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# THE CHARACTERISTICS VARIATION OF THE FLOWERS OF *CAPPARIS SPINOSA* L. DURING THE EXTENDED FLOWERING PROCESS AND THE INFLUENCE OF THE RATE OF SEED-SETTING

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**Abstract**

The reproductive characteristics of *Capparis spinosa* (Capparaceae) were examined at the Turpan Eremophytes Botanical Garden in Xinjiang, China. The flowering period was approximately five months long (from May to mid-October of 2011), during which time, two main and overlap flowering peaks emerged. Several significant differences between the two peaks were found: the number of flowers and duration of the flowering period for male flowers were identical in both peaks, but differed for perfect flowers(contain stamens and pistil); the filaments of both long and short stamens in male and perfect flowers in the first peak were longer than those in the second, whereas anther length showed the opposite trend; the frequency of fruit set and size in the first peak was respectively higher and larger than the second; and the seeds produced in the first peak were smaller and lighter than the second. These results provide that the continuously blooming *C. spinosa* and the variation in the proportion of male and perfect flowers have played a positive role in ensuring a continuous supply of pollen and controlling the investment of fruit.

## Introduction

Plants with an extended flowering period have an increased number of opportunities to mate with a greater number of individuals, and control the investment in flowers and fruits more effectively (Bawa, 1983; De Jong *et al*., 1992). An extended flowering period (Sazima, 1977; Augspurger, 1979) provides a long-term resource (Bertin, 1982; Dobkin, 1984) and reduces the risk of reproductive failure, ultimately affecting the progeny. Thus, extended flowering contributes to reproductive success (Pico & Retana, 2000).

*Capparis spinosa* L. (Capparidaceae) is a winter deciduous, spiny, woody perennial native in the southeastern Mediterranean. Because of its ability to grow under arid conditions, *C. spinosa* (caper) appears to be a suitable candidate for the protection of decertified and degraded areas (Rhizopoulou, 1990; Sakcali *et al*., 2008). The life cycle of the species is completed during the dry season in the Mediterranean Basin (Eisikowitch *et al*., 1986; Rhizopoulou, 1990; Rhizopoulou & Psaras, 2003; Danin, 2010), where new stems sprout in May. There, the nocturnal, short-lived flowers open once and expand at dusk within an hour, from June to August (Rhizopoulou *et al*., 2006). The seeds in Turpan, Xinjiang, however, germinate in late March and the flowering period begins from late April to early May. The best germination percentage of caper seeds, 250 ppm $GA_3$ and 8000 ppm $KNO_3$ and for the strongest seedling 100 ppm $GA_3$ plus 1000 ppm $KNO_3$ can be used (Arefi *et al*., 2012). When maximum temperatures (40.8°C and 41.1°C) occur and rainfall was absent (0 mm), the bud production increased (Aytac *et al*., 2009). Flowering continues for approximately four months. The period from anthesis to fruit ripening is a minimum 30 days (Fici, 2001). *C. spinosa* is andromonoecious, bearing both male and perfect flowers on the same plant (Zhang & Tan, 2008). The male flowers produced larger anthers, larger pollen grains and smaller ovaries than perfect flowers. Two major pollinators (*Xylocopa valga* Gerst and *Proxylocopa sinensis* Wu) did not discriminate between flower morphs and the transfer of pollen similar distances. There were also more seeds per fruit following hand pollination with pollen from male flowers than from perfect flowers (Zhang & Tan, 2009). Flower opening to petal senescence is highly constant, indicating tight temporal control.

Two flowering peaks have been observed in the extended blooming period of the species. However, there is no reported variation in morphological characteristics between the two peaks or their effect on seed set. The present study focused on the reproductive characteristics in different flowering stages of the extended blooming of *C. spinosa*. Any discernible differences in floral morphological characteristics and in the breeding system were evaluated, along with the variation between floral morphological characteristics and its effect on seed set in order to gain a more thorough understanding of the reproductive biology and ecological adaptation.

