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# INTRAFLORAL DIFFERENTIATION OF STAMEN MORPHOLOGY AND FUNCTION OF *CAPPARIS SPINOSA* L.

**YANG MEILIN[1,2], YIN LINKE[1*], YAN CHENG[1] AND CAO QIUMEI[3]**

[1]*Key Laboratory of Biogeography and Bioresource in Arid Land, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China*
[2]*Turpan Eremophytes Botanical Garden, Chinese Academy of Sciences, Turpan 838000, China*
[3]*Xinjiang Agricultural University, Urumqi 830000, China*
[*]*Corresponding author's email:yinlk@ms.xjb.ac.cn; Tel: 086-13609971987*

**Abstract**

In *Capparis spinosa* L. (Capparidaceae), a woody perennial with both male and perfect flowers on the same plant, each flower has both short and long stamens. Flowers of *C. spinosa* were examined for 2 years at the Turpan Eremophytes Botanical Garden in Xinjiang, China. Stamen morphological characteristics, pollen vigor, quantity of pollen, and insect visitation were compared for flowers with short and long stamens to ascertain the function of the two types of stamens. Both types of flowers, male and perfect flowers, had both long and short stamens in the same flower. The number of stamens and pollen grains as well as the color of filaments in a single flower were significantly different between long and short stamens. The number of pollen grains produced by long stamens in a flower was greater than those of shorter stamen in the same flower, although pollen vigor did not differ between pollen from long and short stamens. Insect visitation frequency was higher for long stamens than for short stamens. The pollen of long and short stamens was used for hand-pollination. The rates of fruit and seed set from the pollen of long stamens were higher than those from the pollen of short stamens. While the main function of long stamenswas to provide pollen for visiting insects, short stamens might improve male resources in three ways: by providing a guaranteeof pollen availability in adverse weather conditions, increasingthe space available for pollen capture and increasing the visitation timeofindividual insects.

**Key words:***Capparis spinosa* L.; Long stamen; Short stamen; Morphological differentiation; Function differentiation.

## Introduction

The function of the male parts of plants is to distribute pollen to the stigma; this function drives some of the evolutionary selection pressure on the flower and results in the formation of morphological traits (Willson, 1979; Bell, 1985; Stanton *et al.*, 1986; Barret, 2002, 2003; Zhang, 2004). The morphology and structure of stamens contribute directly to the male function of the plant and exhibit changes caused by evolutionary selection pressures to the degree that a notable disparity in the morphology of stamens may appear in a single flower (Darwin, 1877; Müller, 1882; Luo & Zhang, 2005). The term "heteromorphic stamens" means that the morphology, size and color of the stamens have significant differences, including differences in functions within a single flower (Darwin, 1877; Müller, 1882; Luo & Zhang, 2005).

The fact that many kinds of differentiation occur among heteromorphic stamens has attracted the attention of researchers (Darwin, 1877; Müller, 1882; Foerste, 1888). Not only do stamens vary morphologically, different types of heteromorphic stamens may also differ in function (Jesson & Barrett, 2002a, 2002b; Luo & Zhang, 2005). Stamens can be classified as feeding and pollinating stamens, where feeding stamens attract pollinators and provide pollen, and pollinating stamens create pollen for reproduction (Jesson & Barrett, 2002a, 2002b; Jesson *et al.*, 2003; Luo & Zhang, 2009).

*Capparis spinosa* L. (Capparidaceae), a woody perennial, has both male and perfect flowers on the same plant, a characteristic known as andromonoecy (Zhang & Tan, 2008). This species exhibits both self- and cross-pollination. The main visitors to *C. spinosa* include bees (Hymenoptera) and moths (Lepidoptera) (Zhang & Tan, 2009). We observed that the stamens of male and perfect flowers feature morphological differences and that both types of flowers have long and short stamens in a single flower. The stamens of male and perfect flowers show no differences in morphology or in the quantitative proportion of the kind of stamens the two types of flowers produced (Yang *et al*., 2015).

