



ECOSYSTEMS

Feeding Preference of *Altica deserticola* (Coleoptera: Chrysomelidae: Alticinae) for Leaves of *Glycyrrhiza inflata* and *G. uralensis*

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Abstract: A leaf-disc-test method was used under controlled laboratory conditions to determine the feeding preference of *Altica deserticola* Latreille (Coleoptera: Chrysomelidae) on leaves of two liquorice species, *Glycyrrhiza inflata* Batalin and *G. uralensis* Fisch. ex DC. Leaf hardness and thickness, cuticle thickness, and nitrogen and tannin contents were compared between the two liquorices to explore their feeding resistance to *A. deserticola*. The larvae ate only *G. uralensis* leaves, while the adults fed on the leaves of both species but preferred those of *G. inflata*. The leaf hardness and thickness and cuticle thickness, as well as the nitrogen, total tannins, tannin chemicals contents in leaves, were significantly greater in *G. inflata* than in *G. uralensis*. The larvae having smaller chewing mouthparts could not feed on hard leaves with thick cuticle on both sides. The thicker cuticle and harder texture of *G. inflata* blades may be important physical traits for effective defence against larval phytophagy, while the higher tannin content in its leaves may be an important chemical trait determining their feeding preference. The larger adults, having stronger mouthparts, could consume nitrogen-richer *G. inflata* leaves to obtain the energy needed for flight and reproduction.

Key words: Feeding preference, leaf beetles, leaf texture, liquorice, nitrogen content, tannin.

INTRODUCTION

Liquorice is a perennial herb from the family Fabaceae. *Glycyrrhiza uralensis* Fisch. ex DC. and *Glycyrrhiza inflata* Batalin are two medicinal liquorices listed in the Chinese Pharmacopoeia (Chinese Pharmacopoeia Commission 2015). The former is distributed in China, Mongolia, and Russia, and the latter in China, Kazakhstan, Uzbekistan, Turkmenistan, Kyrgyzstan, and Tajikistan (Chinese Flora Editorial Board of the Chinese Academy of Sciences 1998). Their roots and rhizomes exhibit various pharmacological effects, such as bacteriostatic (Stefan et al. 2011), spasmolytic (Yazdi et al. 2011), anti-inflammatory and detoxifying (Kwon et al. 2010), anticancer (Hwang et al. 2008), and radiation blocking

effects (Shetty et al. 2002), rendering these herbs popular in the pharmaceutical world. In addition to pharmacological value, liquorice is also widely used in the food, tobacco, and cosmetic industries and animal husbandry (Housemna & Lacey 2002, Elghandour et al. 2018). In recent years, the purchase and sale of liquorice has risen sharply, leading to the decline of wild liquorice resources and in some places even their extinction (Liu et al. 2007). The imbalance between the supply and demand in liquorice market has become increasingly prominent and has been effectively alleviated by the cultivation of liquorice. However, frequent pest outbreaks cause a significant loss in the yield and quality of cultivated liquorice (Xu 2017).

Altica deserticola Latreille (Coleoptera: Chrysomelidae) is one of the most harmful pests to liquorice, and is distributed in Russia (Bieńkowski 2010), Turkey (Gok & Cilbiroglu 2005), and China (Zhao et al. 2016). It usually appears in April, enters dormancy at the end of September, and produces 3–4 generations a year (Li & Xing 1989). *Altica deserticola* occurs in both natural populations and cultivated fields of *Glycyrrhiza* species. Both the adults and larvae feed on liquorice leaves, causing serious damage to leaf blades, thereby weakening the photosynthetic capacity of the leaves and reducing the yield and quality of liquorice roots and rhizomes (Xiao et al. 2015). Consequently, farmers express less enthusiasm for liquorice cultivation. At present, chemical control is the only treatment adopted by farmers against *A. deserticola*. However, pesticide residue on plants may endanger the consumers. Therefore, searching for liquorice varieties with higher resistance to *A. deserticola* will positively affect the development of the liquorice and related industries. During field investigations, we observed more frequent outbreaks of *A. deserticola* in *G. uralensis* fields located in Changji Xinjiang (44°02' N, 87°30' E) than in *G. inflata* located in Aksu Xinjiang (41°17' N, 80°27' E). Whether this difference in pest outbreaks is caused by the diversities of biological characteristics of the two liquorices or by the differences in local climate or cultivation management measures (such as different water and fertilizer management) remains unclear.