## Materials and Methods

**Study site and plant material:** The study was conducted in 2011 at the Turpan Eremophytes Botanical Garden (TEBG), located in Turpan of eastern Xinjiang in China (40°51′ N, 89°11′ E; 76–95 m below sea level) (Fig. 1). The climate is characterized by low rainfall, high evapotranspiration, high temperatures and dry winds. The annual mean temperature is 13.9°C with a range from -28.0°C to 47.6°C, the average annual rainfall is 16.4 mm, the annual mean evaporation is 2387.8 mm, and the average annual relative humidity is 41%. There are 26.8 annual gale days with a maximum wind speed of 40 m $s^{-1}$ (Yin, 2004). Meteorological data were supplied by the TEBG (Fig. 2).

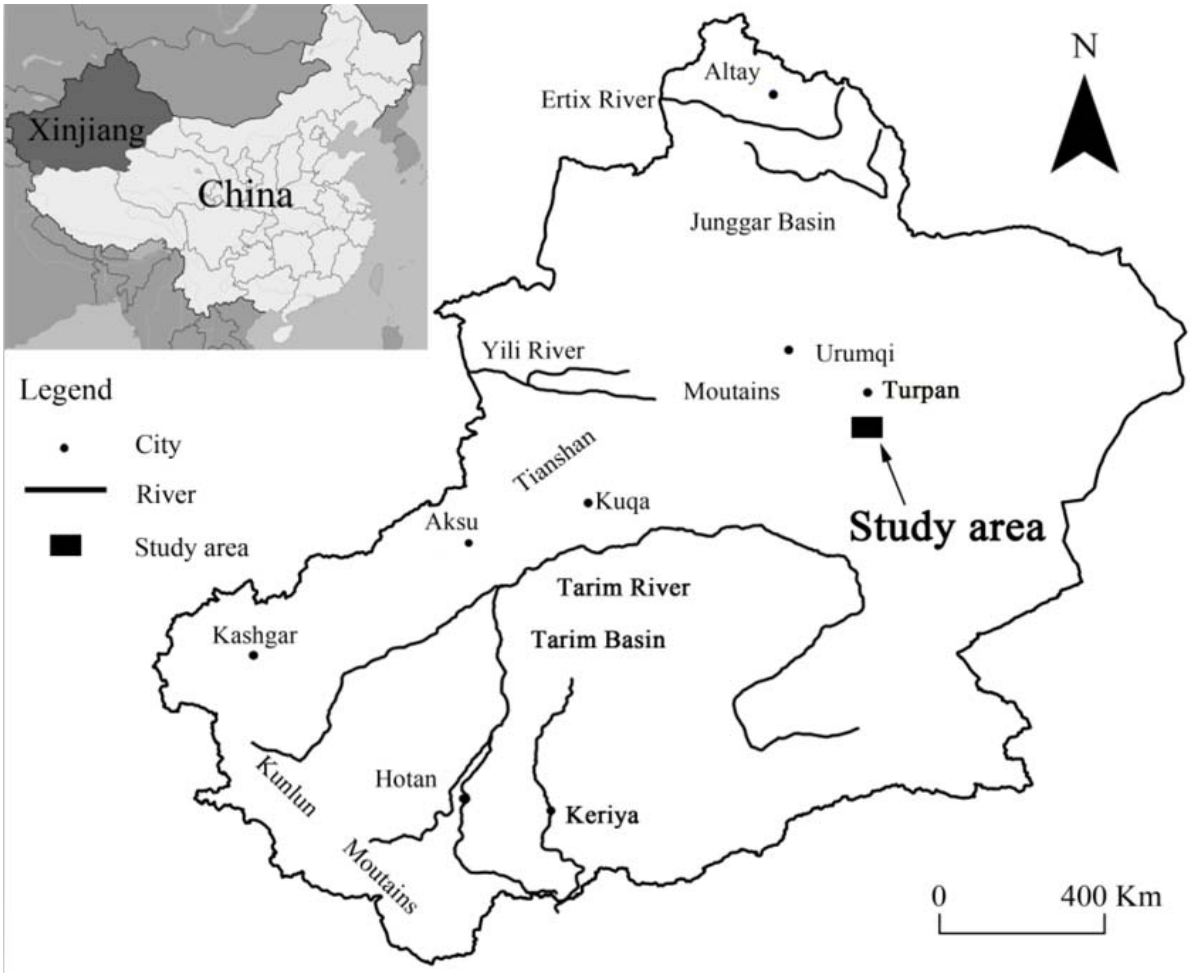


Fig. 1. The map of the study area.