*C. spinosa* has a typical andromonoecious sexual system. This study is aimed to compare the morphology, pollen vitality, as well as the number of pollen grains and insect visits between long and short stamens, and to understand the different functions of the two kinds of stamens.

## Materials and Methods

**Study site and plant material:** Samples for this study were collected from 30 planted shrubs that were more than 30 years old. These grew in the cultivated population of *C. spinosa* in the gardens of Turpan Eremophytes Botanical Garden. The population currently shows normal flowering and healthy growth, with average crowns growing 305 cm tall and 504 cm wide. Flowers were randomly selected from these 30 sample shrubs and used for the experiment.

**Study site:** The study was conducted in 2012–2013 at Turpan Eremophytes Botanical Garden (TEBG)(Fig.1), in Turpan city, eastern Xinjiang, China (42°51′52.5″N, 89°11′06.8″E) at 76–95 m below sea level.

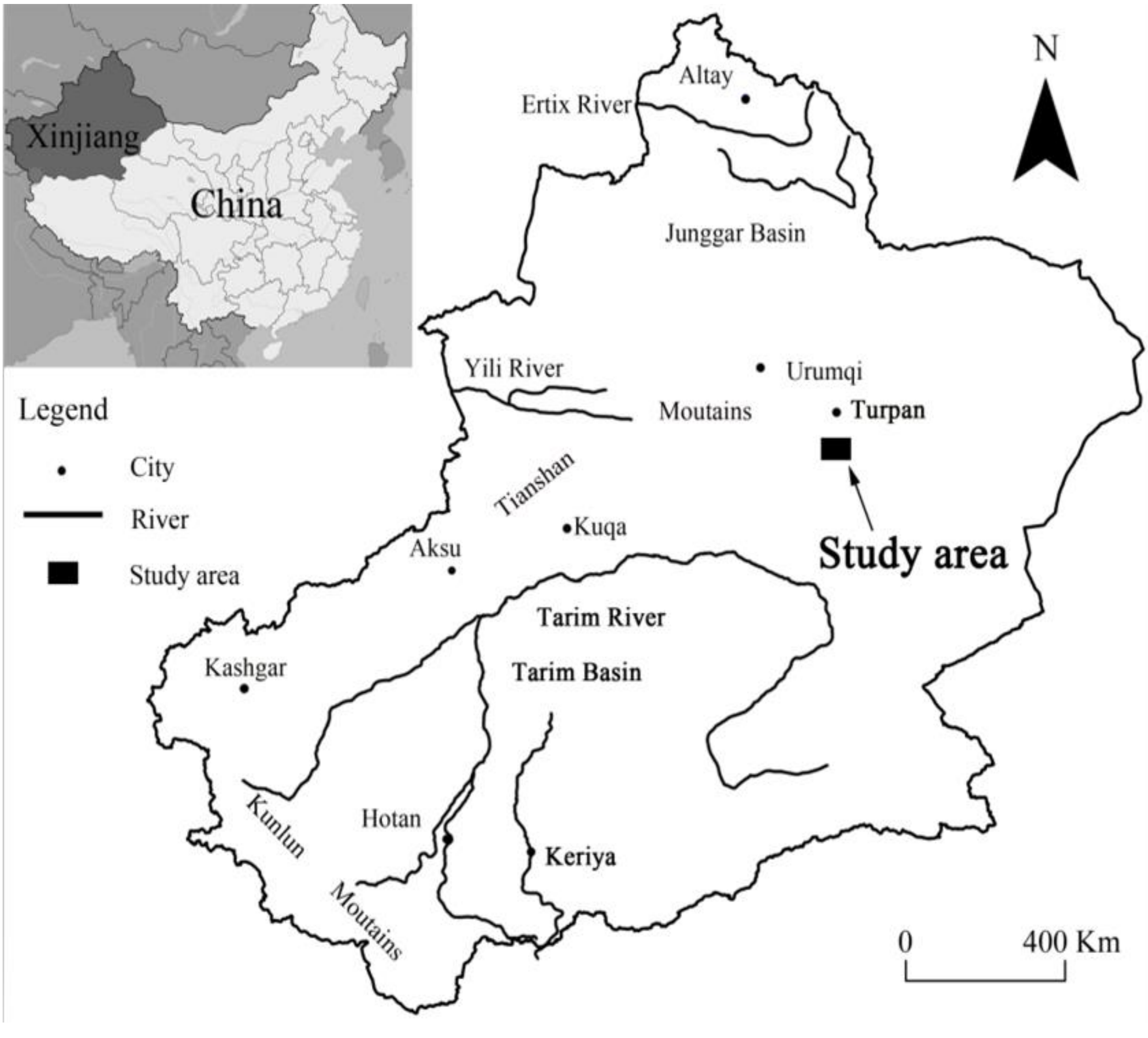


Fig. 1. The map of the study area(Yang*et al.*, 2014).

**Climate:** Meteorological data were collected from an automatic weather station in the garden. The climate is characterized by low rainfall, high evapotranspiration, high temperatures and dry winds. The annual mean temperature of 13.9°C ranged from −28.0°C to 47.6°C with an annual mean evaporation of 2387.8 mm. The site experiences 26.8 windy days annually, with a maximum wind speed of 40 m $s^{-1}$.

**Observation of morphological differentiation of stamens in a flower:** Twenty perfect flowers and 20 male flowers that opened on the same day were randomly selected from the population. Anther and filament lengths of long and short stamens were measured, and their color and morphology were recorded.

**Pollen counts and pollen vitality of longer and shorter stamens:** Twenty perfect flowers and 20 male flowers with anthers that had not dehisced and that had all opened on the same day were randomly selected from the population. Anthers of long and short stamens were crushed and put into methylene blue and ethyl alcohol, with water added to a 2 ml total volume. The pollen was shaken in the solution. The solution and 2 μl of the suspension were examined using a glass microscope slide. Pollen counts were repeated three times under an optical microscope (Olympus). The viability of pollen from long and short stamens was estimated in accordance with Dafni (2005).

