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RESEARCH ARTICLE

Pollen and resource limitations to lifetime seed production in a wild population of the endangered plant *Disanthus cercidifolius* var. *longipes* H. T. Chang (Hamamelidaceae)

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Abstract *Disanthus cercidifolius* Maxim. var. *longipes* H. T. Chang, a plant species that only occurs in a few counties in Hunan, Jiangxi and Zhejiang Provinces and with a relatively small number of individuals, is ranked as a second Class endangered species for conservation in China. We have studied the effect of pollen and resources available to female reproduction, and the reproductive mechanism of "excess flowers with low fruit set" in *Disanthus cercidifolius* Maxim. var. *longipes* H. T. Chang was discussed. Results are as follows:

Pollen from different sources has significant effects on fruit set and seed set of *Disanthus cercidifolius* Maxim. var. *longipes* H. T. Chang. The pollen source rather than pollen numbers significantly affected reproduction of this species. In wild populations, producing one fruit needs about 54.8 flowers, and one satiation seed needs about 6.60 flowers or 83.19 ovules.

After fertilizing, which was propitious to flower development, the abortion rate of flower buds was decreasing, but the flowering rate was increasing. The fruit set and seed set was also significantly increasing, while abortion rate of fruit was significantly decreasing. With the increasing percentages of cutting leaves, the fruit set decreased, but the abortion rate of fruit shows no significant differentiation among treatments. After cutting branches that were puny, broken and insect-infested branches, the flower number seemed to be decreasing, but the fruit set and seed set all increased significantly. After removing some flowers, the fruit set was calculated with respect to the number of flowers remaining after the treatment increased with increasing of percentages of flower removal, whereas fruit set calculated with respect to the initial number of flowers remained constant, and the mean weights of per fruit and per seed all decreased significantly.

Sufficient spatial or temporal heterogeneities in nutrient levels might allow limitation of seed set by resources and pollen in a natural population, while supplying resources may indirectly affect pollination by increasing attraction of the flowers to pollinators. There were very low fruit and seed sets in natural populations of *Disanthus cercidifolius* Maxim. var. *longipes* H. T. Chang. Different factors may have interacted to effect a low fruit set. A joint adoption of the "*selection abortion hypothesis*", "*ovary reserve hypothesis*" and "*male function hypothesis*" seems to be the most likely explanation for the reproductive strategy of "excess flowers with few fruit sets" in *Disanthus cercidifolius* Maxim. var. *longipes* H. T. Chang.

Keywords pollen limitation, resource limitation, hand-pollination, seed set, *Disanthus cercidifolius* Maxim. var. *longipes* H. T. Chang

1 Introduction

Often only a small fraction of the hermaphroditic flowers initiated by a flowering plant become mature fruits, i.e. only an average of 20% of flowers can produce fruits, while in mature fruits 50%–85% of ovules can produce seeds (Martin, 1998). "Excess" flowers seem to contribute little to seed set (Stephenson, 1981; Sutherland and Delph, 1984). This appears usually to be due to initial overproduction of flowers and later reduction of the fruit yield due to limited resource capacity for fruit maturation (Stephenson, 1981). In flowering plants, a low seed set can result from low availability of resources, low pollen transfer, and flower or seed predation (Campbell and Halama, 1993). In the last 20 years, considerable effort has been devoted to assessing the relative importance of those factors. At the same time, evolution biologists

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have paid more and special attention to pollen and resource limitation.

Although pollen limitation is sufficiently recognized in general sex allocation theory, the theory of resource limitation is also embodied in many predictions generated from sex allocation theory (Charlesworth and Charlesworth, 1987). There are also some studies clarifying whether the seed set of a natural population is limited by pollen (Johnston, 1991; Huang et al., 1998; Huang and Guo, 2000). At present, many such studies find that resource and pollen imitations need be mutually exclusive, although a few such studies have detected both pollen and resource limitations at the same time in the same natural population (Campbell and Halama, 1993).