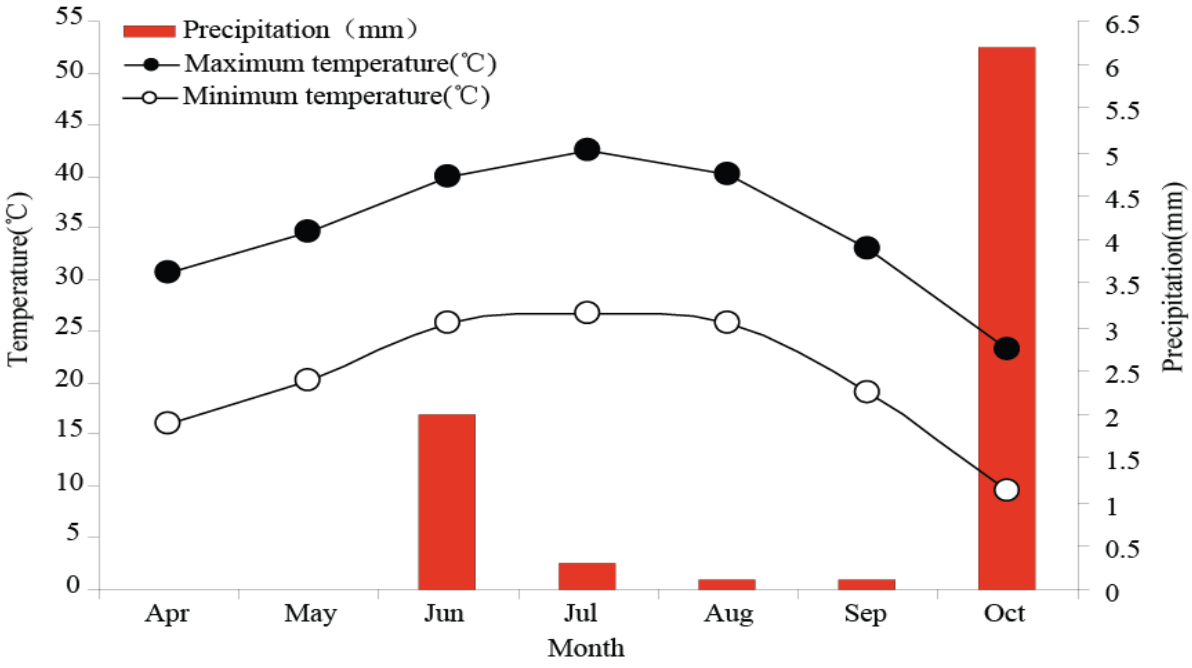


Fig. 2. Temperature and precipitation in TBEG in 2011.

*C. spinosa* was field in TEBG. The population currently shows normal and healthy growth, with average crown dimensions in this study measuring 504 cm high and 305 cm wide. Twenty plants were randomly selected from the population with a minimum distance of 10m between the selected plants. They were monitored daily during the flowering period from early May to mid October of 2011.

**Flowering season division:** Flowers were counted daily over the course of the flowering period. The flowering season was divided by the methodology described in Halevy & Orshan (1973).

**Flower morphology:** After flowering began, one or two male or perfect flowers were randomly collected from each plant for a total of 30 male and 30 perfect flowers in each of the peak flowering periods. Each had opened on the same day. Seven different flower organ measurements were taken from a single petal, petal or anther chosen at random for each flower: sepal length and width, petal length and width, filament length, and anther length and width.

