Conyza blinii responds to the changes of exogenous iron through auxin-terpenoids metabolism pathway

Ming Yang*a, Tianrun Zheng*a,b*, Junyi Zhan*, Maojia Wang*, Wenjun Sunb, Min Zhoua, Zizhong Tang a,b, Tongliang Bua, Qingfeng Lia and Hui Chen a

College of Life Science, Sichuan Agricultural University, Ya’an, People’s Republic of China; bTraditional Chinese Medicine Planting Institute, Chongqing Academy of Chinese Matera Medica, Chongqing, People’s Republic of China; cCollege of Life Science, Nanjing Agricultural University, Nanjing, People’s Republic of China

ABSTRACT
As an essential trace element, iron is a necessary micronutrient for most organisms. Conyza blinii (C. blinii) is a traditional Chinese medicine grown in Sichuan, China. We chose C. blinii as material to explore the way plants respond to iron. Our results showed that iron increased the content of endogenous auxin, glandular trichomes (GTs) density and the content of blinin, the characteristic diterpene in C. blinii. Most of the key enzymes in the blinin synthesis pathway (MEP) were upregulated under iron by RNA sequencing. CbHO-1 (Heme oxygenase gene) was upregulated under exogenous IAA treatment. Taken together, these results suggest that C. blinii respond to iron through auxin-terpenoids metabolism, and this process may be related to CbHO-1.

1. Introduction

Iron is a necessary micronutrient for most organisms. In plants, iron participates in many cellular metabolic processes, chlorophyll synthesis, electron transfer and respiration during the process of plant growth. Iron is a cofactor of many enzymes in the mitochondrial respiratory chain, and AtATM1 regulates the dynamic balance of iron in mitochondria. Yeast ATM1-deficient (atm1) mutants have a phenotype of respiratory defects, leading to excessive iron accumulation in mitochondria and a deficiency of cytochrome C (Sixue 2007). With the development of human industrial activities, heavy metal pollution has become an environmental problem of increasing concern. Studies have shown that excessive iron can lead to iron poisoning in plants because of Fenton reactions, catalyzing the generation of reactive oxygen species (Guerinot and Yi 1994). In rice, excessive iron will lead to yellow leaves, reduced tillers and different degrees of oxidative damage and growth inhibition in pea seedlings (Lobreaux and Briat 1991).

C. blinii is a two-year deciduous herb of Compositae that is mainly distributed in hillsides and sparse forest areas at an altitude of approximately 2000 m in southern Sichuan Province, China. Mineral mining activities in this area are intensive, and the rainy season is relatively concentrated, resulting in acidic soil and enrichment of a large number of ionic metal elements on the surface. Clorane diterpene blinin is the characteristic secondary metabolite of C. blinii (Yang et al. 1989). Studies have shown that terpenoids, as secondary metabolites, play an important ecological role in response to external biological and abiotic stresses. Volatile terpenoids in the leaves and stems of lavender, such as borneol, camphor, and 1,8-cineole, have a pungent smell and have a defensive effect against aggressive insects (J. Li et al. 2021). In addition, terpenoids can also act as phytoalexins to resist the invasion of pathogens (Picman et al. 1990). Terpenoids synthesized during plant growth can also respond to abiotic factors such as temperature and light (Tingey et al. 1980). In our previous studies, it was also found that C. blinii could synthesize more blinin under UV-B stress to resist the damage of excessive UV-B to plants (Zhan et al. 2021).

Auxin, as the primary endogenous plant hormone, is necessary for many physiological processes in plants, such as regulating the development of plant organs and the establishment of physiological morphology (Eva 2003), helping plants form their own apical advantage (Stefan 2005), and promoting the development of plant lateral roots and adventitious roots (Fett-Neto et al. 2001). Studies have shown that auxin, as a hormone signaling molecule, plays a certain regulatory role in plant stress resistance. Spraying different concentrations of auxin on barley at high temperature can alleviate the damage caused by high temperature and restore the anther length and pollen grain number (Sakata 2010). Arabidopsis mutants of important response genes in the auxin signaling pathway air1 (auxin-resistance gene1) and tir1 (transport inhibitor response 1) under cold stress showed slow root growth and abnormal responses to gravity (Shibasaki et al. 2009).

