Differential transcriptome analysis and identification of genes related to resistance to blight in three varieties of *Bambusa pervariabilis* × *Dendrocalamopisis grandis*

Fengying Luo [Equal first author, 1] , **Xinmei Fang** [Equal first author, 1] , **Han Liu** [2] , **Tianhui Zhu** [1] , **Shan Han** [1] , **Qi Peng** [1] , **Shujiang Li** [Corresp. 1, 3]

[1] College of Forestry, Sichuan Agricultural University, Chengdu, Sichuan Province, China

[2] Ganzi Institute of Forestry Research, Kangding, Sichuan Province, China

[3] National Forestry and Grassland Administration Key Laboratory of Forest Resources Conservation and Ecological Safety on the Upper Reaches of the Yangtze River, Chengdu, Sichuan Province, China

Corresponding Author: Shujiang Li
Email address: 14087@sicau.edu.cn

Background. *Bambusa pervariabilis* × *Dendrocalamopisis grandis* is a fast-growing bamboo that is widely introduced in southern China and has great economic and ecological benefits. In recent years, a blight of *B. pervariabilis* × *D. grandis* caused by *Arthrinium phaeospermum* has led to much branch damage and even death of entire bamboo forests.

Methods. To screen for resistance genes in *B. pervariabilis* × *D. grandis* , transcriptome sequencing technology was used to compare the gene expression profiles of different varieties of *B. pervariabilis* × *D. grandis* with variable resistance and the same varieties under different treatments. The Clusters of Orthologous Groups of Proteins (COG) database; the Gene Ontology (GO) database; and the Kyoto Encyclopedia of Genes and Genomes (KEGG) databasehe were used to annotate and analyse the differentially expressed genes.

Results. A total of 26157 and 11648 differentially expressed genes were obtained in the different varieties after inoculation with *A. phaeospermum* and the same varieties after inoculation *A. phaeospermum* or sterile water, respectively. There were 23 co upregulated DGEs and 143 co downregulated DEGs in #3 and #8, #6 and #8, #6 and #3. There were 50 co upregulated DGEs and 24 co downregulated DEGs in the same varieties after inoculation *A. phaeospermum* or sterile water. The results showed that many genes involved in cell wall composition synthesis, redox reactions and signal transduction were significantly different after pathogen infection. Twenty-one candidate genes for blight resistance, such as *pme53*, *cad5*, *pod*, *gdsl-ll* and *Myb4l*, were found. The qRT-PCR results were consistent with the sequencing results, verifying their authenticity. These results provide a foundation for the further exploration of resistance genes and their functions.

1 Differential transcriptome analysis and identification

2 of genes related to resistance to blight in three

3 varieties of *Bambusa pervariabilis* ×

4 *Dendrocalamopisis grandis*

5   Fengying Luo[1†], Xinmei Fang[1†], Han Liu[2], Tianhui Zhu[1], Shan Han[1], Qi Peng[1], Shujiang Li[1,3]

6   [1] College of Forestry, Sichuan Agricultural University, Chengdu, Sichuan Province, Sichuan,

7   P.R. China

8   [2] Ganzi Institute of Forestry Research, Kangding Sichuan, China

9   [3] National Forestry and Grassland Administration Key Laboratory of Forest Resources

10   Conservation and Ecological Safety on the Upper Reaches of the Yangtze River.

12   Corresponding author:

13   Shujiang Li

14   Huimin road, Chengdu, Sichuan Province, 611130, China

15   E-mail address: 14087@sicau.edu.cn

16   †Fengying Luo and Xinmei Fang contributed equally to this work

17 Abstract

18   **Background.** *Bambusa pervariabilis* × *Dendrocalamopisis grandis* is a fast-growing bamboo

19   that is widely introduced in southern China and has great economic and ecological benefits. In

20   recent years, a blight of *B. pervariabilis* × *D. grandis* caused by *Arthrinium phaeospermum* has

21   led to much branch damage and even death of entire bamboo forests.

22   **Methods.** To screen for resistance genes in *B. pervariabilis* × *D. grandis*, transcriptome

23   sequencing technology was used to compare the gene expression profiles of different varieties of

24   *B. pervariabilis* × *D. grandis* with variable resistance and the same varieties under different

25   treatments. The Clusters of Orthologous Groups of Proteins (COG) database; the Gene Ontology

26   (GO) database; and the Kyoto Encyclopedia of Genes and Genomes (KEGG) databasehe were

27   used to annotate and analyse the differentially expressed genes.

28   **Results.** A total of 26157 and 11648 differentially expressed genes were obtained in the

29   different varieties after inoculation with *A. phaeospermum* and the same varieties after

30   inoculation *A. phaeospermum* or sterile water, respectively. There were 23 co upregulated DGEs

31   and 143 co downregulated DEGs in #3 and #8, #6 and #8, #6 and #3. There were 50 co

32   upregulated DGEs and 24 co downregulated DEGs in the same varieties after inoculation *A.*

33   *phaeospermum* or sterile water. The results showed that many genes involved in cell wall

34   composition synthesis, redox reactions and signal transduction were significantly different after

35   pathogen infection. Twenty-one candidate genes for blight resistance, such as *pme53*, *cad5*, *pod*,

36   *gdsl-ll* and *Myb4l*, were found. The qRT-PCR results were consistent with the sequencing results,

37   verifying their authenticity. These results provide a foundation for the further exploration of

38   resistance genes and their functions.

Introduction

40   *Bambusa pervariabilis × Dendrocalamopisis grandis* is the product of the female parent *B.*

41   *pervariabilis* and the male parent *D. grandis*. After 12 years of hybrid cultivation, four excellent

42   hybrid bamboo varieties, #3, #6, #8 and #30, were identified. *B. pervariabilis × D. grandis* is

43   widely used in papermaking and returning farmland to forest, which also promotes the

44   construction of ecological barriers in the middle and lower reaches of the Yangtze River.

45   However, in recent years, it has been found that hybrid bamboo shoot blight caused by

46   *Arthrinium phaeospermum* (*Arthrinium phaeospermum* (Corda) M.B. Ellis) infection has

47   become an important disease in the cultivation area of hybrid bamboo (Ma et al., 2003). After the

48   *B. pervariabilis × D. grandis* is susceptible to the disease, the brown spots first appear near the

49   bamboo nodes, and then the spots gradually expand. When the disease spots surround the

50   bamboo nodes, the branches above the disease spots turn yellow and the bamboo leaves fall off,

51   and the whole plant dies in serious cases. It was found that the shoot blight of hybrid bamboo

52   caused damage to more than 3000 hm^2 of hybrid bamboo, causing large economic losses (Zhu et

53   al., 2009) and greatly threatening the process of returning farmland to forest and the construction

54   of ecological barriers in the Yangtze River Basin.

