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Pollination biology of *Disanthus cercidifolius* var. *longipes*, an endemic and endangered plant in China

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Abstract: *Disanthus cercidifolius* Maxim. var. *longipes* H.T. Chang usually has two inflorescences growing in opposite directions in the axillae, but occasionally three inflorescences grow paratactically. The typical flowering process could be divided into 4 periods: "*Pre-dehiscence*", "*Initial dehiscence*", "*Full dehiscence*" and "*Withering*". Both the natural population and the planted population had a flowering peak of 15–35 days after the first flower bloomed. There were significant differences between the time courses of flowering of the two populations. Out-crossing is the main breeding system in this species. And autogamy decreases the risk of reproductive failure of this species. The main insect pollinators of *D. cercidifolius* var. *longipes* are *Episyrphus balteatus* de Geer, *Scaptodrosophila coracina* Kikkawa and Peng, *Polistes olivaceus* de Geer, *Apis cerana* Fabricius, *Nezara viridula* L. and *Coccinella septempunctata* L., and so on. Among the insects, *S. coracina* and *E. balteatus* are the most important and efficient pollinators, but others are inefficient pollinators. Though wind pollination is not efficient, it guarantees reproduction when insect pollinators are not available. "*Mass flowering*" is an adaptive behavior and reproductive strategy of this species, and "*few fruiting*" could be caused by the lack of pollinators.

Key words: *Disanthus cercidifolius* Maxim. var. *longipes* H.T.Chang; pollen limitation; pollination efficiency; reproductive assurance role; reproductive strategy.

Introduction

Pollination is necessary for sexual reproduction of seeding plants. Insect pollination and wind pollination are the two main pollination systems in terrestrial vascular plants. Wind pollination is very common in gymnosperm. In angiosperm, however, insect pollination, which evolved from wind pollination, is dominant (Tamura & Kudo 2000). As the behaviors of pollination animals are often influenced by the general characteristics of flowers such as pollen stream (Howe & Westley 1997), pollination depending on insects and birds is regarded as more particular and more specialized than wind pollination. Thus, to gain the deeper insight of a flower, we should study the flower as a functional unit evolved for pollination other than a single structural unit (Faegri & van de Pijl 1979; Huang et al. 1999).

Disanthus is a monotypic genus with the species (variation) of *Disanthus cercidifolius* maxim. var. *longipes* H.T.Chang in Hamamelidaceae. Studying the pollilation biology of this genus can help us to gain further understanding of the system development of*Disanthus cercidifolius* var. *longipes* and other species in East Asia. *D. cercidifolius* var. *longipes* is a variation of *D. cercidifolius* var. in the China-Japan floral region (Fu 1989). It exists in a small number of individuals, which

distributed in a few counties in Hunan, Jiangxi and Zhejiang Provinces of China (Fu 1991; Xiao et al. 2002). Currently it is a 2nd Class endangered variety for conservation in China.

In order to discover the factors that are endangering this variation, we have focused our work on its genetic diversity, the relationship between genetic diversity and environmental factors, the dynamics of natural populations and so on for several years (Xiao et al. 2002, 2003, 2004b). The quantity and forestry characteristics of this species in Zhejiang province have been studied (Li et al. 2002), but no other aspects of this species have been studied. In this paper, the general floral characteristics, the types of pollination animals and the pollination efficiency, the factors that limit pollination and the reproductive mechanism of "mass flowering and few fruiting" were studied.

