect interactions that can be beneficial or harmful, depending on the species²⁵⁻²⁷. Plant viruses infect their vectors and likely affect them in at least some instances. For example, the infection with TYLCV is harmful to *B. tabaci* B but beneficial to Q in performance, preference of feeding behaviors and virus transmission^{22,25-27}. In addition, relative to their TYLCV-free B feeding on cotton (a non-host for TYLCV), TYLCV-infected B exhibited

Table 1 | The peak areas ($\times 1000$) of volatile constituents released from TYLCV-infected and TYLCV-free tomato plants (mean \pm SE)

Compound	Retention time	TYLCV-infected plants	TYLCV-free plants	P-value
β -Myrcene	7.33	127.02 \pm 20.20 a	229.38 \pm 24.67 b	0.022
(+)-4-Carene	7.62	0 a	2411.89 \pm 482.71 b	0.008
Thymene	8.37	768.81 \pm 22.34 a	1240.71 \pm 296.90 b	0.036
β -Phellandrene	8.52	5607.10 \pm 217.80 a	9078.92 \pm 2135.28 b	0.038
β -Caryophyllene	19.67	227.70 \pm 14.90 a	375.22 \pm 80.17 b	0.024
α -Humulene	20.63	91.724 \pm 4.18 a	148.30 \pm 35.15 b	0.035
Butylated Hydroxytoluene	21.82	208.16 \pm 42.35 a	351.00 \pm 65.31 b	0.374
α -Phellandrene	7.83	1210.39 \pm 37.56 a	1742.48 \pm 678.30 a	0.097
α -Terpinene	8.12	254.93 \pm 5.89 a	376.00 \pm 133.86 a	0.076
γ -Butyrolactone	5.85	29.52 \pm 15.18 a	53.81 \pm 5.23 a	0.141
α -Pinene	5.93	623.57 \pm 5.65 a	979.58 \pm 267.56 a	0.052

Within each row, different letters indicate significant differences between virus-infected and virus-free plants ($P < 0.05$).



Figure 5 | Selection of healthy vs. TYLCV-infected tomato plants by *Bemisia tabaci*. Photographs by Yong Fang.

significant reductions in survival from egg to adult; fecundity; female and male body size, whereas TYLCV-infected Q showed only marginal reductions²². While Q performed better on TYLCV-infected tomato plants than on uninfected ones, whereas B performed better on uninfected tomato plants than on TYLCV-infected ones²². The transmission of plant viruses by insect vectors has been explored for over a century²⁸. Several studies have shown that virus-induced plant reactions shape the behavior, physiology, and dynamics of the insect vectors, sometimes inducing changes in the insect vectors that favor virus transmission^{25,27}.

Pathogen-induced plant responses may result from the changes of plant volatiles. Plant defensive compounds, specifically terpenoids, play a key role in mediating vector–pathogen mutualistic relationships. Our results show that TYLCV-free plants released significantly more β -myrcene, thymene, β -phellandrene, β -caryophyllene, and α -humulene than TYLCV-infected plants (Table 1, Fig. 4). This result is consistent with that of Luan et al. (2013)²⁹, who reported that elevation in terpenoid levels (via exogenous stem applications) reduced whitefly fitness and that suppression of terpenoid synthesis via gene silencing increased whitefly fitness. Previous study has shown that the monoterpene (+)-3-carene is associated with resistance of Sitka spruce (*Picea sitchensis*) to white pine weevil (*Pissodes strobi*) and that resistant trees contained significantly more (+)-3-carene than susceptible trees³⁰. In the current study, (+)-4-carene was detected in the TYLCV-free tomato plants but not in the infected ones. In addition, virus infection often alters plant morphology, nutrition, and color, and these changes could affect the host preference of herbivorous vectors. With respect to nutrition, virus infection can change the amino acid composition in the phloem or in other ways change the nutritional composition of the plant tissue^{13,31} and thereby change the host selection by herbivorous vectors^{31,32}. Further experiments are needed to investigate how virus-induced changes in plant volatiles, morphology, nutrition, and color affect host selection by *B. tabaci* B and Q.

The status of the vector (virus-infected or virus-free) can also influence its behavior in a way that benefits the virus. Recently, we used the electrical penetration graph (EPG) technique to study the effect of TYLCV infection of tomato plants on vector (*B. tabaci* B and Q) feeding behavior²⁴. Both *B. tabaci* B and Q appeared to find TYLCV-infected plants more attractive than healthy plants, probing them more quickly and exhibiting a greater number of feeding bouts. Interestingly, virus-infected whiteflies fed more often than virus-free insects, and they spend more time in feeding. Because vector salivation is essential for viral transmission, this virus-mediated alteration of behavior should directly benefit TYLCV fitness²⁴.

To our knowledge, we provide the first evidence for a direct effect of a plant virus (TYLCV) on its vector, and the resulting behavioral change in *B. tabaci* Q may have greatly contributed to the spread of TYLCV. However, the cause of the shift in host preference between TYLCV-infected and TYLCV-free *B. tabaci* is unknown and should be investigated.