**Determination of pollen to ovule ratio:** 30 perfect flowers were randomly selected from the 20 plants in each of the peak flowering periods. One or two male and perfect flowers were collected from each plant. The anthers of the flowers had dehiscenced. The number of pollen grains per flower was determined from six individuals for a total of 30 flowers of each floral morph using the method described by Dafni *et al*., (2005). The number of ovules per ovary in the perfect flowers was counted under an optical microscope (Olympus), and the pollen to ovule ratio (P/O) was calculated based on the number of pollen grains and ovules. The type of breeding system was assessed in accordance to Cruden (1977).

**Estimation of pollen vitality and stigma receptivity:** Pollen vitality and stigma receptivity were estimated in accordance to Dafni (2005). Stainability with 3-(4, 5-dimethylthiazol-2-yl)-2, 5-diphenyltetrazolium bromide (MTT) was used to indicate pollen vitality. Initially, the pollen was stained 2 h after anther dehiscence. To test stigma receptivity, after the flower bloomed, hydrogen peroxide was used in two hour intervals until the stigma lost receptivity.

**Fruit and seed characteristics:** Fruits from the same 20 plants were collected in each flowering period. From those, a random sample of 30 fruits was chosen. The fruit was measured in diameter, length and weight, and the number of seeds per fruit was counted. A total of 1000 seeds were selected and measured in 10 replicates each.

## Results

**Flowering period and number of flowers:** *C. spinosa* bloomed from May 1st to October 15th of 2011. Both male and perfect flowers were produced in two distinct peak flowering periods (Fig. 3). The 2 flowering peaks were separated by a short, less-flowering period (Halevy & Orshan, 1973). The peak production of the perfect flowers occurred earlier than the male flowers, whose two peak periods were from May 1st to July 20th and July 21st to October 15th. The duration and number of male flowers produced in each of the two flowering periods was identical, and the maximum number of flowers ($n$=11 and 13, respectively) did not differ significantly. The two peak periods for the perfect flowers ranged from May 1st to June 25th and June 30th to October 15th. The duration and number of perfect flowers produced in each of the two flowering periods differed. There was also a statistical difference ($p<0.05$) in the maximum number of flowers ($n$=18 and 12, respectively) produced. Beginning from June 5th, the number of male flowers began to increase, whereas the number of perfect flowers showed a decrease, and beyond July 15th, the number of male and perfect flowers both showed increasing trends (Fig. 2).