Disanthus cercidifolius Maxim. var. *longipes* H. T. Chang, a plant species found only in a few counties in Hunan, Jiangxi and Zhejiang Provinces and with a relatively small number of individuals, is ranked as a second Class endangered species for conservation in China (Fu, 1992; Xiao et al., 2002). To reveal the endangered mechanism of this species, the authors have studied its population dynamics, breeding system and flowering phenology of natural population (Xiao et al., 2004a; Xiao et al., 2004b; Xiao et al., 2004c). Quantitative distribution and forestry features (Li et al., 2002), along with dormancy and germination (Shi et al., 2002) have also been studied. The results of former studies show that *D. cercidifolius* var. *longipes* display the reproductive phenomena of "excess flower with low fruit set" which may be related to "pollen competition" in the process of pollination (Xiao et al., 2004b). In this study, we test simultaneously for pollen limitation, resource limitation, and their interaction by supplemental hand-pollination, supplement of resources, and/or a reduction of resources in a natural population of *D. cercidifolius* var. *longipes*. The objectives of the paper are as follows:

1) to probe the effects of pollen and resources on female reproduction via investigation of the seed set, seeds per fruit, and the biomass of total seeds;

2) to make clear whether resource supplements have indirect effects on pollination by increasing attractiveness of flowers to pollinators;

3) to reveal the reproductive mechanism of "excess flower with low fruit set".

2 Experiment design and data analyses

2.1 Study site and its natural conditions

This study was conducted in a natural population of *D. cercidifolius* var. *longipes* in the Jinggangshan Natural Reserve located at the middle of the Luoxiao Mountains in Jiangxi Province in China. This area was covered with secondary forests and secondary shrubs after the destroyed subtropical evergreen broad-leaved forest (Xiao et al., 2004a). Details of the study site can be seen in previous studies of the authors (Xiao et al., 2004a; Xiao et al., 2004b).

2.2 Hand pollination

To determine whether the fruit set and seed set in natural populations of *Disanthus cercidifolius* var. *longipes* are limited by type and/or density of pollen, hand pollination was used in this study. As soon as plants began flowering in September 2003, 30 flowering individuals were marked in three treatments as follows:

In each plant, about 260 flowers on 20 reproductive branches were marked, and then all flowers were exposed to different pollen collected from different individuals (see Table 1). Hand pollination was set from "*initial dehiscence*" to "*withering*" phases.

Table 1 Effect on seed production of supplement pollination in *D. cercidifolius* var. *longipes*

Sources of pollens	From the same flower	From different inflorescences in the same plant	From other plants	CK
Number of flowers	400	350	400	1 500
Ovules per flower	12.3 ± 0.11	13.1 ± 0.39	11.9 ± 0.22	12.6 ± 0.67
Total fruits	3^{a}	36^{c}	59^{c}	26^{b}
Fruit set (%)	0.75^{a}	4.59^{c}	4.75^{c}	1.73^{d}
Satiation seeds	25^{a}	373^{c}	452^{d}	257^{c}
Seed set (%)	0.51^{a}	3.14^{c}	3.70^{c}	1.36^{d}
Pollens per stigma	57.3 ± 1.29^{a}	59.6 ± 1.78^{a}	55.7 ± 1.91^{a}	24.1 ± 2.07^{b}

Letters show significant differentiation among treatments.

Five to seven days after hand pollination, five inflorescences (ten flowers) were collected and kept in FAA (40% formaldehyde : 80% alcohol : acetic acid = 1 : 8 : 1), and the numbers of pollen on each stigma was determined. Other flowers in each treatment were used to determine fruit set and seed set.