55   The resistance to plant pathogens varies among plant-resistant and plant-susceptible varieties,

56   which is important for the analysis of pathogenic mechanisms and the utilization of disease-

57   resistant resources. At present, the research in this field in China and abroad mainly focuses on

58   the following aspects: selecting representative varieties to compare and analysing the cell

59   histological changes of different resistant and susceptible varieties after infection (Pereira et al.,

60   2013; Carisse et al., 2000; Vallad, Subbarao, 2008), studying enzymes related to disease

61   resistance (Lin et al., 2014), and revealing the related mechanism of resistant and susceptible

62   varieties through omics technology (Collinge et al., 2008). In particular, the development of

63   omics technology in recent years has guided further exploration of the interaction between plants

64   and pathogens. The resistance of *B. pervariabilis × D. grandis* was induced by pre-inoculation of

65   toxin protein, and then the gene expression before and after induction was compared by

66   transcriptome sequencing. It was found that redox proteins, phenylalanine ammonia lyase and S-

67   adenosine-L-methionine synthase were highly expressed. These results may indicate that these

68   genes are related to the disease resistance level of *B. pervariabilis × D. grandis*. (Peng et al.,

69   2020). Li et al. Separated and identified the proteins before and after *B. pervariabilis × D.*

70   *grandis* infected with *A. phaeospermum* by TMT (tandem mass tag)-labeled quantitative protein

71   technology combined with LC-MS/MS (mass spectrometry), and screened the related proteins

72   that may be involved in *B. pervariabilis × D. grandis* disease resistance, including cinnamyl

73   alcohol dehydrogenase, a protein homologous to maize cysteineprotease 1 and other proteins (Li

74   et al., 2019). After infection with *Candidatus* Liberibacter asiaticus*,* there were differences in the

75   expression of genes related to transcription factors, secondary metabolism, receptor kinase and

76   hormone signal transduction in the resistant and susceptible varieties of grapefruit (Wang et al.,

77   2016). Through subsequent verification, two genes related to the resistance of *C. Liberibacter*

78   *asiaticus, DMR6-like* and *NPR1-like,* were predicted.

79   The transcriptome refers to the collection of all transcription products in cells at a certain

80   developmental stage or under certain physiological conditions and can be used to study gene

81   expression, gene function, and structure. In recent years, this technology has been widely used to

82   screen plant disease-resistance-related substances and identify key differentially expressed genes

83   (Liu et al., 2014; Li et al., 2014; Salgado et al., 2014). Researchers used transcriptome

84   sequencing technology to sequence susceptible and resistant tomatoes after inoculation with

85   *Cladosporium fulvum* and verified the important role of the *Cf* gene in tomato resistance to leaf

86   mould caused by *C. fulvum* (Zhang et al., 2020). Guijiao 9 and Williams are resistant and

87   susceptible to *Fusarium oxysporum*, respectively. After the transcriptome data of Guijiao 9 and

88   Williams infected with *F. oxysporum* were analysed, it was found that genes related to defence-

89   related metabolite synthesis, such as Nb-LRR protein, calmodulin-binding protein and

90   phenylpropanoid biosynthesis genes, were significantly upregulated in resistant varieties, which

91   confirmed the important role of plant hormone regulation and defence-related gene activation in

92   banana disease resistance (Sun et al., 2019).

93   Past forest surveys showed that there were differences in the disease index among different

94   resistant varieties of *B. pervariabilis × D. grandis*. Therefore, by comparing the transcriptome

95   data from different varieties, differentially expressed genes related to disease resistance in *B.*

96   *pervariabilis × D. grandis* could be found, which is the key to disease resistance breeding and

97   biological control of *B. pervariabilis × D. grandis* shoot blight. In this study, transcriptome

98   sequencing technology was used to analyse the transcriptome of different varieties of *B.*

99   *pervariabilis × D. grandis* under different treatment conditions. The gene expression profiles of

100   *B. pervariabilis × D. grandis* between different resistant and susceptible varieties and the gene

101   expression profiles of the same varieties under different treatments were compared to obtain

102   candidate genes for shoot blight resistance. To lay the foundation for further exploration of

103   resistance genes, the functional genes identified here are important genetic resources to improve

104   the resistance of *B. pervariabilis × D. grandis* to shoot blight based on gene technology.

Materials and methods

Plant materials and pathogens.

107   *A. phaeospermum* was stored at the Laboratory of Plant Pathology, Sichuan Agricultural
108   University, and one-year-old *B. pervariabilis × D. grandis* from varieties #3 (moderately
109   resistant), #6 (resistant), and #8 (susceptible) (Li et al., 2018) were planted in the greenhouse
110   near the fifth teaching building of Chengdu Campus of Sichuan Agricultural University.

Inoculation and disease investigation.

112   The preserved hyphae were inoculated on PDA medium, and then inoculated on sugarcane juice
113   medium (sugarcane juice 30-100g/L, magnesium sulfate heptahydrate 1.0g/l, potassium
114   dihydrogen phosphate 1.0g/L, agar 20g/L) and cultured under the dark condition of 25 ℃ for 10
115   days. The spores were washed with sterile water, and the conidial suspension was diluted to 10^6
116   cfu/ml. The 30 one-year-old hybrid bamboos of varieties #3, #6 and #8 were inoculated, with
117   three biological replicates. Five plants of the three varieties inoculated with sterile water were
118   used as controls. The incidence rate and disease index were calculated after 25 days of
119   inoculation.

120    $I(\%) = D / T \times 100$

121   where I, D and T are the incidence, the number of diseased plants and the number of total plants,
122   respectively.

123   The disease classification standard was as follows: 0: no wilt; Level 1: less than 25 % withered
124   branches; Level 2: 25 % – 50 % (including 25 % and 50 %) withered branches; Level 3: 50 % –
125   75 % withered branches (including 75 %); and Level 4: more than 75 % withered branches (Fang.
126   1998).

127    $DI = \Sigma (DN \times L) / (TN \times M) \times 100$

128   where DI is the disease index, DN is the disease level, L is the number of plants at each level,
129   TN is the total number of diseased plants, and M is the maximum disease incidence.

RNA extraction and high-throughput sequencing.