Material and methods

Study plant
Disanthus cercidifolius maxim. var. *longipes* H.T.Chang is a defoliate shrub with approximately 2–4 m tall, branchlets brown, glabrous, lenticellate, petiole 3–5 cm; leaf blade broadly ovate-rounded, membranous, drying gray-white abaxially and green adaxially, glabrous, base slightly

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to deeply cordate, rarely truncate, margin entire, apex emarginate, rarely obtuse, acuminate. *D. cercidifolius* var. *longipes* usually has two head-inflorescences growing in opposite directions in the axillae at the same node, each inflorescence with two opposite bisexual flowers with no peduncle. The peduncles of inflorescence are *ca.* 8–25 mm long; floral cup *ca.* 1 mm, abaxially brown hairy; sepals are ovate, *ca.* 1–1.5 mm long. Petals are red, linear from wider base, and *ca.* 7–21 mm long. Stamens are much shorter than petals; anthers are ovoid. Styles are ca. 1–1.5 mm long. The flowering period is from September to November, and fruits ripen from August to September. Capsules are obovoid, apex subtruncate, usually in August. Seeds are black, shiny, and irregularly ellipsoid.

Study site
One of the sample sites is Caijiatian of Jinggang Mountain in Jiangxi province, P. R. China. The Jinggang Mountain is in the middle of the Luoxiao Mountain range. Its flora belongs to secondary forest or secondary shrub, which has survived the destruction of the subtropical evergreen broad forest – the predominant inhibitors previously in this region. The altitude of the mountain ranges from 600 m to 1300 m, and the soil is red-brown. The temperature ranges from $-13.4\,°C$ to $35.2\,°C$, with a yearly average of $15.1\,°C$. The average temperature is $3.9\,°C$ in January and $23.7\,°C$ in July. The total precipitation is 1,872 mm. There are about 247 to 263 days without frost. The vegetation and climate are similar to those of Longquan Mountain in Zhejiang and Junfeng Mountain in Jiangxi (Fu 1989, 1991; Xiao et al. 2002).

The other sample site is a planted population of this species in Ciping of Jinggang Mountain. This population was planted in 1990. The environmental conditions of the planted site were described in other paper (Xiao et al. 2004a).

Flowering phenology
Fifty individuals with similar heights and crown diameters were chosen in the each sample site. They were marked and observed to study their morphological traits and pollination biology in 2002 and 2003, respectively.

Observations were made every week from Sep. to Nov. And the phenological flowering parameters were calculated: onset (date first flower opened in a population); end date (date last flower opened in a population); duration (difference between date of first and last flower opened in a population); mean flowering date (peak of flowering: the mean of the census dates during which the individual was flowering, with each census date weighted by the number of flowers in that period); mean flower in amplitude (number of flowers produced per unit time (day) in a population, terminology of Newstrom et al. (1994); and synchrony (flowering overlap among individuals).

The synchrony index can be used to calculate the flower synchronization. The equation is as follow according to McIntosh (McIntosh 2002) and Xiao (Xiao et al. 2004a), and the index of synchrony (S) for an individual plant (i) is given by:

$$S_i = \frac{1}{n-1}\left(\frac{1}{f_i}\right)\sum_{j=i}^{n} e_{j\neq i}$$

In the equation, $e_{j\neq i}$ is the number of days that individuals i and j overlap in their flowering; f_i is the total days that individual i is flowering; and n is the total number of individuals in the sample. S_i varies from 0 to 1. If $S_i = 0$, it indicates that individuals don't overlap in flowering time; If $S_i = 1$, it indicates that their flowering time overlaps completely.

All the six parameters taken into account can reflect the condition of the species at the population level. Taking time as the x-axis (Sept. 1 is the first day and Sept. 2 is the second day, and so on) and cumulated flowering percent as y-axis, the flowering course curves were drawn according to the data in 2003. Fifty individuals were observed in both the natural the population and planted population.

Breeding system
To study the breeding system, we separated the tested individuals into six groups in Sep. 2003 and 60 flowers (30 inflorescences) were tagged in each group: emasculated and un-bagged, emasculated and bagged, emasculated and hand self-pollinated, emasculated and hand cross-pollinated, non-emasculated and hand pollinated, non-emasculated and naturally pollination. Six tagged flowers in each group were collected at the 5th day after it flowering, and the pollen grains on each stigmas were counted under light microscope immediately. The fruits were all collected before winter so that they were not dissilient under the frost. Healthy seeds were extracted from the fruits, then the fruit set ratio and the seed set ratio were calculated. This experiment was repeated in Oct. 2003, and their averages were used to discuss.

