Transcriptome Analysis of Hong Yang Kiwifruit in Response to *Bactrocera dorsalis* (Diptera: Tephritidae) Larval Feeding[1]

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Abstract The Oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), is a major pest of Hong Yang kiwifruit (*Actinidia chinensis* Planch cv. *chinensis*) grown in China. Our transcriptome analysis of the interaction between Hong Yang kiwifruit and *B. dorsalis* revealed numerous changes in gene expression level attributable to Oriental fruit fly feeding, resulting in the down-regulation of 112 genes and the up-regulation of 226 genes. Gene ontology analysis revealed that differential expression genes (DEGs) were mainly involved in biological processes (4,568; 56.28%), molecular function (2,297; 28.30%), and cellular components (1,251; 15.41%). By searching against the Kyoto Encyclopedia of Genes and Genomes Pathway database (KEGG), 258 DEGs were assigned to 51 KEGG pathways belonging to five main categories: metabolism (239, 92.64%), genetic information processing (10, 3.88%), organismal systems (5, 1.94%), cellular processes (3, 1.16%), and environmental information processing (1, 0.39%). The numbers of DEGs up-regulated were much higher than those down-regulated. Expression of genes involved in the secondary metabolism was detected, and several key genes showed differential expression. Our results suggest that *B. dorsalis* induced defense response of Hong Yang kiwifruit, including hypersensitive response and immunity triggered by either pathogen/microbe-associated molecular patterns or immunity effectors. Metabolic process was also adjusted to adapt to these responses. Our results provide extensive transcriptome information for *A. chinensis* and valuable clues for elucidating the mechanism of interaction between Hong Yang kiwifruit and *B. dorsalis*, and will facilitate molecular breeding for *Actinidia* crop plants.

Key Words kiwifruit, *Actinidia chinensis*, transcriptome, resistance

Hong Yang kiwifruit was the first red-flesh variety cultivated from *Actinidia chinensis* Planch var. *chinensis* in China and has since developed into an important horticultural crop. With the increasing land area under production for the crop, this commercially grown variety has been increasingly attacked by a variety of native and introduced pests (Hill et al. 2010, Manning et al. 2016). The Oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), ranks as one of the five most damaging and aggressive pest fruit flies in the world (Edwards et al. 2008, Follett et al. 2019). *Bactrocera dorsalis* was first reported in China in the 1980s, and it has since increased in numbers and range (Liu et al. 2016, Wei et al. 2017). The fly attacks a number of fruit crops, causing significant economic losses through direct

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fruit damage, fruit drop, and export limitations associated with quarantine restrictions (Clarke et al. 2005). The larval stages are the most damaging, feeding within the fruit.

The mechanisms of insect-infested tolerance in selected plants have been studied at the gene level. In general, plants possess two broad categories of responses to pest attack: (1) those triggered by pathogen/microbe-associated molecular patterns (PAMP), known as PAMP-triggered immunity (PTI); and (2) effector-triggered immunity (ETI) (Jones and Dangl 2006, Thomma et al. 2011). PTI recognizes molecular microbial determinants, and ETI detects injected effector proteins in the cytoplasm by resistance proteins and elicits further immunity. PTI is considered to be more general and more evolutionarily ancient than ETI, and a recent study speculates that PTI may be the more important defensive response in kiwifruit than ETI (Huang et al. 2013).

Studies on the insect–plant interaction give us the opportunity to examine the mechanism between insect and host, but studies on the response of Hong Yang kiwifruit to *B. dorsalis* are limited (Dubey et al. 2013, Hill et al. 2015). Therefore, we undertook this study investigate the response of Hong Yang kiwifruit to infestation by *B. dorsalis* using Illumina sequencing. Comparative transcriptome analysis was performed to explore the response at the molecular level and to establish a foundation for understanding the defense mechanisms in response to insect attacks.

Materials and Methods

Plant material and insect infestation. Twenty-four clonal *A. chinensis* Hong Yang scions were grafted onto clonal *A. deliciosa* rootstocks in 2012 at Houchang, China. Vines of 5-yr-old clonal *A. chinensis* (Chevalier) Liang & Ferguson were uprooted in 2018, potted in 30-l planter bags, pruned, and held in a shade house (50% shade) under ambient conditions. *Bactrocera dorsalis* were reared on apple (*Malus domestica* Borkh.) and pear (*Pyrus pseudopashia* Yu) in a controlled-environment room (25–28°C, 60–80% relative humidity) at Liupanshui Normal University.