131   RNA was extracted from the shoots of hybrid bamboos (#3, #6 and #8) inoculated with sterile
132   water or pathogens for 25 days. The #3, #6 and #8 *B. pervariabilis × D. grandis* treatment
133   groups inoculated with *A. phaeospermum* were named J3, J6 and J8 respectively, and the #3, #6
134   and #8 *B. pervariabilis × D. grandis* treatment groups inoculated with sterile water were named
135   J3, J6 and J8 respectively. The concentration and purity of the total RNA were determined by an
136   Agilent 2100 analyser (Agilent, Santa Clara, CA, USA). We constructed RNA-Seq libraries
137   following the Illumina protocol for mRNA-sequencing sample preparation. The cDNA library

138 was sequenced using an Illumina HiSeq2000 platform by Shanghai Baipu Biotechnology Co.,

139 Ltd. After processing the original data as previously described in Peng (Peng et al., 2020),

140 Specifically hisat2 (Kim, Langmead & Salzberg, 2015) was used to map reads to the reference

141 genome (Peng et al., 2013)

142 (https://bioinformatics.psb.ugent.be/plaza/versions/plaza_v4_monocots/organism/view/Phyllosta

143 chys+edulis#collapsePanel) and reference transcriptome (GenBank Accession in NCBI:

144 txid38705). Genomic sequences and information of *Bambusa pervariabilis × Dendrocalamopisis*

145 *grandis* were deposited in the NCBI database (BioProject accession number: PRJNA545783,

146 BioSample accession number: SAMN11928018, TSA accession number: GJJA00000000,

147 accessible with the following link: https://www.ncbi.nlm.nih.gov/bioproject/545783).

148 **Differentially expressed gene analysis.**

149 gene expression calculations were performed according to the FPKM method (Peng et al., 2020).

150 The software DEGseq (Wang et al.,2010) was used to conduct differential expression analysis

151 among samples. A false discovery rate (FDR) $\leq$ 0.05 and fold change (FC) > 2 were used as the

152 standards to identify the differentially expressed genes (DEGs) among different treatments.

153 DEGs annotation were collected as previously described in Peng (Peng et al., 2020). Specifically,

154 the DEGs were annotated by NCBI's nonredundant protein sequence database (NR) (Deng et al.,

155 2006), the Clusters of Orthologous Groups of Proteins (COG) database (Tatusov, Galperi &

156 Natale, 2000), the Gene Ontology (GO) database (Ashburner et al., 2000), and the Kyoto

157 Encyclopedia of Genes and Genomes (KEGG) database (Kanehisa et al., 2004). Each database

158 reference link is ftp://ftp.ncbi.nih.gov/blast/db/, http://www.ncbi.nlm.nih.gov/COG/,

159 http://www.geneontology.org/, http://www.genome.jp/kegg/.

160 **Real-time PCR validation.**

161 Primers (Table S1) were designed for 5 randomly selected genes and 21 disease resistance

162 candidate genes. Primer Premier 5.0 (Premier Biosoft International, Palo Alto, CA, USA) was

163 used for qRT-PCR primer design. The primers were synthesized by Tsingke Biotechnology Co.,

164 Ltd. GAPDH was used as an internal reference gene. TransScript® Green One-Step qRT-PCR

165 SuperMix (trans, China) was used for qRT-PCR. The q-PCR system consisted of the following:

166 10uL qPCR SuperMix, 0.4uL RT/RI Enzyme Mix, 0.4uL Passive Reference Dye, 7.4uL ddH2O,

167 0.4 uL F/R, 1 uL RNA. The qPCR was performed: at 45°C for 5 min, 94°C for 30s, 94°C for 5s,

168 and 60°C for 30s. The third step and the fourth step were repeated 40 times, and a dissolution

169 curve was added at the final step. Each treatment group underwent qPCR three times, and the

170 average value was calculated.

171 # Results

172 **Statistics of potted disease experiments performed in the greenhouse.**

173   *B. pervariabilis × D. grandis* of three different resistant varieties grew well before inoculation

174   with pathogens, and there were no symptoms such as withered branches and leaves (Fig.1). 25

175   days after inoculation with the pathogen, #6 the leaves of the high disease resistant variety were

176   slightly chlorotic, #3 the middle resistant variety had brown spots at the bamboo joints, some

177   leaves withered and turned yellow, #8 the susceptible variety had brown spots at the bamboo

178   joints, the branches gradually withered, most of the leaves turned yellow and fell off, and some

179   diseased plants finally died. The incidence and disease index of #3, #6 and #8 hybrid bamboos

180   inoculated with *A. phaeospermum* were statistically analysed (Table 1). The results showed that

181   the incidence was 23.3 %, 7.8 % and 85.6 % and the disease index was 12.2, 2.8 and 62.8,

182   respectively, for hybrid bamboos #3, #6 and #8. According to statistical analysis, #3, #6, and #8

183   hybrid bamboo inoculated with *A. phaeospermum* had significantly different incidences and

184   disease indices (Fig. 2). According to the resistance standard for shoot blight (Li. 2013), hybrid

185   bamboos #3, #6, and #8 showed moderate resistance, full resistance and susceptibility to shoot

186   blight caused by *A. phaeospermum*.

187   **RNA sequence analysis and annotation results between *A. phaeospermum* infection or**

188   **sterile water inoculation in the same varieties.**

189   Comparative analysis of transcriptomic expression data was determined between *A.*

190   *phaeospermum* infection and sterile water inoculation in the same varieties. The results showed

191   that 4387, 6316 and 4159 DEGs were obtained in the #3, #6 and #8 varieties, respectively.

192   Among the 4387 DEGs, 1925 were upregulated and 2462 were downregulated in variety #3 after

193   inoculation. Among the 6316 DEGs found for variety #6 after inoculation, 3148 were

194   upregulated and 3168 were downregulated. Of the 4159 DEGs found for variety #8 after

195   inoculation, 2609 were upregulated and 1550 were downregulated (Table 2).

196   In total, 394 DEGs were shared across the three varieties (Fig. 3); of them, 50 DEGs were

197   upregulated in the three varieties, and 24 DEGs were downregulated (Table S2).

198   In the COG database, 1513, 2776, and 1421 DEGs were found for in the same varieties

199   (including #3, #6 and #8) after inoculation with *A. phaeospermum* or sterile water, respectively.

200   In the comparisons between #3, #6, and #8 inoculated *A. phaeospermum* or sterile water, genes

201   were annotated to 25 functional classifications in the GO database (Fig. S1), including

202   "translation", "ribosomal structure and biogenesis", "translation", "replication, recombination

203   and repair", "posttranslational modification, protein turnover, chaperones", "signal transduction

204   mechanisms" and others. In #6 B. pervariabilis × D. grandis inoculated with *A. phaeospermum*

205   and sterile water, 333, 333 and 316 DEGs were annotated to the classifications "signal

206   transduction mechanisms", "translation" and "replication, recombination and repair" in the COG

207   database (Fig. 4).