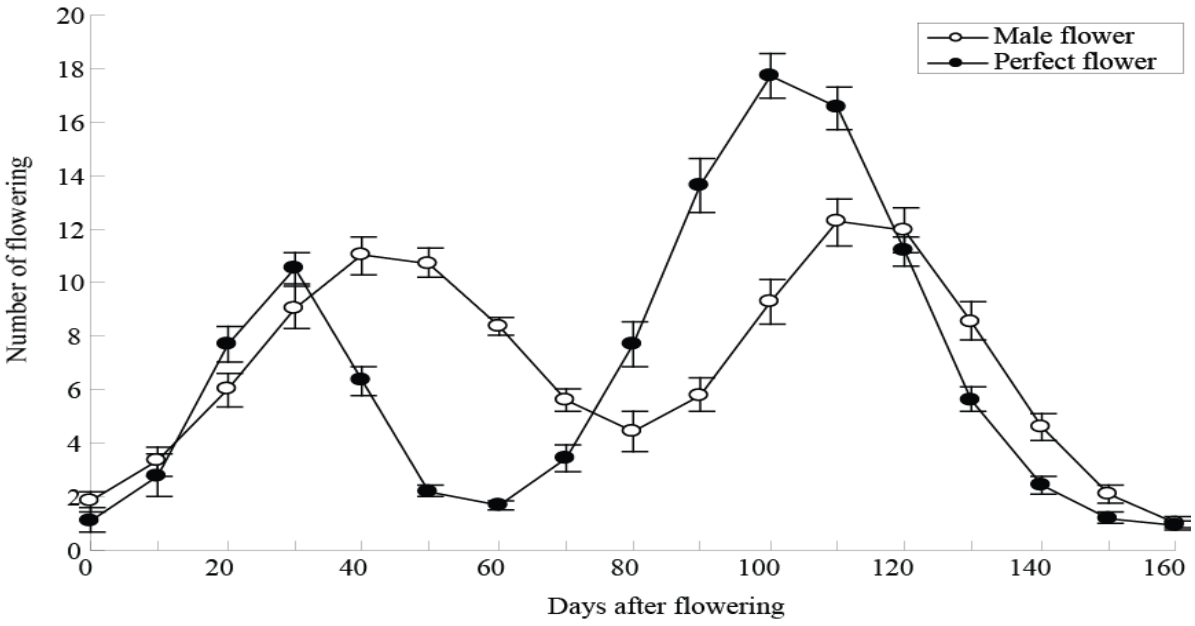


Fig. 3. Variation in the number of male flowers and perfect flowers in *C. Spinosa.*

**Flower morphology:** *C. Spinosa* flowers contain long and short stamens. Short stamens have green filaments and all are positioned close to the two expanded petals, whereas the long stamens have white filaments and are located close to the pair of connate variegated petals (Zhang & Tan, 2008). For both male and perfect flowers, sepal width and the number of long stamens showed a significant difference. For male flowers, filament and anther lengths of both short and long stamens differed between the two peaks ($p<0.01$). For perfect flowers, the filament and anther length of short stamens, and anther length of long stamens alone differed ($p<0.01$). For both stamen types in male and perfect flowers, the filaments were longer in the first peak than in the second, but the opposite was true for anther length (Table 1).

**Table 1. Comparison of floral traits of the *C. spinosa* between two peak flowering period.**

| Organ of flower | | Perfect flower | | | Male flower | | |
|---|---|---|---|---|---|---|---|
| | | First flower season | Second flower season | $P_1$ | First flower season | Second flower season | $P_2$ |
| Petals | Length (mm) | 22.60 ± 2.84 | 23.34 ± 2.83 | 0.41 | 23.09 ± 2.96 | 23.36 ± 3.22 | 0.9 |
| | Width (mm) | 15.16 ± 3.35 | 14.14 ± 2.76 | 0.29 | 12.89 ± 2.98 | 12.51 ± 1.98 | 0.8 |
| Sepals | Length (mm) | 14.78 ± 1.49 | 15.43 ± 1.80 | 0.22 | 14.68 ± 1.79 | 14.91 ± 1.92 | 0.9 |
| | Width (mm) | 8.08 ± 1.35 | 6.98 ± 1.99 | 0.05 | 7.43 ± 1.90 | 6.11 ± 1.07 | <0.01 |
| Long stamens | Number | 32.00 ± 9.77 | 49.38 ± 9.52 | <0.01 | 35.63 ± 13.91 | 48.38 ± 4.81 | 0.03 |
| | Length of filaments (mm) | 25.00 ± 4.00 | 23.44 ±2.85 | 0.09 | 26.04 ± 2.44 | 21.89 ± 2.91 | <0.01 |
| | Length of anthers (mm) | 1.45 ± 0.31 | 2.00 ± 0.60 | <0.01 | 1.31 ± 0.26 | 2.29 ± 0.74 | <0.01 |
| Short stamens | Number | 13.5 ± 4.31 | 15.75 ± 2.49 | 0.22 | 16.38 ± 6.74 | 14.00 ± 2.67 | 0.37 |
| | Length of filaments (mm) | 13.08 ± 2.07 | 11.16 ± 1.33 | <0.01 | 13.21 ± 1.63 | 10.62 ± 1.39 | <0.01 |
| | Length of anthers (mm) | 1.33 ± 0.35 | 1.93 ± 0.73 | 0.01 | 1.31 ± 0.21 | 2.23 ± 0.84 | <0.01 |
| Ovary | Length (mm) | 6.62 ± 0.55 | 6.79 ± 0.38 | 0.43 | 4.58 ± 0.22 | 4.76 ± 0.34 | 0.7 |
| | Diameter (mm) | 2.56 ± 0.12 | 2.79 ± 0.23 | 0.32 | 1.71 ± 0.28 | 1.74 ± 0.25 | 0.8 |
| Gynophore | Length (mm) | 28.89 ± 1.87 | 30.02 ± 1.98 | 0.23 | 7.57 ± 1.98 | 7.85 ± 2.03 | 0.73 |