Feeding behaviour of insects on host plants is often influenced by physical and chemical properties of the plants (Kursar & Coley 2003). For chewing insects, the harder the blade and thicker the leaf cuticle on both sides of the blade, the stronger its ability to resist insect phytophagy (Li et al. 2004, Kasseney et al. 2011). Chemical factors, such as the content of nitrogen and defensive substances, determine

whether insects will continue feeding on the plants (Mattson 1980, Strauss et al. 1999). It is generally considered that feeding on host plants with high nitrogen content contributes to the survival, development, and reproduction of insects (Giulio & Edwards 2010). Plant phenolics, especially tannins are an important defensive substance in plants, which bind to saliva proteins, producing astringent taste and reducing the feeding intensity of herbivorous insects (Makkar et al. 1995). Sun et al. (2008) found a significant negative correlation between tannin content in different poplar varieties and feeding intensity of *Saperda populnea* L. To explore the underlying internal mechanism of the difference in feeding resistance of the two cultivated liquorices to *A. deserticola*, and to provide information on physical or chemical traits for breeding of resistant liquorice varieties, under controlled laboratory conditions, we studied the feeding preference of *A. deserticola* for *G. uralensis* and *G. inflata* leaves by determining leaf hardness and thickness, cuticle thickness, and nitrogen and tannin contents in the two plant species.

MATERIALS AND METHODS

Plant and insect samples

Altica deserticola adults were collected from a population of *G. aspera* Pall. in the eastern suburb of Shihezi, Xinjiang, China (44°32' N, 86°10' E). All adults were housed in a light incubator, under 12 h of illumination at 25 °C and 12 h of darkness at 20 °C, light intensity of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and were fed with fresh leaves daily of *G. aspera*. The fertilized eggs laid by female insects were collected from leaves of *G. aspera* and incubated in a light incubator, and hatched in about 6 days. The larvae were also fed fresh leaves daily of *G. aspera*, and pupated in about 15 days, and emerged into adults after 6 to 8 days. The fully expanded fresh leaves of

G. uralensis and *G. inflata* with the same leaf age (30 days after foliation) required for the leaf-disc test were collected from the Licorice Resource Center of Shihezi University, Shihezi, Xinjiang, China (44°18' N, 86°05' E), where the mean annual precipitation in the region was 125-207.7 cm and the temperature was 6.5-7.2 °C.

A. *deserticola* choice test

A leaf-disc method was used to determine the feeding preference of the adults and larvae of *A. deserticola* for the leaves of *G. uralensis* and *G. inflata*. The leaves of both species were rinsed with clean water, dried with gauze, and discs with a diameter of 1 cm were made by a disc cutter punch. Ten leaf discs of each liquorice species (a total of 20 leaf discs) were placed together in a petri dish (9 cm diameter, Taixing Mingtai Scientific Instruments and Equipment Co., Ltd., Jiangsu, China) over a wet sponge covered with filter paper (Ø9 cm, Hangzhou Special Paper Co., Ltd., Hangzhou, China). The discs were fixed crosswise on the filter paper with pins (0.65*20 mm, Wuyi Jiangnan Cultural and Educational Supplies Factory, Zhejiang, China) to prevent their shuffling during feeding by *A. deserticola*, which will render identification of the varieties of leaf discs difficult. One healthy second-instar larvae (hatched for about 6 days) or new emerged adult after starvation for 5 h were selected and placed into the petri dishes with 20 leaf discs. Petri dishes with leaf discs without *A. deserticola* were used as controls. The larvae were allowed to feed in each experiment for about 24 h. We replicated 30 trials under the same conditions. The leaves were then pressed and dried, and the leaf area consumed (%) were determined by HP scanjet 5300C scanner (Hewlett-Packard, Loveland, CO, USA) and calculated by Adobe Photoshop CS6 (Adobe, San Jose, California, USA).