208   In the GO database, 3506, 5674 and 3414 DEGs of #3, #6 and #8 *B. pervariabilis × D. grandis*

209 were annotated to the cell component, molecular function and biological process categories after
210 inoculation with *A. phaeospermum* or sterile water, respectively (Fig. S2). For #6 hybrid bamboo
211 inoculated with pathogens, the DEGs were mainly enriched in "metabolic process", "cellular
212 process", "single-organism process" and "response to stimulus" in the biological process
213 classification. In the cell component classification, they were mainly enriched in "cell", "cell
214 part", "organelle" and "membrane", and in the molecular function classification, they were
215 enriched in "binding", "catalytic activity", "transporter activity" and "nucleic acid binding
216 transcription factor activity" (Fig. 5).
217 In the KEGG enrichment analysis of DEGs in #3, #6 and #8 *B. pervariabilis × D. grandis*
218 inoculated with *A. phaeospermum* or sterile water, 791, 1505 and 782 DEGs were annotated to
219 121, 125 and 118 metabolic pathways, respectively (Fig. S3). In the KEGG enrichment analysis
220 of the 791 DEGs from hybrid bamboo #3 inoculated with pathogens, most DEGs were enriched
221 in "phenylpropanoid biosynthesis". In the KEGG enrichment analysis of the 1505 DEGs from
222 hybrid bamboo #6 inoculated with pathogens, most DEGs were enriched in "carbon metabolism",
223 followed by "phenylpropanoid biosynthesis" and "starch and sucrose metabolism". In the
224 enrichment analysis of the 782 DEGs from hybrid bamboo #8 inoculated with pathogens, most
225 DEGs were enriched in the "phenylpropanoid biosynthesis" pathway (Fig. 6).
226 **RNA sequence analysis and annotation results between different varieties inoculated *A.***
227 ***phaeospermum* or sterile water.**
228 Firstly, the differentially expressed genes of #6 and #3, #6 and #8, #8 and #3 of the three
229 varieties after inoculation with sterile water were compared (Table S3), and then after
230 inoculation with *A. phaeospermum*, the comparison of #6 and #3, #6 and #8, and #8 and #3
231 excludes the difference after inoculation sterile water. When comparing DEGs from different *A.*
232 *phaeospermum* inoculated varieties, 18401, 18496 and 4070 DEGs were identified between
233 varieties #6 and #3, #6 and #8, and #8 and #3, respectively, including 4856, 5222, and 2380
234 upregulated genes and 13545, 13276, and 1690 downregulated genes. (Table 2). In total, 1401
235 DEGs were shared among #6 and #3, #6 and #8, and #8 and #3 (Fig. 3), of them, 279 DEGs were
236 upregulated, and 528 DEGs were downregulated in all three comparison groups #6 and #3, #6
237 and #8, and #8 and #3(Table S2). By comparing DEGs from the same varieties (including #3, #6,
238 #8) under inoculation *A. phaeospermum* and sterile water treatment respectively, and all
239 differentially expressed genes from #6 and #3, #6 and #8, and #8 and #3 after inoculation *A.*
240 *phaeospermum*, we found that the common DEGs were mainly related to energy metabolism
241 (including photosynthesis and carbohydrate metabolism) and phytohormone biosynthesis, which
242 indicated that energy metabolism and phytohormones played an important role in the resistance
243 of *B. pervariabilis × D. grandis* to shoot blight.
244 After inoculation with *A. phaeospermum*, 1467, 7517 and 7417 DEGs in #3 and #6, #3 and #8,

245   #6 and #8 were annotated into COG database respectively (Fig, S1). After inoculation with
246   pathogens, the DEGs between #6 and #8 were annotated to the most COG database categories
247   (7517 DEGs) across all comparison groups, among which most DEGs were annotated to "signal
248   transduction mechanisms", "translation" and "replication, recombination and repair", with 1093,
249   1057 and 969, respectively (Fig. 4).
250   In the comparisons between #3 and #6, #3 and #8, and #6 and #8 of *B. pervariabilis × D.*
251   *grandis*, there were 17604, 3658 and 17875 DEGs, respectively, annotated to the cell component
252   (Fig. S2), molecular function and biological process categories. In the analysis of hybrid bamboo
253   #6 and #8 inoculated with pathogens, DEGs were enriched in "metabolic process", "cellular
254   process" and "single organism process" in the biological process category. DEGs were mainly
255   enriched in "cell", "cell part" and "organelle" in cell components. "Binding" and "catalytic
256   activity" are molecular functions (Fig. 5).
257   After inoculation of varieties #3, #6 and #8 of *B. pervariabilis × D. grandis* with pathogens,
258   4557, 828 and 4689 DEGs were annotated to 127, 119 and 127 pathways for the comparisons #3
259   and #6, #3 and #8, and #6 and #8, respectively (Fig. S3). Across the three varieties, we found
260   that the transcriptome data of the high-resistance varieties #6 and susceptible varieties #8 were
261   enriched in the most KEGG pathways. These DEGs were mainly enriched in the "ribosome"
262   pathway, followed by "carbon metabolism" and "endocytosis" (Fig. 6). These results suggest
263   that energy metabolism- (including photosynthesis and carbohydrate metabolism) and
264   transmembrane transport-related genes play important roles in the resistance of hybrid bamboo to
265   shoot blight. Therefore, the downregulation of related DEGs may lead to a decrease in the
266   disease resistance of hybrid bamboo, which is sensitive to *A. phaeospermum*.
267   **Selection of candidate resistance genes for hybrid bamboo shoot blight and qRT-PCR**
268   **verification.**
269   Based on GO and KEGG enrichment analysis, the DEGs related to plant resistance in the high
270   enrichment pathway of DEGs were selected as candidate resistance genes. At the same time, the
271   genes significantly differentially expressed in resistant and susceptible varieties and the same
272   variety after inoculation with *A. phaeospermum* or sterile water were also selected as the object
273   of disease resistance gene screening. Finally, through the comparison of existing studies, 21
274   candidate resistance genes were screened (Table 3). The qRT-PCR results of the candidate genes
275   and five randomly selected genes, including P1rcsn, Pod2, Hltfah1, Clbd, and Pod4(Table 4), as
276   well as the results for the reference gene GAPDH, showed a single peak, and the relative
277   expression level was consistent with the transcriptome data (Fig. 7).