The index of pollen limitation $p_i = 1 - (c/p)$ was used to evaluate the effects of pollen on the seed set ratio. (c is the average seeds in a single fruit under natural conditions, and p is the largest number of seeds in a single fruit after hand pollination, respectively).

Pollinators and pollination efficiency
The pollinators were observed at the same spot in the natural population during the flowering duration in 2002 and 2003. In addition, a single plant of *D. cercidifolius* var. *longipes* was selected to study pollen dispersal. To estimate the pollination distance, 10 pieces of microscope glass were covered with vaseline and put on the leeward side of the ground under the selected plant at a interval of 0.5m. 24 hours later, the glass slides were collected and taken back to the laboratory to determine the number of pollen grains on them.

Flowers that were visited by an insect pollinator were fixed by FAA or Carnoy fixative and taken back to the laboratory to determine the number of pollen grains on the stigma. The insect pollination efficiency was estimated by the number of pollen grains that a single insect deposited by one visit.

The total pollination efficiency was calculated with the index of pollination efficiency (Tamura & Kudo 2000):
Index of wind pollination efficiency (w_i): $w_i = n/p$
Index of insect pollination efficiency (I_i): $I_i = (c - n)/p$.
(n indicates the average seeds of a single fruit in gauze bag with natural pollination, c is the average seeds in a single fruit under natural conditions, and p is the largest number of seeds in a single fruit after hand pollination, respectively).

Results

Inflorescence morphological traits
D. cercidifolius var. *longipes* usually has two inflorescences growing in opposite directions in the axillae at the same node, and occasionally three inflorescences growing paratactically (Fig. 1-A). The middle inflorescence might come from the leaf bud in the axillae (the
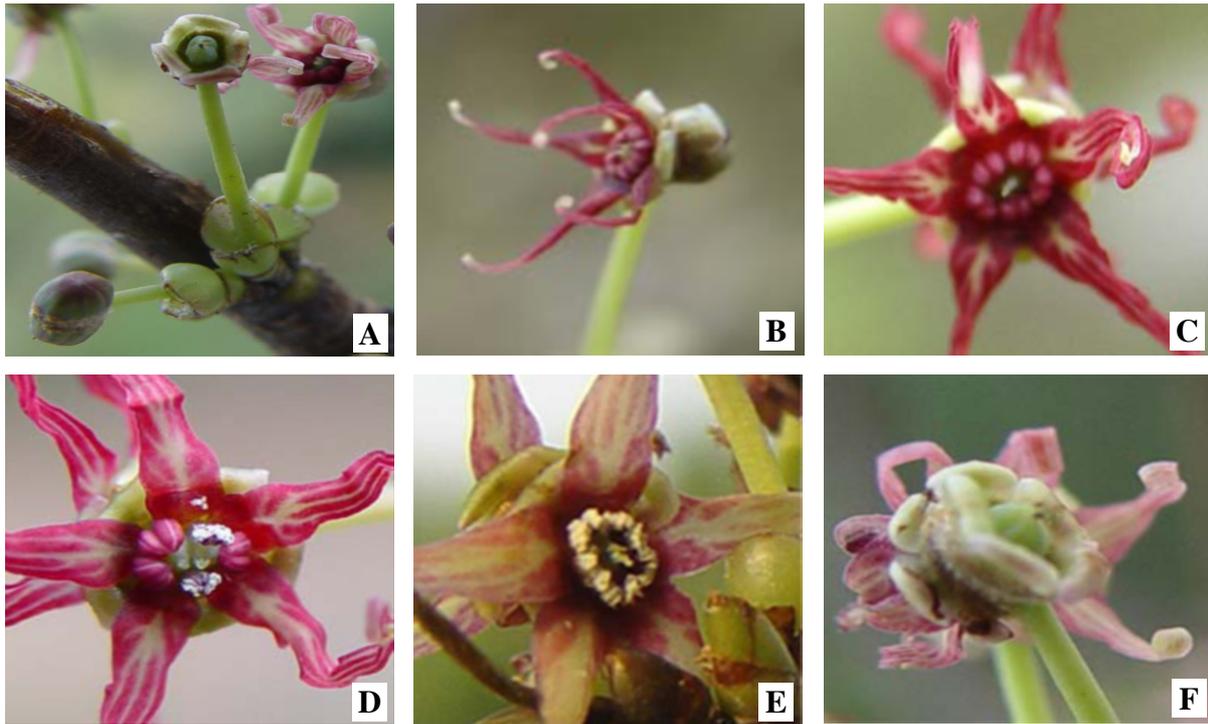
Fig. 1. The floral morphological characteristics observed during the flowering of *D. cercidifolius* var. *longipes*. A – three inflorescences growing paratactically at the axillae, B – the two flowers on the same inflorescence open early or late, C – the two flowers on the same inflorescence are opening at the same time, D – two anther are dehiscing, E – "full dehiscence", showing the "pollen ring", F – the floral morphological characteristics in "Withering period".