Mechanical and chemical properties of leaves of the two liquorices

Leaf hardness: Penetrability of the leaves of *G. uralensis* and *G. inflata* (maximum penetrability value represents the leaf hardness) were determined using a texture analyzer (TA.XT plus, Stable Micro Systems, UK) with its accompanying software Exponent 32 (Stable Micro Systems, UK). The measurements were conducted under the following settings: HDP/CH detection base, SMS P/2N sharp probe, 2 mm s⁻¹ speed before puncture, 1 mm s⁻¹ speed during puncture, 10 mm s⁻¹ speed after puncture, and 20 g puncture trigger value. Randomly selected thirty plants of the two liquorices, respectively, and collected one healthy and fully expanded leaves at the position of the fifth leaf from top to bottom of each liquorice, totalling 30 leaves. Each leaf was tested under the same test conditions three times to obtain the average values.

Leaf thickness and cuticle thickness: Healthy, fully expanded leaves of *G. uralensis* and *G. inflata* from 10 individual plants of each liquorice were cut into small pieces (1 cm × 0.5 cm) and placed in formaldehyde and acetic acid (FAA) solution (70% alcohol: glacial acetic acid: formaldehyde = 18:1:1) for 48 h. Transverse sections of the leaves (8 µm thick) were prepared using conventional paraffin sectioning (Gan & Xu 2019). The sections were stained with safranin and fast green, sealed with optical resin, observed under a light microscope (Olympus BX51, Olympus Optical, Tokyo, Japan), and photographed with an Olympus DP70 system. Leaf thickness and cuticle thickness of the adaxial and abaxial surface were measured by Motic Images Advanced 3.2 (Motic, Hong Kong), calculated their average value.

Leaf nitrogen content: Randomly selected thirty plants of the two licorices, respectively, and collected one healthy and fully expanded leaves at the position of the fifth leaf from top to

bottom of each licorice, totaling 30 leaves. Leaf samples of the two species were dried by oven, pulverized, and sieved through a 1.98 mm mesh, and then weighed to the nearest 0.1 g. Leaf N was measured using a Kjeldahl apparatus (K9840; Haineng Instrument Co., Ltd., Jinan, China) after digestion with sulfuric acid–hydrogen peroxide ($H_2SO_4-H_2O_2$) as described in Kirk (1950). Five samples were tested five times and their average values were calculated.

Tannin content: Randomly selected one hundred plants of the two liquorices, respectively, and collected one healthy and fully expanded leaves at the position of the fifth leaf from top to bottom of each liquorice, totalling 100 leaves. Leaf samples of the two species were dried naturally, pulverized, and sieved through a 1.98-mm mesh and 0.2 g of leaf powder was accurately weighed. The total tannin content was determined using the Folin-Denis procedure (Li et al. 2009) and tannic acid was used as a standard. Four kinds of tannins, tannic acid (Murdiati et al. 1992), ellagic acid (Gasperotti et al. 2010), gallic acid (Ovando-Martínez et al. 2018), and catechin (Persic et al. 2018), were determined by high-performance liquid chromatography (HPLC) (Agilent 1200; Agilent Technologies, California, USA). Five samples of each plant were tested, and their average value was calculated. Setting conditions are as follows:

Tannin acid: the mobile phase was containing solvent A: 0.07% acetic acid 15% and Solvent B: methanol 85%, isocratic elution. The flow rate was 0.5 mL/min and the volume injected was 10 μ L. The temperature of column was 25 °C, and UV detector was set at wavelength of 275 nm.

Ellagic acid: the mobile phase was containing solvent A: 0.1% acetic acid and Solvent B: acetonitrile. The gradient was 12–20% B for 16 min, 20%–25% B for 4min. The flow rate was 1.0 mL/min and the volume injected was 20

μ L. The temperature of column was 30 °C, and UV detector was set at wavelength of 265 nm.

Gallic acid: the mobile phase was containing solvent A: 0.1% acetic acid and Solvent B: acetonitrile. The gradient was 5–7.5% B for 10 min. The flow rate was 1.0 mL/min and the volume injected was 10 μ L. The temperature of column was 25 °C, and UV detector was set at wavelength of 267 nm.

Catechin: the mobile phase was containing solvent A: 0.1% acetic acid 68% and Solvent B: methanol 32%, isocratic elution. The flow rate was 1 mL/min and the volume injected was 10 μ L. The temperature of column was 30 °C, and UV detector was set at wavelength of 254 nm.