2.3 Resource limitation

At the beginning of flower development from the end of June to early July, some plants were marked for treatment as follows:

(1) Supplements of inorganic-resources: To assess the effects of inorganic resources on the fruit set and seed set, we replicated the inorganic-resources supplemental treatments from July to October of 2003. In each treatment, 50 individuals were marked and 1,000 g of fertilizer was applied around the root zone of each plant. The composition of the fertilizer are $NO:P_2O_5:K_2O = 3:3:2$. When the plants were flowering, a solution of 0.5% of the fertilizer was sprayed on the leaves of each plant. 2,000 g of such solutions were used for each plant.

(2) Flower removing: On 60 plants, 0%(Control), 20%, 50%, 80% of all flowers were removed separately. Every attempt was made to ensure that flowers were removed uniformly from all the plant's flower-bearing branches. The numbers of flowers and the fruit set of each plant were calculated before and after the treatment.

(3) Leaf clipping: Clipped plants had their leaf area reduced by cutting off 25%, 50% or 75%. The leaves on 50 reproductive branches per plant were cut in each treatment. There were a total of 45 individuals treated, i.e, 15 individuals per treatment. Unclipped plants were the controls. Those treatments reduced accumulation of organic compounds, allowing us to evaluate whether fruit sets were limited by organic compounds.

Data analyses: To avoid freezing the fruits to death due to low temperatures, all data were recorded before January 15. The seed set is defined as the rate of plump ovules to total ovules.

For each treatment, we compared fruit set, seed set, satiation seeds, abortive fruits, and flowers per individual by one-way analysis of variance (ANOVA). As a post hoc test, Tukey's HSD test was used for analyses. We used analysis of variance to conservatively test the effects of each treatment on fruit set and seed set.

3 Results

3.1 Pollen limitation

Different sources of pollen significantly affected the fruit set and seed set of *D. cercidifolius* var. *longipes* (Table 1). Individuals with self-pollination had the lowest fruit set and seed set, i.e. only 0.75% and 0.51% separately. Cross-pollination had significantly higher fruit and seed sets than any of the other groups. This result indicated that pollen origin had a significant effect on the fruit set and seed set of *D. cercidifolius* var. *longipes*.

In natural pollination, the production of one fruit needs ca. 54.8 flowers, while one seed needs 6.6 flowers or 83.9 ovules.

The number of pollen on stigma with hand-pollination is higher than that with natural pollination, while the fruit set and seed set defined by hand self-pollination were significantly lower than that of natural pollination. There are two stigmas and 12.6 ovules per flower of the species. The average number of pollen grains per flower was at least 48, so the number of pollen grains was significantly higher than that of the ovules per flower. This result indicated that the number of pollen was not the limitation factor to the fruit production of *D. cercidifolius* var. *longipes*.

3.2 Fertilizer addition

Fertilizer addition had a significant effect on the number of abortive flower buds (Table 2). The fertilizer added is helpful to the growth of flower buds, which led to a significantly lower abortive rate of the flower bud and higher rate of blooming. At the same time, fertilizer addition also led to a significantly higher fruit set, seed set and lower abortive rate of fruits.

3.3 Leaf clipping

Leaf clipping had significant effects on the fruit set and seed set of *D. cercidifolius* var. *longipes* (Table 3). Fruit sets were significantly decreasing with an increase in clipped leaf areas. However, there were no significant differences in the rate of abortive fruits among treatments. Cutting the infirm and sick branches led to significantly higher fruit and seed sets, although the total number of blooming flowers decreased.

3.4 Flower removal

When fruit set was calculated with respect to the number of flowers remaining, removal of 20% flowers had no effect (Table 2, 4), while 50%–80% flower removal led to a

Table 2 Effects on bud abortion and seed production with fertilizer-added in *D. cercidifolius* var. *longipes*

Treatment	Flowers per plant*	Percentage of abortive flower buds per plant/%**	Percentage of fruit set/%**	Percentage of abortive fruits/%*	Percentage of seed set/%**
Fertilizing	2666.42 ± 22.13	1.58 ± 0.009	2.61 ± 0.011	68.94 ± 1.165	2.29 ± 0.033
No fertilizing (CK)	2297.57 ± 46.34	0.38 ± 0.015	1.55 ± 0.013	89.62 ± 1.597	1.27 ± 0.012