mechanism needs to be studied further). Each flower blooms 6 to 7 days. The two flowers on the same inflorescence usually blossom at the same time (Fig. 1-C), but sometimes they blossom successively (Fig. 1-B). In this case, the first flower would bloom fully, but the second would probably wither early. In the beginning of the blooming period of each flower, the pistils are longer than the stamens. However, the styles stop growing soon, and the filaments continue to grow until they are as high as the styles. At this point, the anther dehisces into two blades. Usually two filaments lengthen and release their pollen first (Fig. 1-D), and the other three stamens delay pollen release one or two days. This stage was named "*Initial dehiscence*". From 3rd to 5th day, all stamens are releasing pollen, the pollen forms an obvious "pollen circle" (Fig. 1-E), and we named it the "*Full dehiscence*".

The typical flowering process for a flower could be divided into 4 periods: "*Pre-dehiscence*", "*Initial dehiscence*", "*Full dehiscence*" and "*Withering*" (Fig. 1-C~F). "*Pre-dehiscence*", before the pollen grains release at the onset day, the calyces craze and two filaments lengthen, but the petal doesn't stretch completely and the filaments stretch out with no dehiscence (Fig. 1-C). "*Initial dehiscence*", after 2 or 3 days of flowering, the petal stretches completely. Two filaments of the five are now as tall as the styles. One or two anthers start to release their pollen grains (Fig. 1-D). "*Full dehiscence*", is between the third and fifth day of the full blooming period when three or five anthers dehisce, and the color of the stigma changes to yellow, the other sta-

mens release pollen grains, and the pollen grains form an obvious "pollen circle" (Fig. 1-E). Then their stigmas change into yellow. The last period is "*Withering*", that occurs from the sixth to seventh day of the blooming period, when all anthers dehisced, the stamens wither and the color of some stigmas change to brown or black yellow (Fig. 1-F). On the onset day or the second day of the full blooming period of a flower, a little secretion can be found at the base of the petals, but there is not enough to collect. It is probably nectar.

Flowering phenology

It can be seen from Fig. 2 that most flowers bloomed between the 15th~35th day after the first flower bloomed in the population and that the flowering course of the population accorded with a Logistic curve. The planted population bloomed and withered earlier than the natural population and the blooming peak of the former was also earlier than that of the latter.