**Comparison of fertile pollen percentage of the long and short stamens:** Twenty perfect flowers and 20 male flowers with anthers that had not dehisced and that had all opened on the same day were randomly selected from the population. The fertile pollen percentage was calculated using the method described by Chen (1991). Each sample from either long or short stamens was placed on a glass slide, dyed with malachite green-acid fuchsin-Orange G dye solution. and then 6 vision and statistical fertile and abortive pollen counts under the optical microscope (Olympus). If the pollen wall was green and protoplasm was red, the pollen was counted as fertile. If the pollen wall was green and protoplasm was not red, the pollen was counted as abortive.

**Comparing the pollination function of longer and shorter stamens:** Two hundred and seventy perfect flowers from the population were hand-pollinated in different treatments as follows.

1) Long stamens of 30 perfect flowers removed; flowers bagged without hand-pollination.
2) Long stamens of 30 perfect flowers removed; flowers not bagged without hand-pollination.
3) Short stamens of 30 perfect flowers removed; flowers bagged without hand-pollination.
4) Short stamens of 30 perfect flowers removed; flowers not bagged without hand-pollination.
5) All stamens of 30 perfect flowers removed; flowers bagged without hand-pollination.
6) Stamens of 30 perfect flowers removed; flowers bagged with long stamens pollen.
7) Stamens of 30 perfect flowers removed; flowers bagged with short stamens pollen.
8) Only petals removed.
9) Control group; noprocessing.

All bags were removed after the flowering season. Fruit set and number of seeds in each fruit were counted when fruits had matured.

**Observations on flower visitors:** Using the same population of plants, three treatments were established for observing visiting time, pollinator behavior and visiting purpose of insects. These data were recorded from 19:30 of the first day to 12:30 of the next day on five consecutive days. Five to ten flowers were randomly selected from the population every day before they opened and stamen samples were collected in one of three ways: no removal, removal of shorter stamens, removal of longer stamens.

**Data analyses:** All observation data for characteristics of long and short stamens were counted as the means of perfect flowers and male flowers (average of 40 flowers). All data analyses were carried out using Minitab 16.0 & Origin 8.0 statistical tools.