Data analysis

The SPSS 19.0 software (IBM Corp., New York, USA) was used to analyze the data. Difference in leaf area consumed (%), leaf hardness and thickness, cuticle thickness, leaf nitrogen and tannin content between the two liquorices were analysed using a T-test (arcsine transformation of the ratio to make it follow a normal distribution). Multiple comparison analysis was used for comparing the differences in content of the four kinds of tannins for each *Glycyrrhiza* species. The charts were produced using Origin 2016 (OriginLab, Hampton, USA).

RESULTS

Effect of plant type on adult and larval feeding

Adults of *A. deserticola* fed on the leaves of both species, but they consumed nearly 1.7-fold more *G. inflata* leaves when compared with the amount of consumed *G. uralensis* leaves (Fig. 1). In contrast, the larvae fed only on *G. uralensis* leaves, while the leaf discs of *G. inflata* in culture dishes remained intact (Fig. 2).

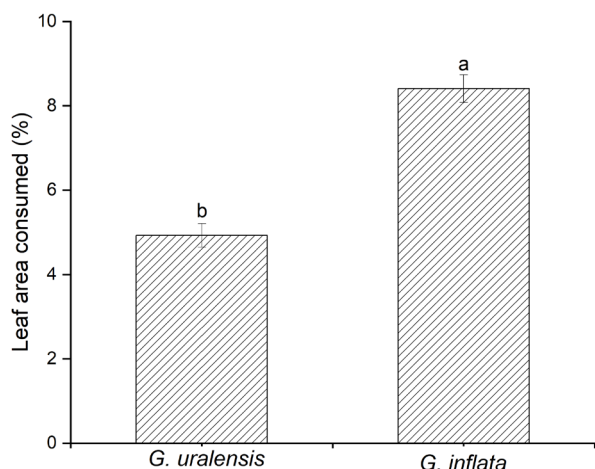


Figure 1. The percentage (%) of the leaf area consumed by adults of *Altica deserticola* in two licorice (*Glycyrrhiza*) species. Different letters denote significant differences between the means of the same color columns ($P < 0.01$).

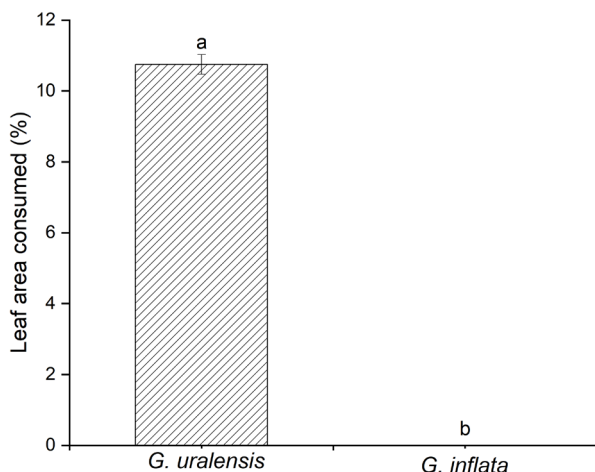


Figure 2. The percentage (%) of the leaf area consumed by larvae of *Altica deserticola* in two licorice (*Glycyrrhiza*) species. Different letters denote significant differences between the means of the same color columns ($P < 0.01$).

Comparison of leaf hardness

The leaf of *G. inflata* was significantly harder ($F = 0.146$, $df = 58$, $P < 0.01$) than *G. uralensis* (Fig. 3)

Comparison of blade thickness and cuticle thickness

The leaves of *G. inflata* were thicker than those of *G. uralensis* (Fig. 4a and c; Table I), and there

was a significant difference in leaf thickness between the two licorices ($P < 0.01$). The leaf cuticle thickness on the adaxial and abaxial side in *G. inflata* was also significantly greater than that in *G. uralensis* (Fig. 4b and d; Table I; $P < 0.01$).

Comparison of nitrogen content

The nitrogen content of *G. inflata* was significantly greater ($F = 0.435$, $df = 8$, $P < 0.01$) than *G. uralensis* (Fig 5.)

Comparison of tannin contents

The total tannin content in the leaves of *G. inflata* was significantly higher than that of *G. uralensis* ($F = 0.544$, $df = 8$, $P < 0.01$; Fig. 6). In both species, the tannic acid was the primary tannin constituent followed by that of catechin, with both accounting for more than 88% of the four kinds of tannins content. The content of gallic acid and ellagic acid in the leaves was only 8% of the four kinds of tannins levels ($P < 0.01$; Fig. 7).