In recent years, auxin has been found to play a role in plant absorption and utilization of iron. When a sufficient amount of iron is present, exogenous application of IAA to cucumber seedlings can promote the transcription of iron reductase genes and iron transporter genes (Bacaicoa et al. 2011). In a study of Malus xiaojinensis, iron deficiency led to a significant increase in IAA content in the stem tip, and the provision of exogenous IAA analogs (NAA) to the...
A stem tip triggered a corresponding iron deficiency reaction. Preventing the transport of IAA from bud to root prevented the iron deficiency reaction (Wu et al. 2012). Downstream of hormone signaling, some chemical signaling molecules also play a key role. Exogenous application of CO in Arabidopsis can alleviate leaf chlorosis and upregulate genes related to iron homeostasis under iron deficiency (Kong et al. 2010). In plant cells, CO mainly comes from haem oxygenase (HO, EC 1.14.99.3), which decomposes haem into CO, Fe²⁺ and biliverdin (BV) (Davis et al. 1999).

Our previous experiments showed that exogenous application of different concentrations of iron could increase the density of GTs on the leaf surface of C. blinii and the biosynthesis of blinin, which may be related to CbHO-1 (Zheng et al. 2020). In this study, we analysed how auxin affects terpenoids metabolism in C. blinii in response to iron from the perspective of plant hormones.

2. Materials and methods

2.1. Plant growth and iron treatments

The seeds of C. blinii were obtained from Hui Chen, Sichuan Agricultural University, China. After 25 °C germination, on the basis of ensuring the plant growth level, hydroponic plant seedlings were cultured in 1/2-strength Hoagland’s solution until 2 months old. Temperature was 26 ± 2 °C and the photoperiod was 16 h light/8 h dark. For iron treatment: 2.78 g FeSO₄·7H₂O, 3.73 g EDTA-2Na₂·H₂O and 100 ml ddH₂O were combined to form a 10 mM iron solution, corresponding amount of ferrous solution was added to the seedlings such that the final concentrations were 50, 100, 200 and 400 μM. The normal 1/2-strength Hoagland nutrient solution was used as a blank treatment. The nutrient solution was replaced every 2 days, and the ferrous iron solution was added every 2 days.

2.2. GTs staining and counting

Leaves were collected avoiding the main vein and were perforated symmetrically. After laying the cut leaves on a glass slide, 0.2% rhodamine B solution was dripped onto them until the whole blade was covered and soaked. After covering with glass, the cells were incubated at room temperature for 30–45 min. The quantity of secretory GTs was then counted under natural light. Images were collected, and the locations of the GTs were marked with arrows for convenience of calculation. The quantity was divided by the view area, and the density of capitate GTs was then calculated.

2.3. Determination of iron content in plant tissues

The plant iron content was determined by Nanjing Jiancheng tissue iron determination kit (A039-2-1). To exclude the influence of plant iron, we subtracted the control group iron before calculating the transfer rate, and analysed leaves, leaves and root iron percentage.
2.4. Extraction of blinin and HPLC analysis

According to Zheng’s method (Zheng et al. 2020), the leaves of C. blinii before and after iron treatment were ground into powder under liquid nitrogen and extracted overnight at 37 °C at a powder:methanol ratio of 1:40. The extract was stored in a 2 ml bottle at 4 °C. HPLC was used to determine the blinin content at a detection wavelength of 210 nm, column temperature of 25 °C, mobile phase of methanol:water:acetonitrile = 40:45:15, and flow rate of 1 mL/min. The peak elution time of blinin was approximately 7 min.

2.5. RNA sequencing and cluster analysis of differentially expressed genes

All leaves of the CK group and 200 μM iron treatment group samples were stored in liquid nitrogen at −80 °C. Three biological replicates were performed in each group. Before RNA extraction, 0.1% RNase solid-phase scavenging agent was used to clean the bench, grinding rod, disposable gloves, and other items. TRIZol Universal Total RNA Extraction Reagent of Tiangen Beijing company was used to extract the total RNA from the C. blinii leaves. Transcriptome sequencing samples were set with three biological repeats.

Eukaryotic mRNA was enriched with oligo (DT) magnetic beads to obtain the final library. After the construction of the library, Qubit 2.0 was used for the initial quantification, and then Agilent 2100 was used to detect the insert size of the library. When the insert size reached the expectation, the effective concentration of the library was accurately quantified by qPCR (the effective concentration of the library was > 2 nm) to ensure the quality of the library. After passing the library inspection, different libraries were pooled according to the requirements of the effective concentration and target disembarkment data volume, and then Illumina HiSeq sequencing was performed.