All the data are "means ± Std. Error"; $^{**}p = 0.01$; $^{*}p = 0.05$

Table 3 Effect on seed production of cutting leaves in *D. cercidifolius* var. *longipes*

Items of observation	Treatments					
	Control	Cutting off 1/4 blade	Cutting off 1/2 blade	Cutting off 3/4 blade	Cutting off whole blade but leafstalk	Clip the infirm branches
Total flowers	3 243^{a}	2 964^{a}	3 867^{a}	3 142^{a}	3 286^{a}	2 591^{b}
Fruits	21^{a}	5.8^{b}	2^{c}	4.25^{b}	2.2^{c}	28^{a}
Fruit set (%)	0.494^{a}	0.202^{a}	0.052^{c}	0.159^{b}	0.091^{c}	1.081^{d}
Satiation seeds	183^{a}	51^{b}	19^{c}	38^{b}	19^{c}	257^{d}
Seed set (%)	0.617^{a}	0.186^{b}	0.049^{c}	0.136^{b}	0.068^{c}	1.083^{d}
Dry weight of satiation seeds (g)	4.983^{a}	1.032^{b}	0.192^{c}	0.257^{b}	0.133^{c}	7.315^{a}
Dry weight per satiation seed	0.027^{a}	0.020^{b}	0.010^{c}	0.007^{c}	0.007^{c}	0.028^{a}
Satiation seeds per fruit	8.714^{a}	8.500^{a}	9.500^{a}	7.600^{a}	6.333^{b}	9.179^{a}

Letters show significant differentiation among treatments.

Table 4 Effect on reproduction of flower removal in *D. cercidifolius* var. *longipes*

Flower removal	Number of flowers		Number of fruits	Fruit-set /%		Dry weight per fruit /g	Dry weight per seed /g
	Initially	After removal		Before removal	After removal		
0%	10 108	10 108	139^{a}	1.38^{a}	1.38^{a}	0.895 ± 0.031^{a}	0.019 ± 0.009^{a}
20%	10 446	8 356	142^{a}	1.36^{a}	1.70^{a}	0.529 ± 0.025^{b}	0.012 ± 0.0013^{b}
50%	12 358	6 178	220^{b}	1.78^{a}	3.56^{b}	0.482 ± 0.019^{b}	0.011 ± 0.0018^{b}
80%	9 670	3 868	206^{b}	2.13^{a}	5.34^{b}	0.341 ± 0.057^{c}	0.010 ± 0.0011^{b}

Letters show significant differentiation among treatments.

significant increase for the set. If the fruit set was calculated with the number of flowers before removing, there were no significant differences in fruit sets among treatments. Flower removal treatments significantly reduced the average weight of single fruits and single seeds.

4 Discussion

4.1 Reproductive mechanisms of pollen and resource limitation in natural population

Most of the previous discussions of pollen and resource limitations have focused mainly on fruit set; minimal attention was given to seed set, biomass of seeds per plant, and flower production. This could be attributed to the fact that pollination levels are not affected by the number of flowers produced within the same season, although elevated seed production can cost a plant or population in terms of flower production in future years. However, this argument depends on the types of inflorescence (Ackerman and Montalvo, 1990; Zimmerman and Aide, 1989). For example, in the orchids' studies by above-mentioned authors, the flowers open only after their bud formation is complete, preventing a compensatory effect on flower production in the same season. Another example is that *Ipomopsis aggregata* has an indeterminate inflorescence, and its flower production responds to nutrient supplements during its blooming season. This means resources available for seed sets may be influenced by flower production and *vice versa* (Campbell and Halama, 1993). In *Raphanus sativus*, investment of resources in fruit set early in the same season would influence later flower production (Stanton et al., 1987). *D. cercidifolius* var. *longipes* belongs to the previous type—its flower open only after the flower bud has completely developed, so that there is no compensatory effect on flower production within the same blooming season.