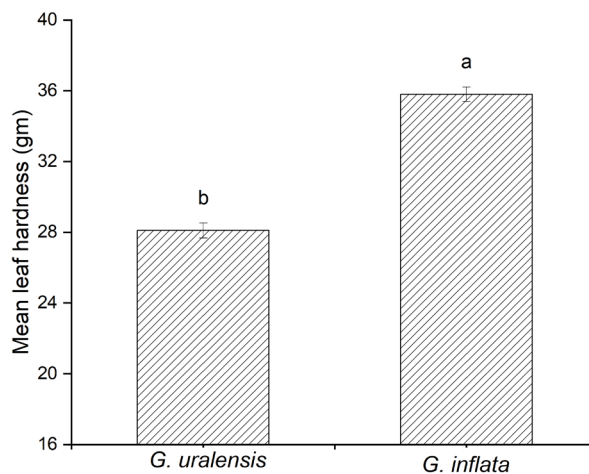


Figure 3. Leaf hardness of two licorice (*Glycyrrhiza*) species. Means with differing letters are significantly different ($P < 0.01$).

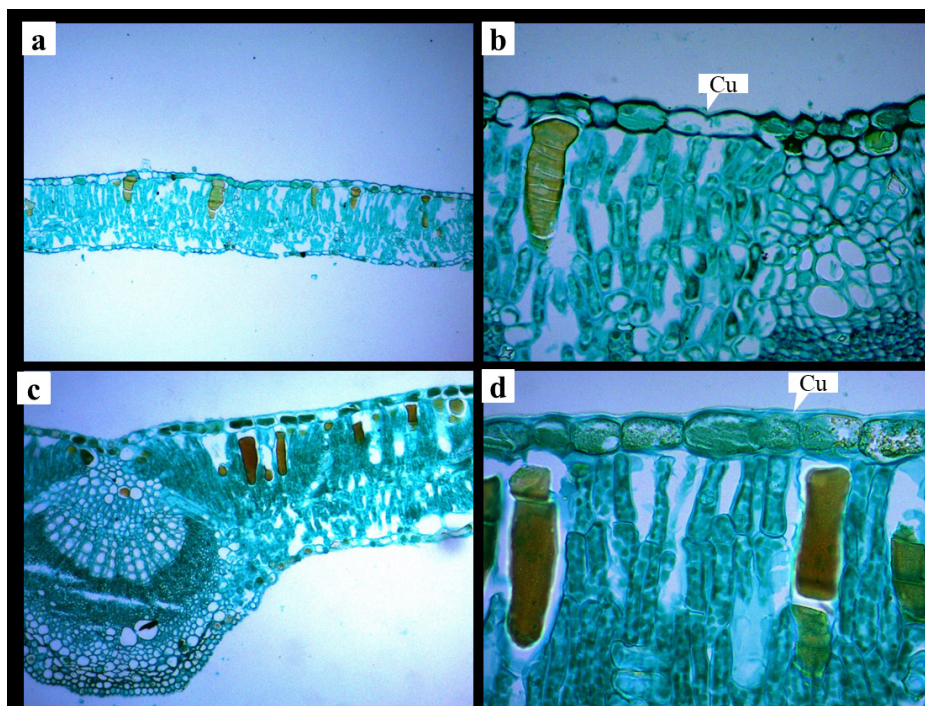


Figure 4. Leaf blade and cuticle thickness in two licorice (*Glycyrrhiza*) species. a: *G. uralensis* leaves 100×; b: *G. uralensis* leaves 400×; c: *G. inflata* leaves 100×; d: *G. inflata* leaves 400×; Cu: cuticle.

Table I. Comparison of leaf thickness and cuticle thickness between two species of *Glycyrrhiza*.

Indexes (µm)		F	df	<i>G. uralensis</i>	<i>G. inflata</i>
Leaf thickness		3.184	18	228.080 ± 0.890b	454.300 ± 1.460a
Leaf cuticle thickness	adaxial	4.459	18	2.330 ± 0.029b	7.687 ± 0.086a
	abaxial	7.264	18	1.836 ± 0.044b	5.811 ± 0.133a

Different letters in the same row indicate significant difference (P < 0.01). Data are presented as means ± standard error (SE).