Hong Yang fruit were infested by releasing approximately 25 *B. dorsalis* larvae per fruit in July 2018 into perforated polyethylene bags enclosing plants with 150-d-old fruit. The bags prevented *B. dorsalis* escape, while the perforations allowed for ventilation. Larvae of the same developmental stage were released into the respective bags containing the fruit plants, with three biological replicates. After 24 h, larvae were removed by brush, and the fruits were pruned and placed in liquid N_2 for eventual total RNA isolation. Three fruits from different insect-infested plants were mixed in equal proportion to serve as material for the insect-infested library (II), and three fruits excised from uninfested trees served as material for the insect-uninfested library (IU).

RNA isolation and sample preparation. Total RNA was extracted from frozen kiwifruit bark and sarcocarp using the TRIzol™ reagent (Thermo Fisher Scientific, Walham, MA) according to the manufacturer's protocol. In this study, the RNA integrity number values of these samples, confirmed using the RNA Nano 6000 Assay Kit of the Bioanalyzer 2100 System (Agilent Technologies, Santa Clara, CA),

were >6.3. The RNA was then subjected to Illumina sequencing using NEBNext® Ultra™ RNA Library Prep Kit (Illumina, Inc., San Diego, CA) at Novogene Bioinformatics Institute (Beijing, China). The mRNA-seq library was constructed for sequencing on the Illumina NovoSeq 6000 sequencing platform.

Sequence data analysis. To obtain high-quality clean read data for further analysis, the sequencing-received raw image data were filtered by masking low-quality reads, discarding the reads with adaptor, reads containing ploy-N, and removing the reads with more than 50% Q $\leq$ 20 bases. Only the reads with a Q20 percentage over 97% and N percentage less than 10% were marked as clean data.

The clean read data were isolated by mapping to the *A. chinensis* genome downloaded directly from the genome website (https://www.ncbi.nlm.nih.gov/genome/16401) (Wu et al. 2019). Index of the reference genome was constructed using Bowtie v2.2.3 (Langmead et al. 2009, Langmead and Salzberg 2012), and paired-end clean reads were aligned to the reference genome using TopHat v2.0.12 (Kim et al. 2013, Trapnell et al. 2012).

Sequence annotation, comparison, and functional classification. The expected number of fragments per kilobase per million mapped reads, or FPKM values, were used to normalize gene expression levels in the differentially expressed genes assay. Differential expression analysis was performed using the DESeq R package (1.18.0) to identify differentially expressed genes between the insect-infested and insect-uninfested samples (Anders and Huber 2010, 2013; Wang et al. 2010). The model based on negative binomial distribution and false discovery rate <0.05 was used to determine differential expression and the significance of gene expression differences, respectively.

To categorize reads by putative function, we utilized the Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) classification scheme. The GO enrichment analysis of differential expression genes (DEGs) was implemented by the GOseq R packages based on Wallenius noncentral hypergeometric distribution with the corrected $P < 0.05$ (Young et al. 2010). The KEGG Orthology-Based Annotation System software (Mao et al. 2005) was used to test the statistical enrichment of DEGs in KEGG pathways (http://www.genome.jp/kegg/) when the corrected $P < 0.05$.

Results

Mapping results of transcriptome sequence. To explore the response of *A. chinensis* to *B. dorsalis* larval feeding, the transcriptomes of fruits infested and not infested by *B. dorsalis* were compared. The total reads output of transcriptome sequencing were 50,846,857 in *B. dorsalis* of infested fruit (II) and 49,920,470 in the uninfested control (IU). The quality control and processing of data resulted in 49,048,281 (IU) and 49,902,681 (II) number of high-quality reads, respectively. After removing adaptors, ploy-N, and low-quality data, 49,242,874 (II) and 48,947,591 (IU) clean reads were obtained (Table 1). Eventually, totals of 7.34 G (IU) and 7.39 G (II) clean bases were generated.

For the mixed transcriptome, 92.85% (II) and 92.71% (IU) of the clean reads were mapped to the host *A. chinensis* genome, respectively. The ratio of the clean reads

Table 1. Mapping results of RNA-Seq reads aligned to the reference genome *A. chinensis*.