Differential expression analysis was performed for the two groups using the DEseq R package (1.10.1). The P value was
adjusted by using the method of Benjamin and Hochberg to control the error detection rate. Genes with adjusted \( P \) values <0.05 found by DEseq were designated differentially expressed.

2.6. GO and KEGG pathway enrichment analysis

Gene Ontology (GO) enrichment analysis of the differentially expressed genes (DEGs) was implemented by the GOseq R package-based Wallenius noncentral hypergeometric distribution (Young et al. 2010), which can adjust for gene length bias in DEGs. We used KOBAS (Mao et al. 2005) software to test the statistical enrichment of the differentially expressed genes in the KEGG pathways.

2.7. Determination of endogenic hormones

Approximately 1.0 g each of root, stem and leaf samples was weighed, ground into powder under liquid nitrogen, and endogenic hormones of C. blinii were extracted with 1 ml methanol to obtain samples. The prepared samples were filtered with an organic phase filter head and detected by HPLC. The conditions were as follows: mobile phase of methanol: 0.6% acetic acid = 50:50; column temperature of 35 °C; flow rate of 1 mL/min; wavelength of 254 nm.

2.8. Treatments of exogenous hormone and hemin

In this experiment, the concentrations of IAA and NPA were 50 and 5 mM, respectively. The concentrations of SA and ABT were 2 and 10 mM, respectively. The concentration of hemin applied was 10 \( \mu \)M and zinc protoporphyrin (Znppix) was 1 \( \mu \)M. 2 months old hydroponic seedlings were selected as the experimental group, 1/2-strength Hoagland nutrient solution was used as a blank. Experimental groups were detected after 7 days of treatment.

2.9. qRT–PCR analysis

According to Zhan’s method (Zhan et al. 2021), leaves were pretreated with liquid nitrogen and stored at -80 °C. cDNA was synthesized using the PrimeScript™ RT Reagent Kit with gDNA Eraser (Perfect Real Time) for reverse transcription. The cDNA reverse procedure was carried out by PCR, which was divided into two steps. The first step was 42°C for 5 min (gDNA eraser 2 \( \mu \)l, 5xgDNA eraser Buffer 4 \( \mu \)l, ddH2O 10 \( \mu \)l, RNA 4 \( \mu \)l). The second step was 37 °C for
15 min and 85 °C for 5 s. The reaction system was 15 μl: 7.5 μl SYBR® Premix Ex Taq™ II (Tli RNaseH Plus), 0.5 μl upstream and downstream primers, CDNA 1 μl, RNase-free H₂O to 15 ml. Three parallel assays were conducted for each sample. A two-step real-time PCR method was adopted, and they were all predenatured at 95 °C for 3 min. Then, all of the samples were annealed at 65 °C. After 0.5 – 95 °C for every 5 s, the samples were kept for 5 s, and the fluorescence signals were collected for fusion curve analysis. The 2⁻ΔΔC method was used to calculate the level of gene expression.

2.10. Correlation analysis

The Hmisc (version 4.5–0, https://hbiostat.org/R/Hmisc/summaryFuns.pdf) R package was used to calculate the correlation between C. blinii GT density, blinin content and hormone content.

3. Results

3.1. Growth of C. blinii under exogenous iron treatment

In order to research the response in C. blinii to iron, we treated C. blinii with different concentrations of iron, and counted the iron content in plant tissues. It was found that the exogenous iron resulted in the dissimilar growth in C. blinii (Figure 1A), iron content in leaves was lower than roots (Figure 1B). The iron transportation rate of leaves showed a similar trend (Figure 1C). Excessive accumulation of iron in plant tissue will destroy the structure and function of plant cells, induce the production of a variety of reactive oxygen species, cause iron toxicity and affect plant growth (Hameed et al. 2016). When the iron concentration reaches 400 μM, the excessive accumulation of iron in leaves leaded to iron poisoning in plant tissues, which was characterized by leaves chlorosis, wilting and black spots.
Iron content of leaves in *C. blinii* was increased under 200 μM iron in 7 days (Figure 1D), but this group showed a better growth, which was the same as our previous experimental results (Zheng et al. 2020).