**Results**

**The morphological differentiation characteristics of long and short stamens:** The morphological characteristics of the same type of stamen did not differ between male and perfect flowers. The number of long stamens per flower was greater than that of short stamens ($p<0.01$). The average filament lengths of long and stamens differed significantly, at 24.61 mm and 13.17 mm, respectively ($p<0.01$). The lengths of the anthers did not differ significantly. The long stamens were arranged on the external side of each flower and had white filaments, while the shorter stamens were arranged inside and had green filaments. The anthers were all white (Table 1).

**Pollen counts, pollen vitality and fertile pollen percentage of long and short stamens:** The pollen counts of individual anthers did not differ significantly between long and short stamens in *C. spinosa*. The total pollen count of long stamens was higher than that of short stamens ($p<0.01$; Table 2).

Pollen vitality of *C. spinosa* was highest (>80%) 2–6 h after anthers dehisced, and pollen grains remained viable for 20 h. No difference was observed in the pollen vitality of long and short stamens (Fig. 2).

**Table 1. Comparison the characteristics of diadelphous stamens in male and perfect flowers.**

| | Long stamens | Short stamens | *P* |
|---|---|---|---|
| Number | 45.90 ± 4.72 | 19.15 ± 2.30 | <0.01 |
| Length of filaments (mm) | 24.61 ± 2.84 | 13.17 ± 1.22 | <0.01 |
| Length of anthers (mm) | 2.34 ± 0.40 | 2.18 ± 0.45 | 0.60 |
| Colour of filaments | White | Green | - |
| Colour of anthers | White | White | - |

**Table 2. Pollen number of diadelphous stamens in male and perfect flowers.**

| | Long stamens | Short stamens | *P* |
|---|---|---|---|
| Number of pollenper anther ($\times 10^3$) | 75.55 ± 6.94 | 76.75 ± 5.48 | 0.55 |
| Number of stamenspollen per flower ($\times 10^4$) | 343.82 ± 106.64 | 146.02 ± 112.89 | <0.01 |

**Table 3. Different pollination effect on fruit formation and development of *C. spinosa*.**

| Perfect flowers | Treatment | Fruit rate (%) | Fruit length (mm) | Fruit diameter (mm) | Fruit weight (g) |
|---|---|---|---|---|---|
| Removal longer stamens | Bagged without pollination | $10.00 \pm 4.71^{d}$ | - | - | - |
| | No Bagged without pollination | $25.00 \pm 2.36^{c}$ | $12.78 \pm 1.58^{c}$ | $8.83 \pm 1.13^{c}$ | $0.48 \pm 0.23^{d}$ |
| Removal shorter stamens | Bagged without pollination | $8.34 \pm 2.35^{d}$ | - | - | - |
| | No Bagged without pollination | $33.34 \pm 4.72^{c}$ | $15.96 \pm 0.70^{b}$ | $10.73 \pm 0.77^{b}$ | $1.00 \pm 0.15^{c}$ |
| Removal all stamens | No Bagged without pollination | $11.67 \pm 2.35^{d}$ | - | - | - |
| | Crossed with longer stamens pollen | $63.33 \pm 2.72^{a}$ | $20.35 \pm 2.51^{a}$ | $13.13 \pm 1.39^{a}$ | $2.01 \pm 0.62^{a}$ |
| | Crossed with shorter stamens pollen | $35.00 \pm 7.93^{c}$ | $14.42 \pm 1.97^{bc}$ | $10.18 \pm 1.30^{b}$ | $1.01 \pm 0.30^{c}$ |
| Remove the petals | | $46.67 \pm 4.72^{b}$ | $20.44 \pm 2.16^{a}$ | $13.13 \pm 1.86^{a}$ | $1.95 \pm 0.16^{b}$ |
| Control group | | $55.00 \pm 2.36^{ab}$ | $21.17 \pm 1.45^{a}$ | $13.27 \pm 0.67^{a}$ | $2.56 \pm 0.27^{a}$ |