Sample Name	Insect-infested Fruit	Insect-uninfested Fruit
Total reads	50,846,857	49,920,470
High-quality reads	49,902,681	49,048,281
Clean reads	49,242,874	48,947,591
Clean bases (G)	7.39	7.34
Total mapped, n (%)	45,720,513 (92.85)	45,381,206 (92.71)
Multiple mapped, n (%)	1,742,437 (3.54)	1,726,712 (3.53)
Uniquely mapped, n (%)	43,978,076 (89.31)	43,654,494 (89.19)

multiple mapped to the host genome was <5%, while the ratio of the clean reads uniquely mapped to the host genome was >89%. To facilitate the access and use of the *A. chinensis* transcriptome sequencing data, the raw sequence data can be found in the National Center for Biotechnology Information GenBank (http://www.ncbi.nlm.nih.gov/genbank) with accession numbers SRR14134522, SRR14134523, SRR14134524, SRR14134525, SRR14134526, and SRR14134527.

Analysis of differentially expressed genes. All distinct reads were annotated through comparison with the reference genome of *A. chinensis*. The expression levels of these annotated genes were quantitatively analyzed as their corresponding reads copy number, and they were classified into up-regulation, down-regulation, and no significance change genes. Fig. 1 shows the distribution of differentially expressed genes, the upper regions with red and green dots reveal

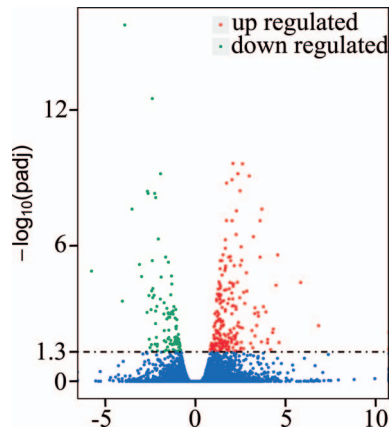

Fig. 1. Highly up- and down-regulated genes after infestation by *B. dorsalis* in comparison with controls.

those genes with markedly expression difference, and the lower regions with blue dots show those genes with no obvious expression diversity. The right-hand and upper regions with red dots display the up-regulated genes, in which 226 genes could be annotated. The left-hand and upper regions with green dots display the down-regulated genes, of which 112 genes could be annotated.

Expression level of each read was calculated and DEGs between insect-infested samples (II) and insect-uninfested samples (IU) were identified. Cluster analysis of reads of the two samples is shown in Fig. 2. Compared with the insect-uninfested sample (IU), the expression pattern of the insect-infested sample (II) was obviously different and presented the greater number of DEGs.

Functional classification of differentially expressed genes. Enrichment and classification of the DEGs were performed by searching GO and KEGG database. Within the overall category of biological process, GO classifications of biological process (201, 4.40%), metabolic process (161, 3.52%), and cellular process (137, 3.00%) characterized the most DEGs (Fig. 3). In the category of molecular function, molecular function (208, 9.06%), binding (135, 5.88%), and catalytic activity (125, 5.44%) characterized the most DEGs. Cellular component (111, 8.87%), cell (69, 5.52%), and cell part (69, 5.52%) were the most DEGs in the category of cellular component. Most of the GO terms in the category of biological process had more DEGs up-regulated by *B. dorsalis* treatment than those down-regulated, which was also seen in the cellular component category and the molecular function category.

A total of 8,116 DEGs were found in this study, of which 2,192 were down-regulated and 5,924 were up-regulated. Of the 6,551 DEGs identified in II and IU, the up-regulated DEGs (1,292) were greater than those down-regulated DEGs (273). Among the most differentially expressed genes, we identified DEGs participating in oxidoreductase activity (43, 0.53%), oxidation-reduction process (42, 0.52%), transferase activity (46, 0.57%), and hydrolase activity (38, 0.47%), which were all related to insect-infested resistance of plant. There also were many DEGs participating in biosynthesis of secondary metabolites, carbohydrate metabolism, and genes of plant immunity system PTI and ETI.

The 258 DEGs could be assigned to 51 pathways that belonged to five main categories, including metabolism (239, 92.64%), genetic information processing (10, 3.88 %), organismal systems (5, 1.94%), cellular processes (3, 1.16%), and environmental information processing (1, 0.39%) (Table 2). Of the 51 identified pathways, 9 pathways with up-regulated (117, 87.31%) and down-regulated (17, 12.69%) DEGs were identified between II and IU, and 14 DEGs identified in 13 pathways were down-regulated and 110 DEGs identified in 29 pathways were up-regulated. The KEGG classification showed that the number of up-regulated DEGs was greater than the number of down-regulated DEGs.