Discussion

279   Transcriptome sequencing technology is an important means to explore genes and a powerful

280 tool to identify the interaction network between plants and pathogens. The xylogenesis formation
281 of Moso bamboo shoot was studied by transcriptome sequencing (Zhang et al., 2018), the
282 transcriptome of *Dendrocalamus latiflorus* Munro was sequenced and de novo analyzed using
283 Illumina platform, and many key candidate genes related to the growth and development of
284 *Dendrocalamus latiflorus* were found (Liu et al., 2012). In this study, transcriptome sequencing
285 technology was used to study the reaction of three varieties of hybrid bamboo inoculated with
286 water or pathogens. Transcriptome sequencing analysis showed that under six different
287 conditions (S3, J3, S6, J6, S8, J8), many DEGs may be potential resistance genes in *B.*
288 *pervariabilis × D. grandis*. Combined with gene functional annotation, candidate disease
289 resistance genes were determined; these genes may be the key to determining the disease
290 resistance mechanism of *B. pervariabilis × D. grandis* regarding shoot blight. In addition, 21
291 candidate genes and five randomly selected genes were verified by qRT-PCR, and the results
292 showed that these genes had 100 % similarity with the transcriptome sequencing results,
293 confirming their authenticity.
294 Plant resistance to pathogens involves several different mechanisms. On the one hand, some
295 structural and chemical components of plants have disease resistance functions, such as cutin,
296 wax, embolus, lignin and special stomatal structures of the cell wall; on the other hand, plants
297 show disease resistance reactions through the regulation of resistance genes when infected by
298 pathogens (Dhaliwal, Uchimiya, 1999).
299 The cell wall is the first barrier against pathogen invasion, and pectin is the main component of
300 the primary cell wall (Caffall, Mohnen, 2009). Pectin methylesterase (PME), also known as
301 pectinesterase, is one of the main enzymes that modifies pectin. This enzyme plays an important
302 role in the synthesis of the cell wall and the regulation of elasticity and permeability. Studies
303 have shown that PME activity in Arabidopsis thaliana is significantly enhanced under pathogen
304 infection (Bethke et al., 2013). PME not only regulates the growth and development of the plant
305 cell wall but also participates in the pathogenic process of pathogens. PME participates in the
306 demethylation process of pectin, promotes the further decomposition of pectin, and reduces the
307 strength and hardness of the cell wall. In *A. thaliana*, *AtPME3* was upregulated after infection
308 with *Botrytis cinerea* and *Pectobacterium carotovorum*, and the expression of *AtPME3* was
309 considered a susceptibility factor in *A. thaliana* (Raiola et al., 2011). However, oligogalactic acid
310 (OG) is an elicitor-active substance, and its degraded products can be recognized by downstream
311 kinase receptors and further activate downstream defence responses, thereby improving plant
312 disease resistance (Villegas et al., 2016). In this study, the expression level of the
313 PH01004943G0040 gene (annotated as pectinesterase 53-like) was significantly increased in the
314 high-resistance varieties #6 after inoculation, indicating that this gene may be closely related to
315 the resistance of *B. pervariabilis × D. grandis* to shoot blight. However, whether the

316 downstream defence response was activated by producing OG in *B. pervariabilis × D. grandis*
317 needs further experimental confirmation. There was almost no expression of pectinesterase 53-
318 like after inoculation with *A. phaeospermum* in varieties #3 and #8, indicating that the expression
319 level of pectinesterase 53-like increased with increasing resistance in hybrid bamboo infected
320 with *A. phaeospermum*, which further indicated that *pectinesterase 53-like* might be involved in
321 the resistance response of hybrid bamboo to *A. phaeospermum*.
322 In plant-pathogen interactions, the increase in lignin is an important mechanism for plants to
323 resist pathogens and enhance disease resistance, as lignin is involved in a varieties of
324 physiological and biochemical reactions in plants. Cinnamyl alcohol dehydrogenase (CAD) was
325 isolated from tobacco stems for the first time in 1992 (Knight et al., 1992); this enzyme was
326 previously found to be involved in lignin synthesis and played a key role in lignin synthesis
327 (Wyrambik, Grisebach, 1975). The number of CAD family members in different plants varies,
328 and 9, 12, 16, 15, 14 and 17 CAD family members have been reported in Arabidopsis, rice,
329 Populus trichocarpa, Populus hybrida, sorghum and alfalfa (Kim et al., 2004; Tobias, Chow,
330 2005; Kim et al., 2004; Shi et al., 2010; Barakat et al., 2009; Saballos et al., 2009). Many factors
331 in the natural environment, such as hormones, mechanical damage, fungi and mineral elements,
332 can induce CAD to participate in the plant lignification defence process (Kim et al., 2007), which
333 reduces the adverse effects of external factors on plants and plays an important role in plant
334 growth and development. *CAD-C* and *CAD-D*, the main genes for lignin biosynthesis in *A.*
335 *thaliana*, were found to be important genes for defence against strong and weak varieties of
336 *Pseudomonas syringae pv. tomato*. In this study, new_gene_84366 (annotated as cinnamyl
337 alcohol dehydrogenase 5) was significantly upregulated after pathogen inoculation of the
338 hyperactive cultivar #6, indicating that the gene may be closely related to the resistance of *B.*
339 *pervariabilis × D. grandis* to shoot blight.
340 After plants are infected with pathogens, the metabolic balance between the production and
341 elimination of reactive oxygen varieties in the body is damaged. Excess reactive oxygen varieties
342 can trigger and aggravate membrane lipid peroxidation. The cell structure is destroyed, and the
343 metabolic system is disordered, which will lead to plant cell death in serious cases. POD is the
344 key enzyme in the protective enzyme system that is responsible for scavenging reactive oxygen
345 varieties in plants. The increase in POD activity indicates that the ability to scavenge free
346 radicals is enhanced and that membrane lipid peroxidation is reduced, thereby maintaining the
347 normal metabolism of cells. In addition, POD plays an important role in the synthesis of
348 antibacterial substances such as lignin, phenols and phytoalexin (Hwang et al.,1997; Yubedee.
349 2013; Green. 1975; Cao et al., 2013) In the transcriptome data for the different treatments of *B.*
350 *pervariabilis × D. grandis*, we found that the expression levels of PH01000966G0470 and new
351 gene_67872 (annotated as peroxidase-like) increased after inoculation in #3 and #6 hybrid

352   bamboo, especially in the highly resistant varieties #6, indicating that the POD synthesis reaction

353   was activated during the resistance of *B. pervariabilis × D. grandis* to shoot blight, and this

354   reaction was more significant in resistant varieties. This gene may be closely related to *B.*

355   *pervariabilis × D. grandis* resistance to shoot blight.