### 3.2. Iron improves the blinin content and GTs density in *C. blinii*

As an exocrine structure of the plant epidermis, glandular trichomes can secrete and store secondary metabolites (Ping et al. 2013). GTs with exuberant surface coating are the characteristics of *C. blinii*, we attempted to explore whether GTs or blinii were involved in iron response. We found that 200 μM exogenous iron was able to increase GTs density over time, whether adaxial or abaxial surface (Figure 2A–J). The blinii content showed an upward trend under the same conditions, reaching 0.83 mg/g at 7 d (Figure 2K).

### 3.3. RNA sequencing identifies the key genes and processes of blinin synthesis under iron in *C. blinii*

To research the potential mechanism of the increase in blinin content of *C. blinii* under iron, we conducted RNA sequencing for comparison between the CK treatment and 200 μM iron.
iron treatment samples of 2-month-old *C. blinii* using the Illumina HiSeq platform. According to the RNA sequencing results, all 1034 differentially expressed genes (DEGs) were obtained. Among them, 609 genes were upregulated, while the remaining 425 genes were downregulated (Figure S1).

After GO enrichment of the differentially expressed genes, all DEGs were annotated into two parts: biological process (BP) and molecular function (MF). However, no cell components (CC) were noted. The identified genes are mainly involved in cell homeostasis and cell redox homeostasis biological processes. Their function at the molecular level is mainly to participate in redox reactions (Figure S2).

Furthermore, all DEGs were also clustered by KEGG pathway analysis. The most significant enrichments of all DEGs were in 'plant hormone signal transduction', 'phenylpropanoid biosynthesis' and 'starch and sucrose metabolism' (Figure 3A). In addition, 'plant hormone signal transduction', 'phenylpropanoid biosynthesis', 'processing in endoplasmic reticulum', and 'phenylalanine metabolism' were enriched in the upregulated DEGs (Figure 3B), although the most significant enrichments of the downregulated DEGs were 'starch and sucrose metabolism', 'plant hormone signal transduction' and 'phenylpropanoid biosynthesis' (Figure 3C).

### 3.4. Expression profiling of key enzyme genes associated with blinin biosynthesis under iron in *C. blinii*

Blinin is a diterpene compound produced by the MEP pathway. Here, we investigated the effect of iron on the gene expression of the blinin synthesis pathway. We screened differentially expressed genes related to the blinin synthesis pathway from the transcriptome (Figure 4). A total of 49 genes were screened, including 12 DXS genes, 7 DXR genes, 2 CMS genes, 5 MCS genes, 6 HDS genes, 5 HDR genes, 10 GGPPS genes and 3 CPS genes. Twelve genes were upregulated, including Cluster-16989.19467, Cluster-16989.13324, Cluster-21337 in DXS, Cluster-16989.1874 in CMS, Cluster-39009.0, Cluster-16989.21544 and Cluster-16989.24592 in HDR, and Cluster-16989.20219 in HDS, Cluster-37013.0 in GPS, Cluster-16989.4030 in CPS. The upstream limiting enzyme gene *CbDXS* is upregulated and can utilize more pyruvic acid and glycerol 3-phosphate in the MEP pathway. Meanwhile, the upregulation of *CbHDR* converts more IP and DMAPP to GPP and GGPP, which is an intermediate of blinin.

### 3.5. The contents of endogenous IAA and SA were increased under iron

‘Plant hormone signal transduction’ was significantly enriched in KEGG pathway analysis (Figure 3A). Then, we selected and measured the contents of six endogenous plant hormones (Figure 5A). The contents of IAA, SA, ABA and BR increased under iron. Correlation analysis showed that IAA and SA had a higher correlation with blinin synthesis and GTs density. In summary, we found that IAA and SA were potential factors related to blinin synthesis and GTs density.

### 3.6. IAA promotes the development of GTs and blinin synthesis in *C. blinii*

To explore the effect of endogenous IAA and SA in *C. blinii* under iron, we sprayed IAA and SA and their inhibitors NPA and ABT on *C. blinii* leaves. The results showed that exogenous IAA and SA increased the GTs density on adaxial and abaxial surfaces (Figure 6A–C), but the GTs density did not decrease after ABT treatment (Figure 6A,D,E). The blinin content results showed that exogenous IAA and SA improved the blinin content in *C. blinii* leaves by 200%, and the blinin content decreased after adding NPA and ABT (Figure 7A,B).