The category with the largest number of DEGs was metabolism, wherein metabolic pathways (74, 30.96%), photosynthesis (28, 11.72%), biosynthesis of secondary metabolites (24, 10.04%), photosynthesis - antenna proteins (21, 8.79%), and carbon metabolism (11, 4.60%) pathways were found to be most represented. Other pathways influenced by insect-infested treatment included environmental adaptation and translation (Table 2).

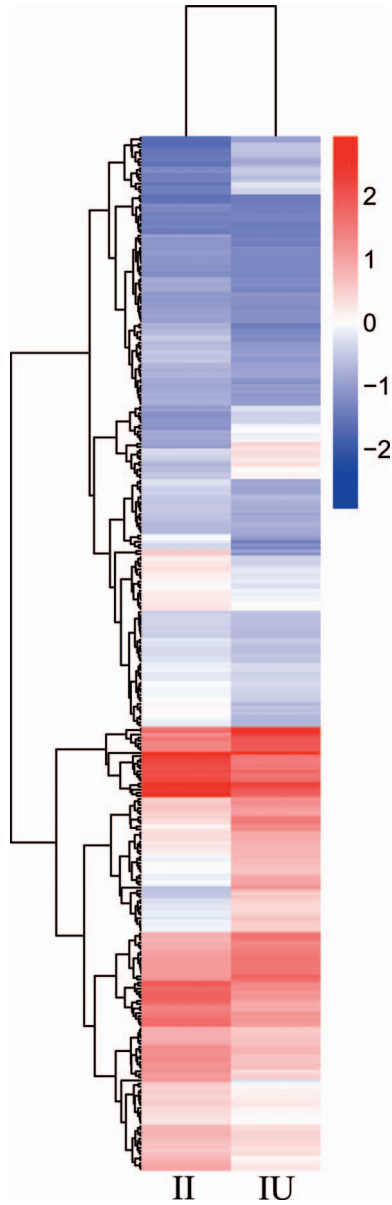

Fig. 2. Cluster of significant differentially expressed genes generated from the insect-infested and insect-uninfested *A. chinensis*. The FPKM (expected number of fragments per kilobase of transcript sequence per millions base pairs sequenced) values of reads were used for hierarchical cluster analysis. Expression levels are shown by different colors: the redder the higher expression, and the bluer the lower.