**Table 4. Different pollination effect on seed setting rate and development of *C. spinosa*.**

| Perfect flowers | Treatment | Seed number (n) | Seed length (mm) | Seed diameter (mm) | Thousand seed (g) |
|---|---|---|---|---|---|
| Removal longer stamens | Bagged without pollination | - | - | - | - |
| | No Bagged without pollination | 52.43 ± 8.20$^{c}$ | 2.17 ± 0.15$^{b}$ | 1.87 ± 0.12$^{bc}$ | 2.60 ± 0.04$^{d}$ |
| Removal shorter stamens | Bagged without pollination | - | - | - | - |
| | No Bagged without pollination | 84.40 ± 16.04$^{bc}$ | 2.42 ± 0.28$^{a}$ | 1.92 ± 0.26$^{abc}$ | 2.71 ± 0.02$^{cd}$ |
| Removal all stamens | No Bagged without pollination | - | - | - | - |
| | Crossed with longer stamens pollen | 174.75 ± 87.46$^{a}$ | 2.21 ± 0.28$^{b}$ | 1.76 ± 0.18$^{c}$ | 2.84 ± 0.07$^{c}$ |
| | Crossed with shorter stamens pollen | 83.80 ± 20.54$^{bc}$ | 2.29 ± 0.18$^{ab}$ | 1.83 ± 0.15$^{bc}$ | 3.10 ± 0.31$^{b}$ |
| Remove the petals | | 102.90 ± 10.41$^{b}$ | 2.15 ± 0.18$^{b}$ | 2.05 ± 0.17$^{a}$ | 3.10 ± 0.20$^{b}$ |
| Control group | | 175.30 ± 22.64$^{a}$ | 2.27 ± 0.22$^{ab}$ | 1.96 ± 0.27$^{ab}$ | 3.72 ± 0.24$^{a}$ |

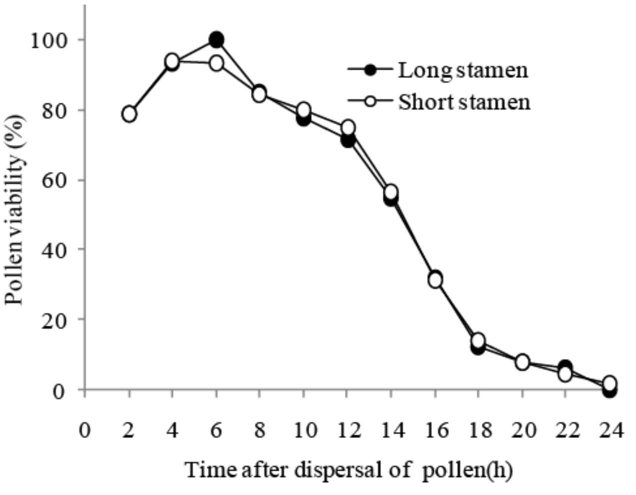


Fig. 2. Dynamic curve of pollen viability of longer and shorter stamens.

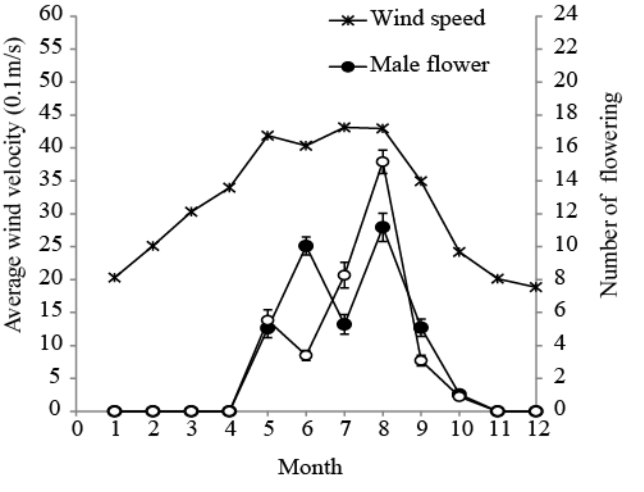


Fig. 3. The relationship between average wind speed of Turpan and the number of flowering of *C. spinosa*.