356   Plant GDSL lipase is a large gene family and plays an important biological role in plant growth,

357   morphogenesis, lipid metabolism and the defence response (Kondou et al., 2008; Takahashi et al.,

358   2010). The expression of GDSL lipase can change in response to biotic and abiotic stresses. The

359   expression of GDSL lipase in plants can be induced by hormones such as pathogens, salicylic

360   acid, ethylene, jasmonic acid and abiotic stress factors, indicating that this gene may be involved

361   in plant disease resistance and stress responses (Oh et al., 2005; Kram et al., 2008; Lee, Cho,

362   2003; Kim et al., 2013). GDSL lipase can regulate or directly destroy the integrity of fungal

363   spores through signal transduction, limiting the growth and reproduction of pathogens in infected

364   areas (Oh et al., 2005; Kwon et al., 2009). PH01151705G0010 and PH01000743G0130

365   (annotated as GDSL-like lipase) were detected in the three varieties, and their expression levels

366   increased with increasing disease resistance, especially in highly resistant varieties. Their

367   expression levels increased significantly after inoculation, indicating that GDSL lipases may be

368   involved in the disease resistance process of *B. pervariabilis × D. grandis* against shoot blight,

369   and this gene family may be the key resistance genes in *B. pervariabilis × D. grandis*.

370   In addition, in the transcriptome data analysis, we also found a gene encoding MYB protein in

371   the highly resistant varieties #6. The MYB family is the most abundant transcription factor

372   family in plants and can regulate plant development, metabolism, physiological rhythm

373   regulation and key factors for biological and abiotic stress responses (Dubos et al., 2010; Hosoda

374   et al., 2002; Dubos et al., 2010). Studies have shown that many MYB genes are involved in the

375   plant response to stress. The molecular expression characteristics of 60 MYB genes in wheat

376   under high salt, ABA and PEG stress showed that the expression of *TaMYB48* with a MYB

377   domain was first upregulated and then downregulated (Zhang et al., 2012). Hiroshi (Abe et al.,

378   1997) found that a MYB protein (ATMYB2) can activate the expression of the rd22 gene and

379   ABA gene in Arabidopsis thaliana, thereby improving plant resistance. In this study, the

380   expression level of the PH01000008G1560 gene (annotated as myb-related protein Myb4-like)

381   was significantly higher in the highly resistant varieties #6 than in the susceptible varieties #3

382   after inoculation, indicating that the PH01000008G1560 gene may be closely related to the

383   resistance of *B. pervariabilis × D. grandis* to shoot blight. At the same time, we found that the

384   expression level of Myb4-like was lower after inoculation with *A. phaeospermum* than after

385   treatment with sterile water in the susceptible varieties #8 and the moderately resistant varieties

386   #3, which may be due to the inhibition of Myb4-like expression by ABA accumulation. The

387   specific result needs further experimental confirmation.

388 In this study, many DEGs involved in lignin and phytoalexin synthesis, redox reactions,

389 photosynthesis and signal transduction were found to be potentially important disease resistance

390 genes. The results of this study provide a basis for the further study of resistance genes and

391 related molecular functions in *B. pervariabilis × D. grandis* related to shoot blight caused by *A.*

392 *phaeospermum* and provide a basis for further study of its regulatory mechanism. The

393 transcriptome data of *B. pervariabilis × D. grandis* were uploaded for the first time and laid the

394 foundation for molecular breeding of *B. pervariabilis × D. grandis* in the future.

Conclusions

396 *The B. pervariabilis × D. grandis* transcriptome was first sequenced and uploaded to the public

397 database. *B. pervariabilis × D. grandis* with different resistance varieties showed different levels

398 of disease resistance after being infected with *A. phaeospermum*. # 3, # 6 and # 8 showed disease

399 resistance, high resistance and susceptibility, respectively. After inoculation with *A.*

400 *phaeospermum* in # 6 resistant varieties, many genes related to disease resistance were also

401 significantly expressed, especially those related to transcription, energy metabolism and cell wall

402 composition synthesis. The results showed that the expression of 21 genes such as *Gdsl-ll*, *Myb4*,

403 *Pec53*, *Cad5* and *Pod16* was significantly increased after inoculation with varieties # 6. These

404 genes may be involved in the resistance response of *B. pervariabilis × D. grandis* shoot blight

405 caused by *A. phaeospermum*, and they are important potential resistance genes. The specific

406 functions of these genes in the resistance process of *B. pervariabilis × D. grandis* need further

407 experimental verification.

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588

Statistical table of the disease index of the three varieties

Data are the means of three repetitions; data in the same column followed by different lowercase letters indicate significant differences among different varieties after inoculation by the LSD test (p<0.05)

1   **Table 1** Statistical table of the disease index of the three varieties

Species	Incidence (%)	Disease index
#8	85.6 ± 1.7^{a}	62.8 ± 2.1^{a}
#3	23.3 ± 3.3^{b}	12.2 ± 1.7^{b}
#6	7.8 ± 1.7^{c}	2.8 ± 0.4^{c}

2   Data are the means of three repetitions; data in the same column followed by different lowercase letters indicate

3   significant differences among different species after inoculation by the LSD test ($p<0.05$)

Statistical table of the number of DEGs

J indicates inoculated *A. phaeospermum*, S indicates inoculated sterile water.

1 **Table 2** Statistical table of the number of DEGs

Comparison	Number of DEGs	Upregulated	Downregulated
J3-vs-S3	4387	1925	2462
J6-vs-S6	6316	3148	3168
J8-vs-S8	4159	2609	1550
J6-vs-J3	18401	4856	13545
J6-vs-J8	18496	5222	13276
J3-vs-J8	4070	2380	1690

Candidate genes screened from common DEGs

1   **Table 3** Candidate genes screened from common DEGs

Gene ID	Gene name	Annotation
PH01000030G0570	*Tfbl*	transcription factor bHLH96-like
PH01000322G0910	*Lrr-rlk2*	leucine-rich repeat receptor-like protein kinase IMK2-like
PH01000356G0220	*Cer1l*	ECERIFERUM 1-like
PH01000743G0130	*Gdsl-ll1*	GDSL-like lipase
PH01000967G0060	*Prp4l*	proline-rich protein 4-like
PH01001075G0100	*Scl45*	serine carboxypeptidase-like 45
PH01001222G0140	*Faah*	fatty acid amide hydrolase
PH01001261G0170	*Klp*	kinesin-like protein FLA10
PH01001610G0170	*Plbp*	putative lipid-binding protein
PH01002098G0130	*Xth28*	xyloglucan endotransglucosylase/hydrolase protein 28
PH01002765G0010	*C2agdcp*	C2 and GRAM domain-containing protein
PH01002901G0100	*Laoh*	L-ascorbate oxidase homologue
PH01003226G0090	*Atlp3*	auxin transporter-like protein 3
PH01151705G0010	*Gdsl-ll2*	GDSL-like Lipase
PH01000966G0470	*Pod4l*	peroxidase 4-like
PH01000008G1560	*Myb4l*	myb-related protein Myb4-like
PH01004943G0040	*Pec53*	pectinesterase 53-like
newGene_56747	*B-bwip1*	Bowman-Birk type wound-induced proteinase inhibitor WIP1
newGene_63038	*Egl20*	endoglucanase 20-like
newGene_67872	*Pod16*	peroxidase 16
newGene_84366	*Cad5*	cinnamyl alcohol dehydrogenase 5