Methods

Plant and insect rearing. *B. tabaci* B was originally collected from infested cabbage, *Brassica oleracea* L. cv. Jing feng 1, in Beijing, China in 2004³³. *B. tabaci* Q was collected from poinsettia, *Euphorbia pulcherrima* Wild. ex Klotz., in Beijing, China in 2009²⁰. B and Q whiteflies were reared on healthy tomato plants, *Solanum lycopersicum* Mill. cv. Zhongza 9, in separate, whitefly-proof screen cages in a greenhouse under natural lighting and controlled temperature ($26 \pm 2^\circ\text{C}$) for six generations. The purity of each *B. tabaci* was monitored by sampling 15 adults per generation using a molecular diagnostic technique, CAPS (cleavage amplified polymorphic sequence), and a molecular marker, mitochondrial cytochrome oxidase I genes (*mtCOI*)³⁴. Tomato plants were grown in insect-proof cages under natural lighting and ambient temperatures. Inoculation was mediated by *Agrobacterium tumefaciens* using a cloned TYLCV genome (GenBank accession ID: AM282874), which was originally isolated from tomato plants in Shanghai, China¹⁸. Similar plants were not inoculated with the virus. TYLCV-infected and uninfected tomato plants with the same height were selected for experiments. Healthy and TYLCV-inoculated tomato plants at the seven true-leaf stage were used to test for TYLCV with a triple antibody sandwich enzyme-linked immunosorbent assay (TAS-ELISA). A 0.1-g sample of leaf tissue (the third leaf from the top) was ground in 1 ml of extraction buffer. Each of the two treatments was represented by 12 replicates²². A kit supplied by Adgen Phytodiagnosics (Neogen Europe (Ayr), Ltd) was used, and the manufacturer's protocol was followed. Absorbance was read with a fluorescence microplate reader at 405 nm (SpectraMax M2e, Molecular Devices). The samples were considered positive for TYLCV when the mean optical density (OD) values at 405 nm were greater than three times those of the healthy controls.

Detection of TYLCV in insect and plant samples. Genomic DNA was extracted from individual whiteflies according to De Barro and Driver (1997)³⁵ and Frohlich et al. (1999)³. The nucleic acids from plants were extracted using the Plant Genomic DNA Extraction Kit (BioTeke Biotechnology, Beijing Co, Ltd). A ~410-bp TYLCV DNA fragment was amplified using the primer pairs C473 and V61³⁶. The resultant PCR products were electrophoresed on a 2.0% agarose gel in a $0.5 \times$ TBE buffer and visualized by Gelview staining.

Acquisition of TYLCV by *Bemisia tabaci* B and Q. Plants selected to be infected with virus were inoculated at the three true-leaf stage and were assumed to be infected with TYLCV when they developed characteristic leaf-curl symptoms; TYLCV was confirmed by molecular analysis as described in the previous paragraph. About 1000 newly emerged (0–8 h post-emergence) B or Q whiteflies were placed in small cages containing the TYLCV-infected tomato plants or healthy tomato plants for 72 h.

Two-choice bioassays to assess *Bemisia tabaci* B and Q preferences. We determined the proportion of TYLCV-infected and TYLCV-free whiteflies that settled on TYLCV-infected and virus-free plants after 24 h. Two tomato plants of similar size and with same number of true leaves (one infected with TYLCV and the other virus free) were placed in a cage (60 cm long, 55 cm wide, 70 cm high), and about 150 *B. tabaci* adults of one biotype (B or Q) and one infection status (virus-infected or not infected) were released into the center of the cage (Fig. 5). The position of the two plants in the cage was randomized, and cages were kept under laboratory conditions ($25 \pm 1^\circ\text{C}$, natural lighting). There were eight replicate cages for each of the four kinds of whiteflies: 1) infected B whiteflies ($n = 8$ replicates); 2) uninfected B whiteflies ($n = 8$); 3) infected Q whiteflies ($n = 8$); and 4) uninfected Q whiteflies ($n = 8$). The number of *B. tabaci* settling on each plant was recorded 3, 6, 9, 12, and 24 h after release.

Volatile collection and analysis. Leaf samples were collected from five TYLCV-free and five TYLCV-infected tomato plants. There were thus two treatments: volatile compounds released by the healthy tomato plants ($n = 5$ replicates); volatile compounds released by the TYLCV-infected tomato plants ($n = 5$). A 0.3-g quantity of leaf from each plant was subjected to gas chromatography–mass spectrometry (GCMS-2010, Shimadzu) using a VF-5MS column ($0.25 \text{ mm} \times 30 \text{ mm}$, J&W Scientific, Folsom, CA). The temperature program was as follows: an initial temperature of 50°C was held for 1 min, increased at $5^\circ\text{C}/\text{min}$ to 240°C , held for 2 min, and then increased at $30^\circ\text{C}/\text{min}$ to 300°C and held for 5 min. The injection temperature was 270°C . Relative quantification was based on the peak area of each component of the volatiles. The mass spectrometer was operated in EI ionization mode at 70 eV. The temperature of the source was kept at 200°C , and the interface temperatures were 280°C .

Data analysis. One-way ANOVAs were used to compare the viral load in the healthy and TYLCV-infected tomato plants. The host-settling preference between *B. tabaci* B and Q was tested by repeated-measures ANOVA. The concentration of individual volatile compounds emitted by TYLCV-free (healthy) versus TYLCV-infected



tomato plants was compared with a Student's *t*-test. Statistical analyses were performed with SPSS (version 13.0; SPSS Inc., Chicago, IL, USA).

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Author contributions

Y.J.Z., Y.F., H.P.P. designed the experiment. Y.F., X.B.S., G.C. performed the experiment. W.X., S.L.W., Q.J.W., Q.S., X.Y. contributed reagents/materials. Y.F., X.G.J., H.P.P., Y.J.Z. wrote the paper.

Additional information

Competing financial interests: The authors declare no competing financial interests.

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