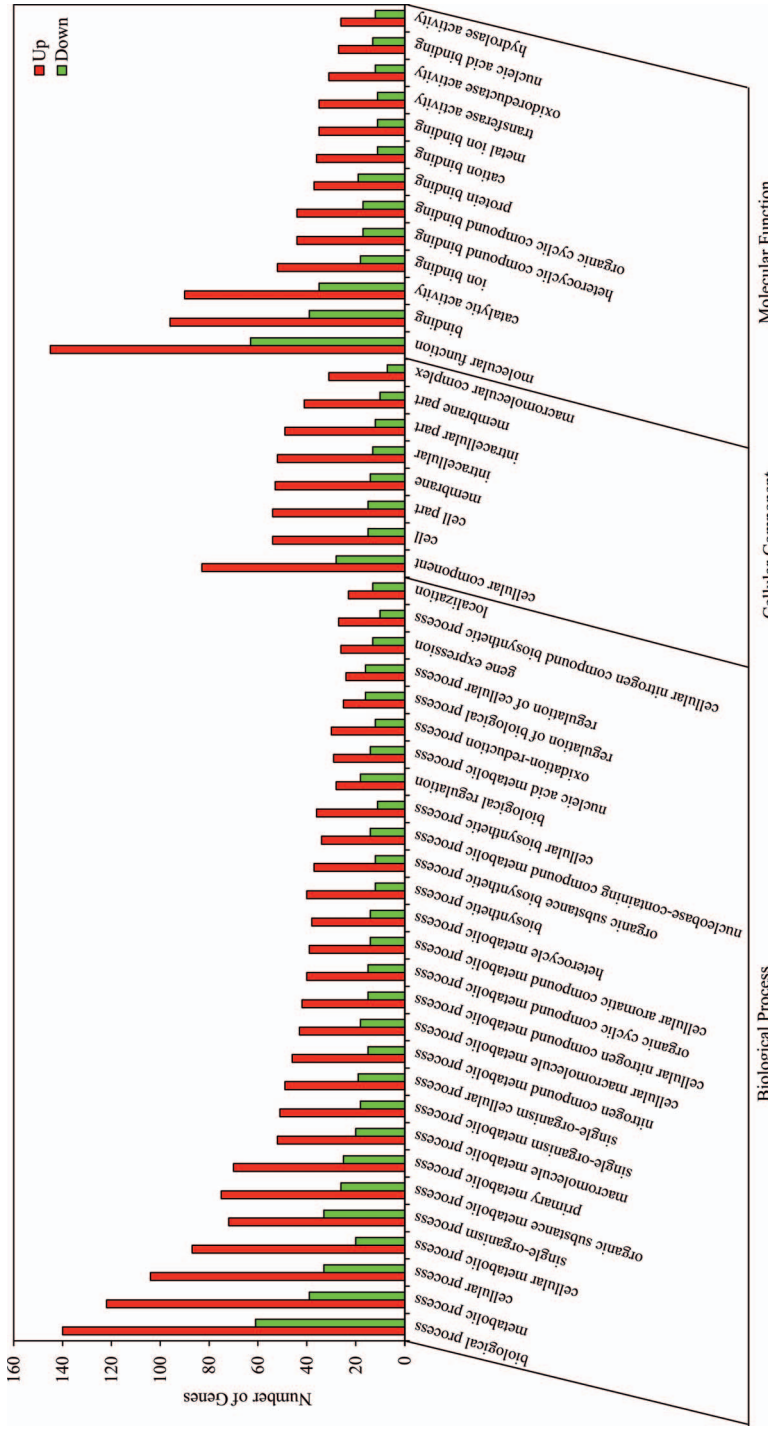

Fig. 3. Gene Ontology classification of differentially expressed genes.

Table 2. The enriched differential progress top 25.

Category I	Category II	Pathway	Pathway ID	DEGs* With Pathway Annotation (258)		All Genes With Pathway Annotation (7,179)
				up	down	
Organismal systems	Environmental adaptation	Circadian rhythm - plant	ath04712	3	0	36
		Plant–pathogen interaction	ath04626	2	0	164
Genetic information processing	Translation	RNA transport	ath03013	2	2	169
Metabolism	Amino acid metabolism	Glycine, serine, and threonine metabolism	ath00260	3	0	69
		Tyrosine metabolism	ath00350	1	1	40
	Carbohydrate metabolism	Glycolysis/gluconeogenesis	ath00010	5	1	112
		Fructose and mannose metabolism	ath00051	5	0	52
		Glyoxylate and dicarboxylate metabolism	ath00630	5	0	63
		Pentose phosphate pathway	ath00030	5	0	54
		Starch and sucrose metabolism	ath00500	4	1	188
		Amino sugar and nucleotide sugar metabolism	ath00520	4	0	122

Table 2. Continued.

Category I	Category II	Pathway	Pathway ID	DEGs* With Pathway Annotation (258)		All Genes With Pathway Annotation (7,179)
				up	down	
	Energy metabolism	Photosynthesis	ath00195	28	0	77
		Photosynthesis - antenna proteins	ath00196	21	0	22
		Carbon fixation in photosynthetic organisms	ath00710	6	0	69
		Oxidative phosphorylation	ath00190	3	0	162
		Nitrogen metabolism	ath00910	2	0	42
	Global and overview maps	Biosynthesis of secondary metabolites	ath01110	22	2	995
		Carbon metabolism	ath01200	10	1	243
		Biosynthesis of amino acids	ath01230	5	1	255
		Metabolic pathways	ath01100	67	7	1,861
	Lipid metabolism	Fatty acid degradation	ath00071	1	1	40
	Metabolism of cofactors and vitamins	Porphyrin and chlorophyll metabolism	ath00860	5	0	45

Table 2. Continued.

Category I	Category II	Pathway	Pathway ID	DEGs* With Pathway Annotation (258)		All Genes With Pathway Annotation (7,179)
				up	down	
		Ubiquinone and other terpenoid-quinone biosynthesis	ath00130	2	0	32
	Metabolism of other amino acids	Taurine and hypotaurine metabolism	ath00430	0	2	14
		Glutathione metabolism	ath00480	2	0	93

* DEGs, differential expression genes.