Parameters such as the first day of blooming, the last day of blooming and the duration of the blooming (the number of days of florescence) of the same population were not statistically different between 2002 and 2003. However, difference existed between the two populations (Table 1). The natural population in Caijiatian bloomed later than the planted population in Ciping during 2003. The date of the end of the blooming period was later, too. As far as the number of flowers on the first day of blooming and the number of flowers on the "blooming peak day", there are significant differences between the two populations. The number of flowers on
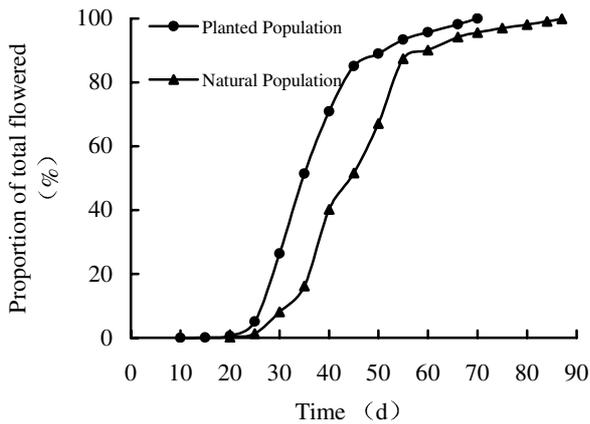
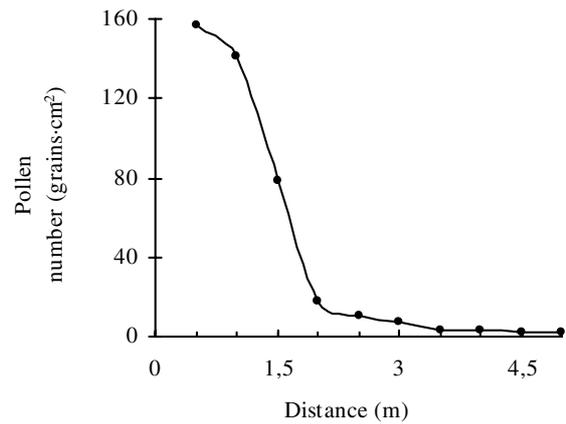Fig. 2. Course of flowering of *D. cercidifolius* var. *longipes.*

Fig. 3. Effect of wind on the pollen dispersal.

the first day of blooming of the planted population was less than that of the natural population ($r^2 = 0.612$, $p = 0.001$) and the number of flowers on the "blooming peak day" was more than that of the latter ($r^2 = 0.793$, $p = 0.0001$).

Breeding system
According to the results of the bagging experiment (Table 2), *D. cercidifolius* var. *longipes* has no agamospermy. Under natural conditions, the seed set ratio was only about 2.75%, which is consistent with the results of field investigations of many years. The self-pollinated plants achieved seed set irregularly. The plants that were artificially cross-pollinated had a seed set ratio of about 45%. These results show that out-crossing is the main breeding system.

Pollen had an important effect on the seed set ratio. The pollen limitation index is 0.9312 ± 0.0509.

Effects of wind on pollen dispersal
As is shown in Fig. 3, when the distance increased from 0.5 m to 2.0 m, the amount of pollen decreased sharply from 160 to 20 grains. Therefore, the efficiency of wind pollination is very low.

The indices of wind pollination efficiency (w_i) in 2002 and 2003 were 0.0012 and 0.0015, respectively. There was not significant difference between 2002 and

2003. These results further prove that wind pollination is low efficient.

Insect pollinators and their behavior
The main insect pollinators of *D. cercidifolius* var. *longipes* are *Episyrphus balteatus* De Geer, *Scaptodrosophila coracina* Kikkawa et Peng, *Polistes olivaceus* De Geer, *Apis cerana* Fabricius, *Nezara viridula* L. and *Coccinella septempunctata* L.