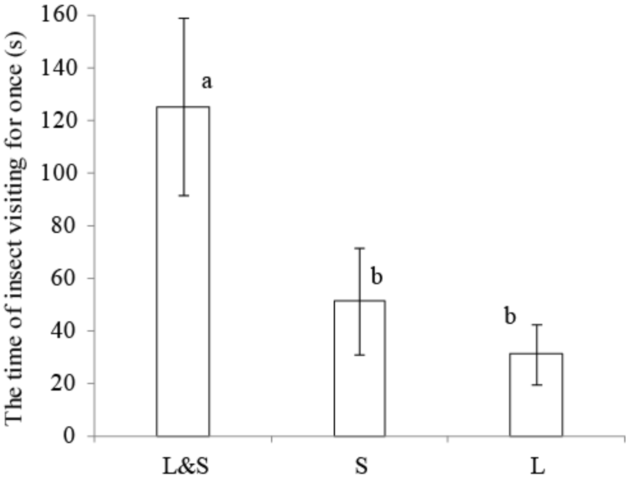


Fig. 4. Statistical the time of insect visiting for once(L&S: Remain longer stamens and shorter stamens; L: Remain longer stamens; S: Remain shorter stamens).

**The functional differentiation of long and short stamens in single flower:** Table 3 demonstrates the viability of perfect flowers of *C. spinosa* when all stamens had been removed or when either long or short stamens had been removed from an individual flower; in all three of these cases, the flowers had been bagged before they opened. All of these flowers could produce fruit, but fruit set was low in all cases. Pollen from both long and short stamens were able to fertilize eggs and result in the production of seeds. The results from observation of insect visitation showed that both kinds of stamens were visited by insects, and their pollen was transferred to perfect flowers. The bag mark experiment showed that when all stamens were removed from perfect flowers of *C. spinosa* and the flowers were not bagged, these flowers could produce fruits with seeds.

The perfect flowers sampled with all stamens present were hand-pollinated with pollen grains from either long or short stamens. The fruit set of flowers pollinated using long stamens was higher than those pollinated with short stamens, and was also higher than the fruit set of flowers pollinated naturally by insects or wind. The size and mass of fruits pollinated by long stamens were larger than those of fruits produced from pollen of short stamens, but slightly smaller than flowers pollinated naturally (Table 3). As pollen viability did not differ significantly between pollen from either long or short stamens, we believe the main function of longer stamens was to provide pollen.

More seeds were produced by pollen from long stamens than by pollen from short stamens, but the size and mass of seeds were lower for fruits pollinated by short stamens; the quality of seeds produced by pollen from long or short stamens was inferior to that of plants growing naturally (Table 4).

**Insect pollination frequency for long and short stamens:** The number of flower-visiting insects per flower was higher on sunny than on cloudy days. Visiting frequency was not significantly different for fruits hand-pollinated by long and short stamens. In breezy conditions, insects visited the flowers an insignificant number of times. Longer stamens had higher spatial locations within an individual flower than shorter stamens and appeared to experience larger amplitudes of oscillation under windy conditions, while insects visited shorter stamens more frequently than longer stamens under windy conditions. The relationship between local average wind velocity and the flower phenology of *C. spinosa* has been previously analyzed; the results showed that the flowering season of *C. spinosa* was from May to October, with two main overlapping flowering peaks (Yang *et al*., 2014). These two flowering peaks coincided with the months of maximum wind velocity (Fig. 3). This proved that shorter stamens provided more stable pollination environments and were more conducive to food acquisition by insects on windy days.

Long stamens were visited by insects an average of 11 times per minute and five to six times per minute for short stamens; the visiting frequency was higher in long stamens. This proved that insects visited different types of stamens with different frequencies, but the insects were attracted to long stamens more frequently and obviously.

Observations on insect pollination revealed that most insects visited the long stamens counterclockwise and individually (one stamen at a time). When many insects were on the long stamens of a single flower, short stamens acted as a bridge for insects to reach the opposite long stamen. If short stamens were removed, insects would rarely reach the opposite long stamens and would fly away (Fig. 4).