IAA or SA, which is more likely to be affecting the blinin content and GTs density? We conducted an inhibitor experiment in which NPA and ABT were separately added to *C. blinii* under iron. The NPA group showed a decline in the GT density of the adaxial and abaxial surfaces, but there was no decline in the ABT group. Moreover, we screened three differentially expressed ARF transcription factors in the transcriptome (Cluster-16989.13207, Cluster-16989.6331, and Cluster-16989.9486). Cluster-16989.6331 and Cluster-16989.9486 were more similar to the key enzyme expression of the blinin synthesis pathway (Figure S3). The above results...
showed that IAA, not SA, promoted GT development and blinin synthesis in *C. blinii* (Figure 8).

### 3.7. The effect of IAA on GTs development and blinin synthesis depends on the expression of *CbHO-1*

The heme oxygenase-1 system plays a critical role in photosynthesis, root development and stress physiology. Heme is decomposed into CO, BV and Fe²⁺ by haem oxygenase (Davis et al. 1999). First, we found that the expression of *CbHO-1* was increased by IAA under iron treatments and was inhibited after ABT addition (Figure 9D). Second, after adding IAA and Znppix, the expression of *CbHO-1* did not significantly change. The effects of IAA on GTs density and blinin content in *C. blinii* leaves were similar to the *CbHO-1* expression pattern. Both of them were increased after adding IAA and were inhibited after adding NPA (Figure 9A–C). On account of these results, we speculate that IAA is located upstream of *CbHO-1*, regulating GTs development and blinin biosynthesis in *C. blinii*.

### 4. Discussion

#### 4.1. Auxin is a messenger of *C. blinii* in response to iron

Researchers have shown that plants can adapt to environmental changes by regulating their hormone levels (Peleg and Blumwald 2011), including auxin and other plant hormones that are involved in the absorption and balance of iron (Schmidt et al. 2000). In rice, Osarf16 showed dwarfism, photosynthesis attenuation, iron content decline and changed root structure (A et al. 2015). KEGG enrichment of DEGs in the transcriptome showed that ‘plant hormone signal transduction’ was significantly enriched; among our candidate plant hormones, IAA increased with the duration of iron treatment. The GTs density and blinin content were inhibited to varying degrees when exogenous IAA and NPA were added, as was NPA alone (Figure 5). These results suggest that IAA acts as a messenger in the *C. blinii* response to iron.

In addition to IAA, other plant hormones also participate in the maintenance of plant iron homeostasis. Excessive iron affects the growth of plant primary roots by preventing the extension and division of Arabidopsis root cells, and ethylene alleviates the damage to plants by increasing the expression of iron chelation genes (Li et al. 2015). Cytokinin (CK) can negatively regulate plant iron uptake by inhibiting AtIRT1 and AtFRO2 (la et al. 2010). Abscisic acid (ABA)-mediated corking negatively regulates iron acquisition (Marie et al. 2016). SA treatment reduces the level of plant hormones in wheat seedlings, preventing decreases in IAA and cytokinin contents, which reduces plant growth inhibition under salt stress (Shakirova et al. 2003). In some sense, this explains why the blinin content decreased after we added ABT, but the GT density on the leaf surface did not show a downward trend. IAA may indirectly affect GT density and blinin content through other plant hormones.
Downstream of hormone signaling, NO is a chemical signaling molecule that can activate the activity of iron chelate reductase (FCR) in the roots of iron-deficient Arabidopsis, improving the absorption and utilization of iron (Chen et al. 2010). CO affects the accumulation and transport of auxin in root tips by changing the distribution of auxin transport proteins PIN1 and PIN2 under iron salt stress to control the lateral root structure (L. Yang et al. 2016). Our experiments found that the expression of CbHO-1 increased with iron treatment. As the decomposition product of heme, CO may be involved in the response of C. blinii to iron.

Figure 9. The effects of IAA on the GTs density and blinin content are based on CbHO-1. (A,B) Changes of adaxial and abaxial GTs densities under IAA, hemin and their inhibitors for 7 days. (C,D) Changes of CbHO-1 expression and blinin content under exogenous IAA, hemin and inhibitors for 7 days in C. blinii.