The most frequently encountered pollinator was *S. coracina* with an average of 2.57 ± 0.62 per flower. However, *S. coracina* usually crawled slowly on the flower and sometimes stayed on one flower for 15∼30 minutes or more. If the flower was exposed to sunshine, *S. coracina* would either fly away or hide in the bracts at the base of the peduncles or in other shady spots. While on the flower, the pollinators moved to all parts of the flower, sometimes resting on the styles, sometimes on the stamens, sometimes on the petals, but most of the time they extracted nectar between the petals and the stamens. Occasionally *S. coracina* crawled to the stigma. Judging by the small amount of the pollen grain at their mouthparts and trunk legs, *S. coracina* can be considered an inefficient insect pollinator for *D. cercidifolius* var. *longipes*. However, *S. coracina* is an effective pollinator for the extremely high number of individuals in this ecosystem.

Table 1. Flowering phenology of *D. cercidifolius* var. *longipes* at the plant and population levels.

Items of observation	Caijiatian population		Ciping population	
	2002a	2003a	2002a	2003a
Onset day	22/9	18/9	12/9	8/9
Number of flowers on the onset day	63	66	70	75
Flowers duration (d)	61	70	65	65
The blooming peak day	21/10	23/10	15/10	16/10
Number of flowers on blooming peak day	280	298	229	237
Flowering amplitude (Flowers $\cdot$ plant^{-1} $\cdot$ day^{-1})	61	78	69	61
Endset day	21/11	26/11	15/11	12/11
Number of flower on endset day	7	3	3	9
Mean synchrony	0.65	0.69	0.78	0.81
Variations among synchrony	0.60∼0.77	0.56∼0.78	0.69∼0.82	0.72∼0.85

Table 2. The results of emasculated of *D. cercidifolius* var. *longipes* (means ± SE).

Treatment	Number of pollen grains on each stigma	Mean seed set ratio (%)
Emasculated, bagged, no pollination	0.00	0.00
Emasculated, un-bagged, natural pollination	11.6 ± 0.52	4.60 ± 2.10
Emasculated, bagged, hand cross-pollination	63.9 ± 2.30	45.01 ± 2.73
Emasculated, bagged, hand self-pollination	57.9 ± 1.90	2.73 ± 0.06
Non-emasculated, bagged, natural pollination	19.1 ± 1.49	1.13 ± 0.09
Non-emasculated, un-bagged, natural pollination	23.5 ± 1.23	2.75 ± 0.29

Table 3. Efficiencies of different insect pollinators of *D. cercidifolius* var. *longipes* (means ± SE).

Pollinators	*Scaptodrosophila coracina*	*Episyrphus balteatus*	*Polistes olivaceus*	*Apis cerana*	*Nezara viridula*	*Coccinella septempunctata*
2002a	0.56 ± 0.131	23.81 ± 1.974	11.34 ± 2.330	16.21 ± 1.072	0.60 ± 0.050	0.59 ± 0.094
2003a	0.39 ± 0.054	25.62 ± 1.348	13.10 ± 1.914	18.40 ± 1.584	–	–

Fig. 4. The main efficient insect pollinator of *D. cercidifolius* var. *longipes*. Note: It is showing the pollintion of *Episyrphus balteatus* De Geer.

Sometimes *E. balteatus* visited *D. cercidifolius* var. *longipes*. There were usually 3–5 individuals per plant were found (Fig. 4). They always flew in one or more circles around the flower and then landed on it with their limbs holding the anther and their mouthparts extracting nectar. They often visited the centralized flowers of a few smaller branches and the adjacent plants, spending about 20–90 s (mean 53.7 s) on each flower. After visiting the flowers of a few branches, *E. balteatus* would fly to the adjacent leaves to rest (usually <30 s), and then move to other branches or return to the flowers that they had just visited. 85% of the flowers visited by *E. balteatus* were initially dissilliant or full dehiscence. Therefore, *E. balteatus* is also an effective pollinator.

The other insect pollinators were inefficient pollinators. The visiting frequency of these pollinators was very low. They were seen occasionally when the flowers were exposed to sunshine but not found during the blooming stage. Further study is needed to determine whether or not there were night pollinators.