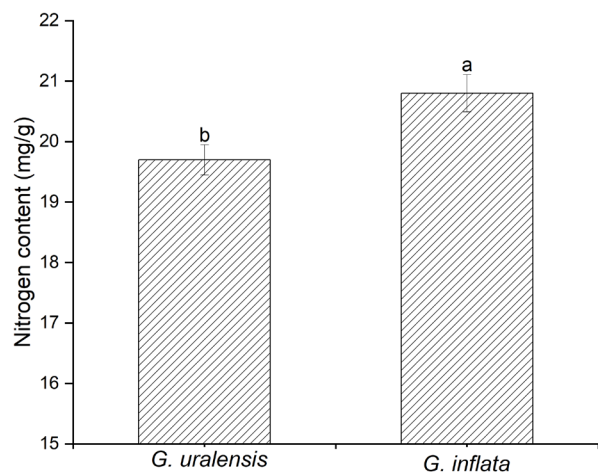


Figure 5. Leaf nitrogen content of two licorice (*Glycyrrhiza*) species. Means with differing letters are significantly different (P < 0.01).

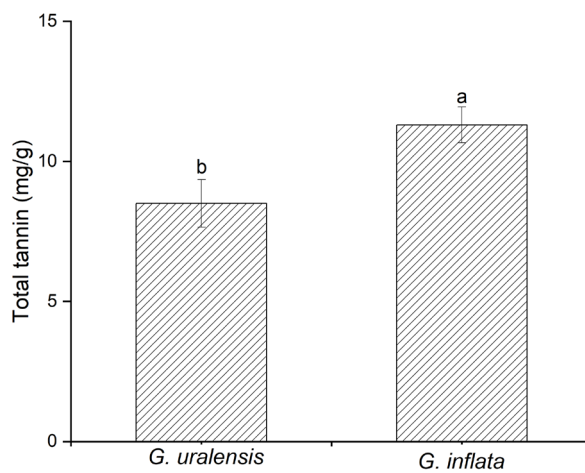


Figure 6. Total tannin content in the leaves of two licorice (*Glycyrrhiza*) species. Means with differing letters are significantly different (P < 0.01).

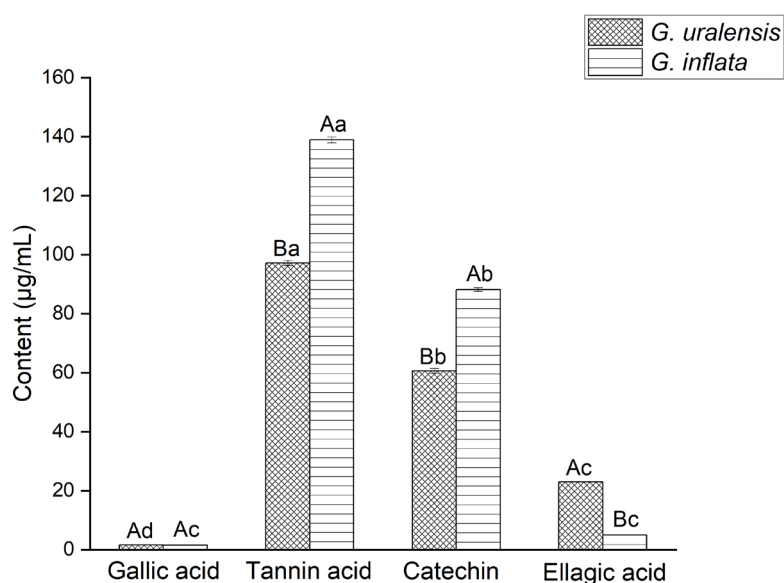


Figure 7. The content of four kinds of tannins in the leaves of two licorice (*Glycyrrhiza*) species. Different uppercase letters denote significant differences between means of the columns ($P < 0.01$), and different lowercase letters denote significant differences between means of the four kinds of tannins in the same licorice species ($P < 0.01$).

DISCUSSION

Leaves are the main photosynthetic organs of plants, and any damage to leaves may reduce the accumulation of biomass, affecting the normal plant growth and development (Mauricio et al. 1993). Field investigations suggested the presence of a large number of larvae and adults in the above-ground parts of licorice (Figures S1 and S2 - Supplementary Material). Both growth stages of the insect feed on licorice leaves, affecting the photosynthesis and biomass accumulation and even resulting in plant death. Therefore, it is of important scientific and economic significance to study the feeding preferences and feeding mechanisms of *A. deserticola* on licorice leaves. Our study indicated that the feeding preference of *A. deserticola* for licorice leaves is likely to be related to the physical and chemical properties of their leaves.