Five genes that were randomly selected to verify the expression level

1   **Table 4** Five genes that were randomly selected to verify the expression level

Gene ID	Gene name	Annotation
PH01087490G0010	*PIrcsn*	photosystem I reaction centre subunit N
PH01000445G0570	*Podbd2*	peroxidase
PH01000974G0460	*Hltfah1*	histone-like transcription factor and archaeal histone
PH01000040G1380	*Clbd*	calreticulin-like
PH01000445G0440	*Podbd4*	peroxidase

Figure 1

Symptom map of *B. pervariabilis* × *D. grandis* before inoculation.

a, b, c #3, #6 and #8 *B. pervariabilis* × *D. grandis* stems, respectively. **d, e, f** #3, #6 and #8 *B. pervariabilis* × *D. grandis* leaves, respectively.
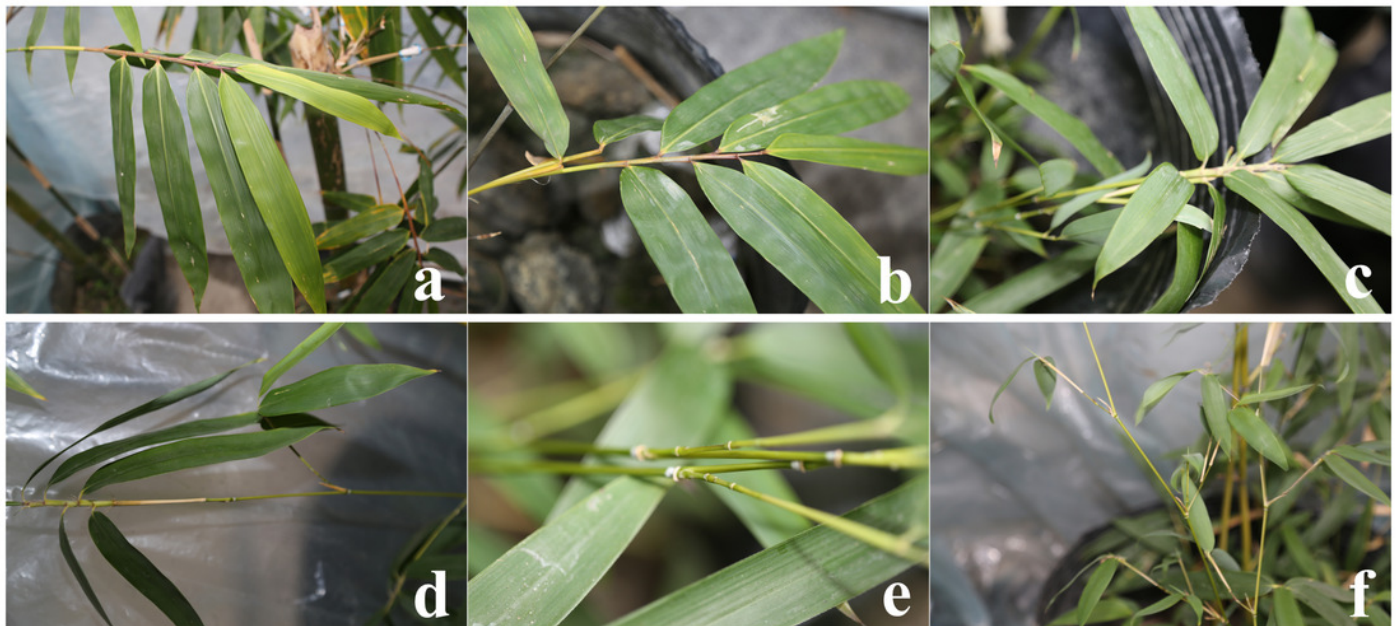
Figure 2

Symptom map of *B. pervariabilis* × *D. grandis* after inoculation.

a, b, c #3, #6 and #8 *B. pervariabilis* × *D. grandis* stems were inoculated for 25 days, respectively. **d, e, f** #3, #6 and #8*B. pervariabilis* × *D. grandis* leaves were inoculated for 25 days, respectively.

Figure 3

Venn diagram of DEGs.

a Venn diagram showing the DEGs between the sterile water and spore suspension treatments for varieties #3, #6 and #8 **b** Venn diagram showing the DEGs between varieties #3, #6 and #8 after spore suspension treatment. (J indicates inoculated *A. phaeospermum*, S indicates inoculated sterile water.)
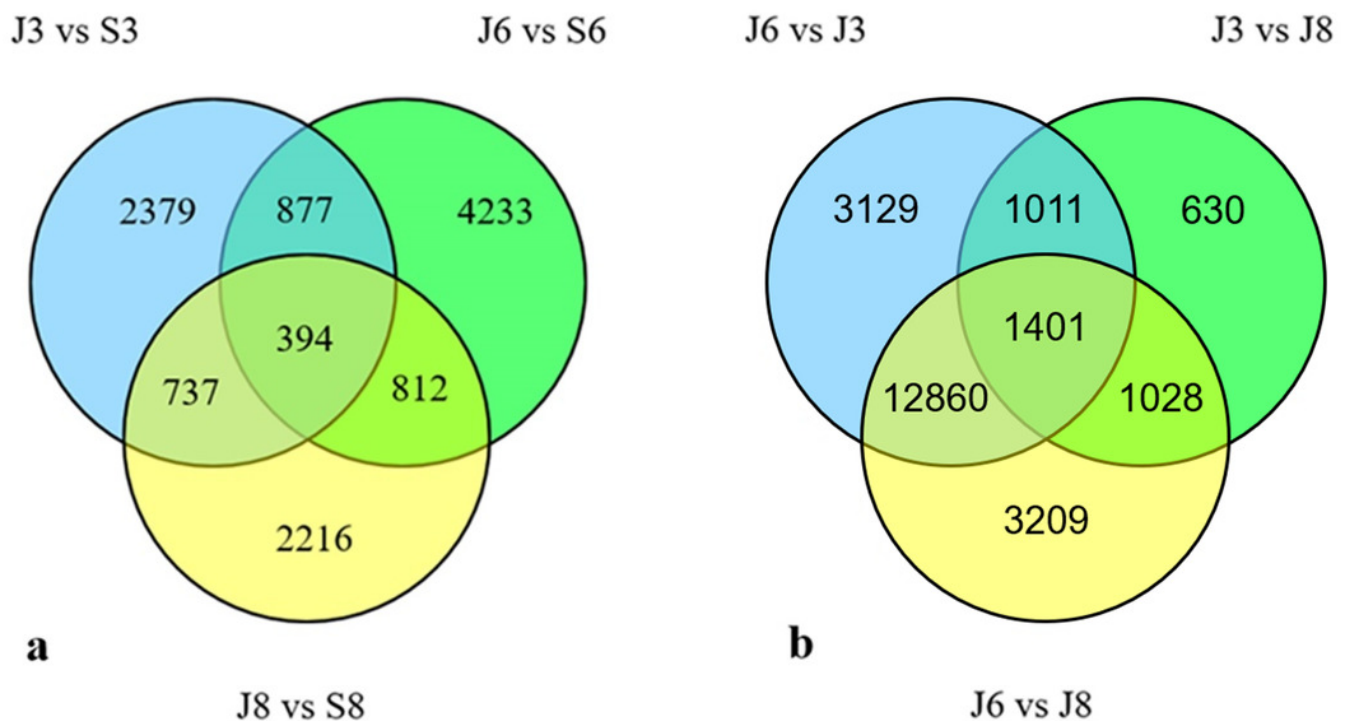
Figure 4