The visiting frequency of insects to short stamens was not affected by removal of long stamens; however, insects did visit long stamens that had dropped on the ground. The frequency of insect visits to long stamens was not affected by the removal of short stamens; insects were not observed visiting short stamens that had dropped on the ground.

## Discussion

In different plant species, long and short stamens vary in different ways, and the diversity of stamen morphology indicates the importance of adaptation. The dimorphic stamens in *C. spinosa* were differentiated by the filament length, with some filaments being either relatively long or short. This type of stamen differentiation is by far the most widespread in the plant world.

Long stamens of *C. spinosa* mainly serve as pollen providers, i.e. their anthers were "pollinating" anthers. There were more long stamens arranged on the outside of a flower than there were short stamens arranged on the inside of the flower. This stamen arrangement not only improves the pollen productivity of a flower, but it also conserves pollen resources and maximizes male reproductive function. In limited space, the efficient male resource conservation of this species allows for maximization of pollination production in space and of the percentage of flowers fertilized, thus improving the male reproductive function. Increasing the availability of male resources and the efficiency of their production has a positive effect, showing evolutionary adaptation (Harder & Barrett, 1993; Escaravage *et al.*, 2001).

The white anthers of long and short stamens of *C. spinosa* matched the white color of most of the bees and moths that are the main visitors of *C. spinosa* (Guan *et al.*, 2005). Insects visited long stamens, those arranged externally on a flower, more frequently than short stamens always found in the flower center. The long and short stamens had white and green filaments, respectively.

The insect visitors almost always visited the long stamens in a counterclockwise direction individually, but when there were many insects on the long stamens, the short stamens appeared to act as a "bridge" and "waiting area." If short stamens were removed from an individual flower, the arriving insects would infrequently move across to longer stamens briefly and then fly away. This proved that the presence of shorter stamens not only increased the pollination area but also helped increase the time insects spent visiting a flower.

When a plant produces a large number of stamens this forces a differentiation in resource allocation and an adjustment in the flower. The changes in the number and viability of pollen grains produced in a plant exhibiting heteromorphic stamen differentiation are the result of resource allocation and functional differentiation (Ren *et al.*, 2012). The quantity and quality of pollen may directly affect the production of fruit and seed (Medrano *et al.*, 2000; Kliber & Eckert, 2004; Wang *et al.*, 2010). In the present study, pollen viability did not differ significantly between plants modified to have only long or short stamens. However, the total number of long stamens was greater than that of short stamens and long stamens had a higher frequency of visits by insects. Because the above stamen differences greatly improve the ability of a plant to distribute pollen to the stigmas, the relative proportions of fruit and seed set from long stamen pollen was higher than that from short stamen pollen.

The stamens of *C. spinosa* differentiated into long and short stamens and this has played the role of "bet-hedging." With these dimorphic stamens, on sunny days more pollen from long stamens would be transmitted by the visitors than that from short stamens. On breezy days, insects were observed to have great difficulty staying on the anthers of long stamens, in which case they preferred the short stamens. Short stamens were protected from the wind by the perianth, while the long stamens were more affected by strong winds. Short stamens appeared to provide a stable landing platform for visitors compared with long stamens and the insects benefited by still being able to acquire edible pollen under adverse weather conditions. When some pollen was in a protected position so that insects could distribute it to the stigmas, this guaranteed a higher percentage of fructification and seed-set in unfavorable weather conditions.

Tian (2013) found that both long and short stamens of *Glycyrrhiza glabra* and *Glycyrrhiza uralensis* were "pollinating" stamens. Also, while both long and short stamens of *C. spinosa* were "pollinating" stamens, these two types of stamens had functional differences. Long stamens were mainly pollen providers and were visited more frequently, but short stamens mainly increased the pollination rate of an individual flower and provided a "protective" pollination environment by providing a platform where pollinators could land and maneuver. In addition, the presence of short stamens helped improve the fitness of offspring by using minimal reproductive resources while maximizing the available pollination space and increasing the pollination rate to improve the male reproductive function.

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