*$P_1$ is the variance yields of perfect flower; $P_2$ is the variance yields of male flower

**Pollen/ovule ratio:** The number of pollen grains per male and perfect flower and per long and short stamen was almost identical, and no significant differences in these traits between the two periods were observed ($p>0.05$). The number of ovules per perfect flower also showed similarity (Table 2).

**Pollen vitality and stigma receptivity:** Pollen vitality of *C. spinosa* was highest (>80%) 2-6 h after anther dehiscence, as pollen grains remained viable for 20h. No difference in the pollen vitality of both male and perfect flowers was observed.

The stigma receptivity of perfect flowers was highest 4-8 h after the flower opened. It lost receptivity 16–18 h after opening and the petals had wilted. No difference in stigma receptivity between the two peak flowering periods was apparent.

**Fruit and seed characteristics:** The length, diameter, weight and seed number of each fruit differed between the two peaks ($p<0.01$). The fruit that developed and number of seeds produced in the first peak flowering period were respectively larger and greater than in the second period (Table 3). The length, diameter and weight of 1000 seeds all differed between the two flowering peaks ($p<0.01$). The seeds produced in the first peak were smaller and lighter than those of the second period. There was a 55% frequency of fruit in the first period and only 41% in the second.

**Table 2. Pollen numbers and pollen-ovule ratios of the *C. spinosa* between two peak flowering periods.**

| Organ of flower | | Perfect flower | | | Male flower | | |
|---|---|---|---|---|---|---|---|
| | | First flower season | Second flower season | $P_1$ | First flower season | Second flower season | $P_2$ |
| Number of pollen per anther ($\times10^3$) | Long stamens | 74.56±8.75 | 74.50±8.17 | 0.98 | 73.00±5.79 | 75.11±5.97 | 0.46 |
| | Short stamens | 73.72±8.17 | 76.00±12.58 | 0.52 | 74.44±2.56 | 73.67±4.44 | 0.66 |
| Number of pollen per flower ($\times10^4$) | | 485.17±81.13 | 479.96±84.31 | 0.1 | 491.12±79.32 | 487.21±91.53 | 0.76 |
| Number of ovules | | 293.44±20.30 | 297.00±31.60 | 0.34 | - | - | - |
| P/O value($\times10^4$) | | 1.66 | 1.62 | - | - | - | - |

*$P_1$ is the variance yields of perfect flower; $P_2$ is the variance yields of male flower

**Table 3. Comparison of fruits and seeds of the *C. spinosa* between two peak flowering periods.**

| | | First flower season | Second flower season | *P* |
|---|---|---|---|---|
| Fruit | Length (mm) | 29.69 ± 4.28 | 21.93 ± 4.23 | < 0.01 |
| | Diameter (mm) | 18.16 ± 2.19 | 14.07 ± 2.93 | < 0.01 |
| | Weight (g) | 5.26 ± 1.77 | 2.73 ± 1.39 | < 0.01 |
| | seed number | 293.1 ± 65.00 | 173.1 ± 63.1 | < 0.01 |
| Seed | Length (mm) | 2.20 ± 0.16 | 2.45 ± 0.18 | < 0.01 |
| | Diameter (mm) | 1.73 ± 0.16 | 2.06 ± 0.34 | < 0.01 |
| | Thousand seed | 2.58 ± 0.32 | 3.95 ± 0.10 | < 0.01 |