Efficiencies of insect pollinators
The pollination efficiency of *S. coracina*, *N. viridula* and

C. septempunctata was very low. They could bring no more than 0.5 pollen grains to the stigma. *P. olivaceus* and *A. cerana* could bring 11–18 pollen grains to the stigma each time while *E. balteatus* brought an average of 24 pollen grains to the stigma. There was no significant difference in the pollination efficiency. The pollination efficiencies of the insects in 2002 were not significantly different from those in 2003. ($r^2 = 0.997$, $p = 0.05$).

The indices of insect pollination efficiency in 2002 and 2003 were 0.056 ± 0.001 and 0.079 ± 0.003 respectively ($r^2 = 0.611$, $p = 0.01$). There was significant difference between years (Table 3).

Discussion

There are many factors that limit the survivability of self-fertilizing plants. For example, self-fertilization plants can not evolve into out-crosses plants. This inability can cause species to decline because it limits the plants' capacity to form new species when out-cross is impossible (He & Liu 2003). However, self-pollination has obvious advantages. It can guarantee the success of reproduction (Fausto et al. 2001; Takebayashi & Morrell 2001). *D. cercidifolius* var. *longipes* has a self-pollination and out-cross compatible breeding system. Based on the fact that self-pollination evolved from out-cross (Wyatt 1983; Wang 2001), it can be deduced that *D. cercidifolius* var. *longipes* has out-cross breeding system first. Later, the self-cross and out-cross compatible breeding system evolved because of environmental pressures such as the inefficiency of wind pollination and the insect pollination.

E. balteatus is an effective pollinator. Though they were encountered in small numbers, the visiting frequency (per flower) and pollination efficiency (per flower) of them were high. *S. coracina* is another effective pollinator because of its large numbers and high visiting frequency (it spends almost all of its time on flowers). Even if *A. ceran* have relatively high pollination efficiency (per flower), they have low total polli-

nation efficiency due to their small numbers and extremely low visiting frequency. The *P. olivaceus* was found visiting the flower only once a time during the experiment. *N. viridula* and *C. septempunctata* are not regular pollinators and have the lowest pollination efficiency. Therefore, *P. olivaceus*, *A. ceran*, *N. viridula* and *C. septempunctata* are regarded as inefficient pollinators. Though wind pollination efficiency is very low, it can guarantee reproduction when there are no enough insect pollinators.

Fishbein point out that pollination should be observed at different times throughout the year. The results of research will be inaccurate if the pollination efficiencies of different pollinators are only measured during a single season (Fishbein & Venable 1996). According to the observation on *D. cercidifolius* var. *longipes* in 2002 and 2003, it can be seen that there is no significant difference between the index of wind pollination efficiency in 2002 and that in 2003. However, both the index of insect pollination efficiency and the fruit set ratio of insect pollination were higher than those of wind pollination. In short, insect pollination is a more effective method of pollination. Wind pollination is, however, a way of ensuring reproductive success when insect pollination is not available.

Like other endangered species, *D. cercidifolius* var. *longipes* has the reproductive mechanism of "mass flowering but few fruiting". Many factors affect the reproductive success of flowering plants (Anderson & Hill 2002). Among these factors, timing, frequency, and duration of the flowering period are obviously of great importance (Rathcke & Lacey 1985; Anderson & Hill 2002). The reasons for the variation could be that there are few effective pollinators. As far as the reproductive mechanisms of "mass flowering" and "centralized flowering" are concerned, they are effective in attracting a lot of effective pollinating insects such as *E. balteatus*, thus decreasing the risk of the plant coming endangered (Stanton et al. 1986). *D. cercidifolius* var. *longipes* has evolved a "few fruiting" reproductive strategy respond to the limited types and quantities of pollination insects and low pollination efficiency. The lack of effective pollinators is probably an important reason why *D. cercidifolius* var. *longipes* is endangered.

Acknowledgements

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