Our study found the relation of the feeding preference of *A. deserticola* larvae with leaf hardness and thickness and cuticle thickness—the larvae preferred to feed on thinner, softer leaf blades with thinner cuticles. This is similar to the results of Xia et al. (2013), who found that evergreen plants *Symplocos lancifolia*, *Loropetalum*

chinense, and *Myrica rubra*, defended against insect phytophagy by increasing leaf thickness and hardness. However, this is inconsistent with the feeding preference of the adult forms for the two licorice species, which may be attributed to differences between the larvae and adults, such as their sizes, morphology of their mouthparts (Li & Xing 1989, Aslan et al. 2004, Bieńkowski 2010). We speculated that leaf hardness and thickness and cuticle thickness are only partial factors affecting the feeding preference of *A. deserticola* for the two types of licorice leaves. Other leaf characteristics such as leaf shape, colour, and nutrition may affect the feeding preference of *A. deserticola*, which requires further research.

Nitrogen is recognized as the most important limiting nutrient element for herbivorous insects. The average nitrogen content in most plants is 2%, while that in insects is as high as 7% (Wiesenborn & William 2011). To meet such high nitrogen needs, the insect must feed on nitrogen-rich plants. The nitrogen content in the leaves of *G. inflata* is significantly higher than that in *G. uralensis*, which is consistent with the feeding preference of *A. deserticola* adults, indicating that the leaf nitrogen content is an important factor for feeding preference of this insect.

However, the larvae fed only on the leaves of *G. uralensis*, probably due to lower leaf hardness and thickness. Wheeler et al. (1998) reported that the larvae of *Spodoptera pectinicornis* increased their consumption 3-fold when feeding on *Pistia stratiotes* leaves with low nitrogen content, whereas the feeding time of *Pieris rapae* larvae was significantly shortened with increasing nitrogen content in cabbage (Loader & Damman 1991). *Altica deserticola* larvae might compensate for the deficiency of nitrogen in *G. uralensis* by increasing the amount of consumed food or by the extension of their feeding time during their feeding process. In contrast, the relatively well-developed mouthparts in adults support their preference for *G. inflata* leaves, which are characterized by higher nitrogen content compared with the leaves of *G. uralensis*.

In general, more nutritious food provides a more effective nutrient supply to insects. However, whether insects favour certain food depends on their digestibility and absorption efficiency to the food. Tannins are an anti-nutritional factor that binds to proteins in the digestive tract of insects, forming insoluble compounds, which are thus not conducive to digestion and absorption of the nutrients by insects (Stienezen et al. 1996). Previous studies reported that liquorice contains tannins such as tannic acid, catechin, ellagic acid, and gallic acid (Cheel et al. 2013, Hamad et al. 2015, Komes et al. 2016, Rahman et al. 2018). Besides, some researchers found that insects' feeding preference for host plants was negatively correlated with tannin content (Zhou et al. 1996, Fonseca et al. 2018). We determined the contents of total tannins and their four components in the leaves of the two liquorices using the Folin-Denis method and HPLC. Our results showed that the higher tannin contents the *Glycyrrhiza* leaves had, the less likely were they eaten by *A. deserticola*.

In summary, the feeding preference of *A. deserticola* for leaves of the two liquorice is the

result of a combination of various factors. The difference in feeding preference between adults and larvae may be due to different factors playing different roles in different stages of insect life history. During the larval stage, leaf hardness and thickness and cuticle thickness played a greater role on the feeding of insects, whereas during the adult stage, nitrogen content and tannin content of the leaves played a greater role. Therefore, in the process of cultivation of *Glycyrrhiza*, different pest management plans should be made according to the feeding preference of *A. deserticola* in different growth stages and the corresponding physical and chemical properties of *Glycyrrhiza* leaves. Besides, to gain more accurate results about the harm of *A. deserticola* to the two *Glycyrrhiza* species, the survival and growth rate of the larvae on the two *Glycyrrhiza* species should be further studied.

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SUPPLEMENTARY MATERIAL

Figures S1 and S2.

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