## Discussion

Plants with an extended flowering period may serve as a long-term resource (Bertin, 1982; Dobkin, 1984), which allows the presence of a constant population of pollinators (Stiles, 1977; Waser & Real, 1979). This flowering strategy promotes cross-pollination (Sazima, 1977; Augspurger, 1979) and offers plants the following potential advantages (Bawa, 1983; De Jong *et al*., 1992): reduced risk of reproductive failure (Zubair *et al*., 2013); the possibility of mating with more individuals in the population and better control over relative investment in flowers and fruit. Halevy and Orshan (1973) found similar double peak flowering patterns in *Acaciae raddiana*, a predominant host of *L. acacia*; one in June and one in November. In some *A. raddiana* plants, the two flowering peaks were separated by a short, non-flowering period. The 2011 flowering season of *C. spinosa* in Turpan ranged from May 1st to October 15th. Both the male and perfect flowers exhibited two peak flowering periods, of which the peaks overlapped between the two flower types. Some phenological characteristics, such as flowering time or length of the flowering season(s) of different species, are controlled by harsh weather conditions (De Jong et al, 1992) and environmental factors, e.g., temperature, and precipitation (Biere & Honders, 1996). Temperature seems to be the most important environmental factor, according to this study. When comparing Figures 1 and 2, an inverse relationship can be detected between the maximum temperatures that occurred in July and the least number of flowers of the two flower types produced during that time (day 60), with exception to the initial and final flowering stages.

The flowering season of individuals that produce a greater number of flowers is longer than that of individuals that produce fewer flowers (Dieringer, 1991). The number of perfect flowers produced in the second peak was higher than the first, thus the duration of the second peak flowering period was longer. However, the number of male flowers did not differ between the two periods, and the length of the periods was identical.

The corolla is long, tubular and curved (Gill & Wolf, 1978; Mcdade & Kinsman, 1980), and the distance from the stigma to the flower entrance is relatively long. Seasonal changes in flower size could be a result of climate and environmental conditions (including temperature, humidity and rain) and may be considered adaptations for arid conditions (Yiftach Vaknin *et al*., 1996). Obvious differences in flower morphology were observed between the two peaks. The number of long stamens for male flowers and perfect flowers between the two peaks was statistically different. For all long and short stamens, the filaments were longer in the first peak flowering period than in the second, whereas anther length showed the inverse. The latter indicated that a higher number of pollen grains were produced in the second peak flowering period than in the first.

In perfect flowers, the pollen/ovule ratio can reflect the mating system (Barrett & Harder, 1996). The pollen/ovule ratio of *C. spinosa* was in the range (1.62-1.66) × $10^4$. According to Cruden (1977), *C. spinosa* exhibits obligate xenogamy. The pollen retained vitality for 20h, and vitality was highest (>80%) 2-6 h after anther dehiscence. The stigma receptivity of perfect flowers was highest 4–8h after the flower opened and was lost after 16-18h, which was when the petals started wilting. No difference was observed between the two peak flowering periods.

Flowering phenology affects reproductive success (Ollerton & Diaz, 1999). Higher flower to fruit production ratio is a universal phenomenon in plants and the low frequency of fruit production might reflect resource constraints and pollen limitation (Cao *et al*., 2005). Huang (2003) conducted a bagging experiment and observed the pollination ecology of *Sagittaria guyanensis* subsp. *lappula*, an andromonoecious taxon, and found that bagging perfect flowers did not reduce the fruit-bearing frequency, whereas removing the stamens did. In addition, fewer pollinators visited the flowers. Huang considered that the presence of stamens in perfect flowers might have provided reproductive assurance under inadequate pollination conditions. For *C. spinosa*, the frequency of fruit differed between the two flowering peaks, with the first peak producing more than the second. This result reflects the fact that the proportions of male and perfect flowers were almost identical in the first peak flowering period, but the number of male flowers was lower in the second peak flowering period. Thus, the lower fruit set might have been caused by a lack of male resources. The size of fruits and seeds also differed. Compared with the second peak, the fruits in the first peak flowering period were larger, there were more seeds per fruit, and the seeds were lighter. This result suggests that, because of additional nutrient availability, the seeds produced in the second peak were larger than the first, but the number of seeds was lower due to a lack of male resources.

These results provide that the extended flowering phenomenon of *C. spinosa* could allow flexibility in the relative investment in flowers and fruit, improve the pollination frequency of individual flowers, and provide more efficient resources.

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