COG classification map of DEGs.

a COG classification diagram showing the DEGs between the sterile water and spore suspension treatments for variety #6; **b** COG classification diagram showing the DEGs between varieties #6 and #8 after spore suspension treatment.

Figure 5

GO classification map of DEGs.

a GO classification diagram showing the DEGs between the sterile water and spore suspension treatments for variety #6; **b** GO classification diagram showing the DEGs between varieties #6 and #8 after spore suspension treatment.
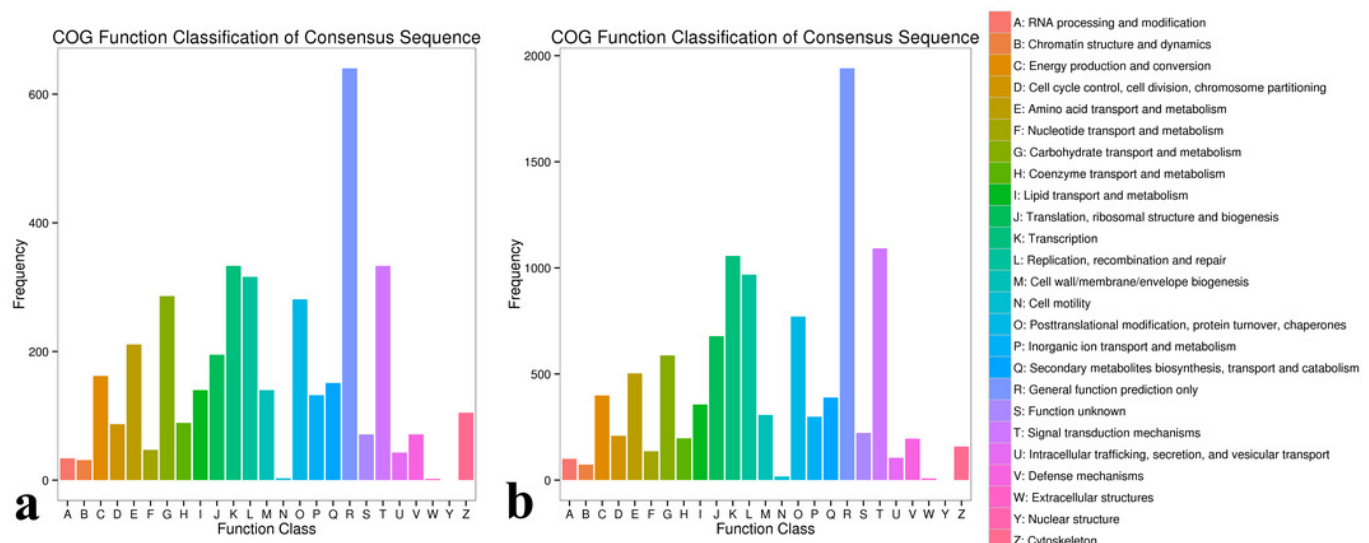
Figure 6

Summary of the KEGG enrichment maps of DEGs.

a KEGG classification diagram showing the DEGs between the sterile water and spore

suspension treatments for variety #6; **b** KEGG classification diagram showing the DEGs

between varieties #6 and #8 after spore suspension treatment.
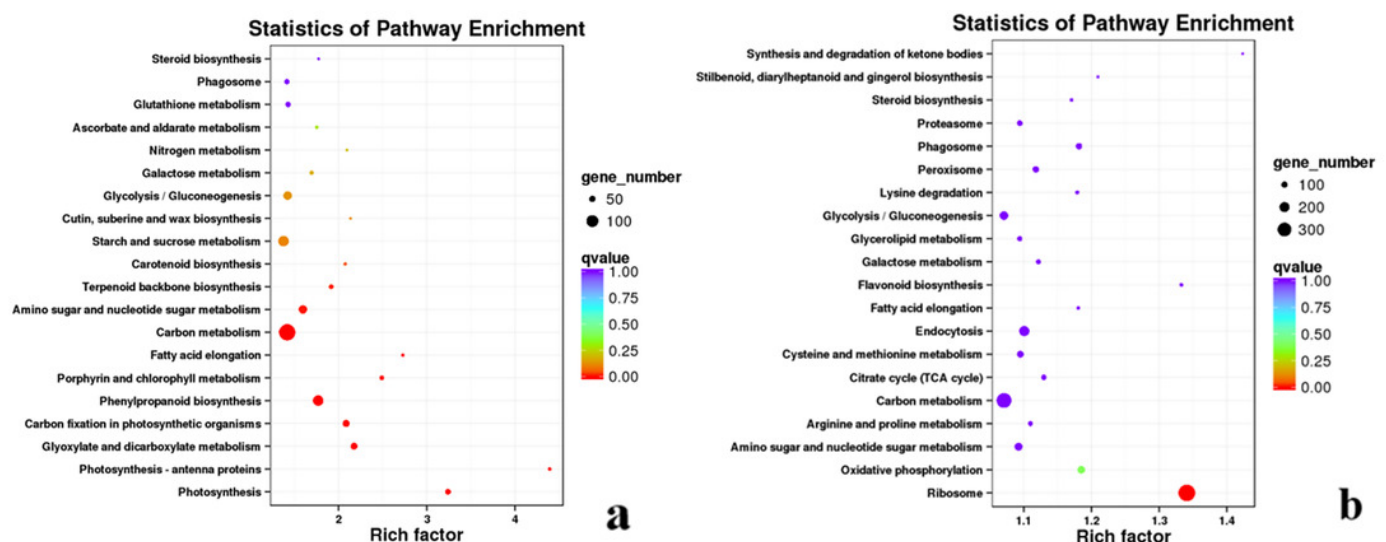
Figure 7

Column map of J8, J6 and J3 gene expression measured by qRT-PCR