Figure 10. IAA dominated the response to iron in C. blinii. The solid arrow is the promotion effect, and the dotted line is the process to be verified. The right part is the iron condition, and the left part is the iron-free condition.
4.2. Blinin is needed for C. blinii in response to iron

With the increasing concentration of iron ions in soil, plant roots will absorb more iron and transport it to the leaves, resulting in many reactive oxygen species in cells, which will destroy the cell structure and affect the growth and development of plants (Asch et al. 2010). A study on the effects of iron stress on different plants showed that tolerance to iron varies greatly among different species (Albano et al. 1996; Audebert and Sahrawat 2000; Brown and Ambler 2010). In this experiment, we found that under 200 μM iron treatment, C. blinii did not exhibit plant tissue damage but there was increased blinin content and GT density. This may be because a soil environment with a high iron content has allowed C. blinii to develop a tolerance to iron.

The tolerance of C. blinii to iron may be related to its characteristic secondary metabolite blinin. Our previous experiments also proved similar results; the blinin content gradually increased with iron treatment, and they both showed a significant correlation (Zheng et al. 2020). RNA sequencing analysis showed that key enzyme genes of the MEP pathway were upregulated to varying degrees under iron. GTs serve as a site for the synthesis and secretion of multiple secondary metabolites (Yan et al. 2016), and their increase in density on the leaf surface also provides evidence for the response to iron in C. blinii.

4.3. Blinin is a potential active component that maintains the stability of photosynthesis

Our previous study found that iron could cause an accumulation of chlorophyll, improving the photosynthetic capacity (Zheng et al. 2020); too much lighting energy is generated in a short time and not dissipated, it will cause oxidative damage to plant photosystem II (PSII) (Long 1994; Barber and Barber 1995). Excessive iron in the leaves will also reduce the chlorophyll content and electron transfer rate, inactivating the photosystem II reaction center and reducing the net photosynthetic rate of plants (Xu et al. 2015). Blinin alleviates oxidative damage and maintains light stability under UV-B stress (Zhan et al. 2021), also confirming that blinin has the same function under iron.

Overall, we propose the following hypothesis: When the exogenous iron content increased, iron absorbed by roots was transported to leaves. With the improvement of photosynthesis, the synthetic auxin is transported to other parts, which improves the development of GTs, providing more places for the synthesis of blinin. Blinin, in turn, maintains the stability of photosynthesis (Figure 10).

5. Conclusion

In conclusion, the enhancement of endogenous IAA upregulated the expression of key enzyme genes of the blinin synthesis pathway and increased the GTs density and blinin content in C. blinii under iron. Meanwhile, the upregulation of CbHCO-1 decomposed heme and produced more CO, helping IAA present molecular signals. Taken together, our experiments explored the way responds to exogenous iron in C. blinii, that is, auxin-terpenoid metabolism pathway, which provides a new perspective for the study of plant iron response.

Author’s contributions

J.-Y. Z, H. C and T.-R. Z designed the research; J.-Y. Z, T.-R. Z, M. Y, M.-J. W, W.-J. S and M. Z performed the research; J.-Y. Z and T.-R. Z analysed the data; Z.-Z. T, T.-L. B and Q.-F. L were responsible for project administration. M. Y and T.-R. Z wrote the paper. All authors read and approved the final manuscript.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

Notes on contributors

Ming Yang, College of Life Science, Sichuan Agriculture University Sichuan, People’s Republic of China.

Tianran Zheng, Chongqing Academy of Chinese Materia Medica, Chongqing, People’s Republic of China.

Junyi Zhan, College of Life Science, Nanjing Agricultural University, Nanjing, People’s Republic of China.

Maojia Wang, College of Life Science, Sichuan Agriculture University Sichuan, People’s Republic of China.

Wenjun Sun, College of Life Science, Sichuan Agriculture University Sichuan, People’s Republic of China.

Min Zhou, College of Life Science, Sichuan Agriculture University Sichuan, People’s Republic of China.

Zizhong Tang, College of Life Science, Sichuan Agriculture University Sichuan, People’s Republic of China.

Tongliang Bu, College of Life Science, Sichuan Agriculture University Sichuan, People’s Republic of China.

Qingfeng Li, College of Life Science, Sichuan Agriculture University Sichuan, People’s Republic of China.

Hui Chen, College of Life Science, Sichuan Agriculture University Sichuan, People’s Republic of China.

ORCID

Zizhong Tang http://orcid.org/0000-0002-3508-6057

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