Discussion

For plants, the tolerance to biotic stresses is a defense response involving multiple genes, and our understanding of the fruit–pest/pathogen interaction can assist in efforts to improve the characters of fruits. In this study, we reported the transcriptomic changes of Hong Yang fruit in response to *B. dorsalis* larval feeding. Although fine-scale feeding does not cause extensive physical damage to the plant, 338 differentially expressed genes were identified to be involved in response to *B. dorsalis* infestation. We found a greater number of up-regulated genes than the down-regulated genes in these infested fruits. Comparable results were recently reported with transcriptomic analyses of other fruit–pest/pathogen interactions, for example, kiwifruit–bacterial canker (*Pseudomonas syringae* pv. *actinidiae* Takikawa, Serizawa, Ichikawa, Tsuyumi, and Goto) (Wang et al. 2018), kiwifruit–lataniae or palm scale (*Hemiberlesia lataniae* (Signoret)) (Hill et al. 2015), and cotton (*Gossypium hirsutum* L.)–aphids and whiteflies (Dubey et al. 2013).

DEGs participated in oxidoreductase activity, oxidation-reduction process, transferase activity, or hydrolase activity that are necessary to host defense to biotic and abiotic stresses (Dubey et al. 2013, Hill et al. 2015). We found that 26 DEGs and 16 DEGs participated in response to stimulus and response to stress, respectively. Only one DEG was identified to be involved in innate immune response.

KEGG annotations of 258 DEGs showed that most of the DEGs were related to metabolism processes, especially metabolic pathways (Table 2). We determined that the majority of DEGs were assigned to the categories of global and overview maps (117, 45.35%), followed by energy metabolism (60, 23.26%), carbohydrate metabolism (33, 12.79%), and other functions. After infestation by *B. dorsalis*, the DEGs related to amino acid metabolic pathways of glycine-, serine-, threonine-, alanine-, aspartate-, glutamate-, arginine-, and proline-related reads were enriched (Table 2), consistent with data in aphid-infested cotton plant during the initial phase of infestation (Dubey et al. 2013). Photosynthesis has been found to be up-regulated in response to *B. dorsalis* attack, a result much different with the photosynthesis in response to water and drought stress (Berger et al. 2007, Janda et al. 2014) which may be caused by the difference between biotic and abiotic stresses.

Secondary metabolites play important roles in regulation of plant defense to different kinds of pests (Bennett and Wallsgrove 1994, Wang et al. 2018). Plants deploy numerous secondary metabolites to facilitate interaction with biotic and abiotic factors (Elsayed 2011). To that end, we found 24 DEGs that were identified to be involved in biosynthesis of secondary metabolites. Expression changes of genes involved in biosynthesis of terpenoid backbone (1, 0.42%), ubiquinone and other terpenoid-quinones (2, 0.84%), and flavonoid biosynthesis (1, 0.42%) indicated that secondary metabolites may play an important role in interaction between kiwifruit and *B. dorsalis*.

Expressions of genes involved in PTI and ETI were detected, and several important genes showed differential expression in *B. dorsalis*–infested kiwifruit. *Rboh* is involved in the plant–pathogen interaction pathway, and PAMP-induced genes showed increased expression in *B. dorsalis*–infested kiwifruit. This gene

regulates the production of reactive oxygen species (Kurusu et al. 2015, Wang et al. 2018) which induces hypersensitive response.

WRKY transcription factors, one of the largest families of transcriptional regulators found exclusively in plants, are involved in diverse biotic stresses (Eulgem 2005, Naoumkina 2008). In our study, we found only one *WRKY* gene (*WRKY19*) was up-regulated in response to infestation by *B. dorsalis*. *WRKY19* was also found to be up-regulated in transgenic *Arabidopsis* induced by abiotic stresses (Niu et al. 2012).

These results have provided a foundational database of knowledge of the interaction between Hong Yang kiwifruit and its pest the Oriental fruit fly, *B. dorsalis*. The extensive transcriptome information for *A. chinensis* and for its response to infestation to *B. dorsalis* will facilitate future genetic and genomics studies as well as molecular breeding for *Actinidia* crop plants.

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