In our study, both hand-pollination and fertilization increased the number of seeds per fruit and per flower. In addition, different sources of pollen have different effects on seed sets. There was competition among different sources of pollen. Under natural conditions, a majority of pollen grains on the stigma come from flowers within the same plant, which causes few seed sets (Xiao et al., 2004b). This indicated that reproduction of *D. cercidifolius* var. *longipes* was not only limited by pollen supplies, but also by nutrient supplies. Sufficient spatial or temporal heterogeneities in nutrient levels can cause the limitation of the seed set by pollens and/or nutrient resources, although the effect was subtle.

Another way that both nutrient resources and pollens can limit seed sets is that the availability of a resource itself influences attractiveness of flowers to pollinators. In *I. aggregata*, fertilization increases the nectar product rate by increasing the contents of P and K in the soil (Campbell and Halama, 1993; Rathcke, 1992). As in *D. cercidifolius* var. *longipes*, no nectar content was measured before fertilizing, while 0.312 μL (average of nectar among 50 flowers) of nectar content was tested on the third day of blooming after fertilizers were added. The diameter of the flower increased significantly ($r^2 = 0.735$, $p = 0.01$) and had brighter colors. Associated with higher nectar production is a higher rate of visitation by pollinators in natural populations (Campbell et al., 1991). Such increase in visitation by pollinators obviously had an effect on seed sets (Table 2). Our results indicated how resource addition would indirectly influence pollination by increasing the attractiveness of flowers to pollinators.

4.2 Ecological and evolutionary implications of pollen and resource limitation theory

Diane had suggested that it is overly simplistic to attempt to classify a plant species as pollen limited or resource limited. That populations can differ in the relative importance of these two factors has been confirmed in both insect-pollinated and hummingbird-pollinated plants (Johnston, 1991; Campbell, 1987). Our studies indicated that both processes could also occur in the same population, requiring a cautious explanation to either pollen or resources limitation. In our results, there is the possibility of indirect affects by pollinator attraction, so we would not conclude from a resource supplement experiment that seed sets will not be limited by low pollen transfer. Meanwhile, the increasing number of seed sets after hand-pollination would not indicate that supplied resources could not increase it further.

Although increases of fruit sets by hand-pollination may be driven by the decrease of fruit sets of the other flowers or of the number of flowers within a plant, hand-pollination is an important approach to show that seed sets would be limited more or less by the quantity and (or) quality of the pollen the stigma received (Zimmerman and Pyke, 1988).

However, to our knowledge, the temporal patterns of pollen and resource limitation would not be opened out. In our view, future research must consider the modular approach, and production of flowers and balancing the allocation of resources between the male and female function within a flower after resource supplements are applied.

4.3 Reproductive mechanism of "excess flower with low fruit set" of *D. cercidifolius* var. *longipes*

Many hypotheses have been put forward to explain the reproductive mechanism of "excess flower with low fruit set" in endangered plants, such as "*selective abortion hypothesis*", "*ovary reserve hypothesis*", and "*male function hypothesis*", *etc*. (Guitian, 1993).

The "*selective abortion hypothesis*" prescribes that plants could selectively abort "poor quality fruits" (Stephenson, 1981). According to this hypothesis, flower removal limited selection and the choice of fruits to abort (Stephenson and Winsor, 1986; Sutherland, 1987), leading to a greater likelihood of survival for more "poor quality" fruits. In this species, the fruit set is significantly higher, but the weight of a single fruit and single seed is significantly lower in plants where flowers were removed compared with those without flower removal in control plants. Based on the findings that seed weight is positively correlated with its progeny vigor (Richardson and Stephenson, 1991), our results provide support for the "*selective abortion hypothesis*".

In the experiments of flower removal, fruit sets calculated with respect to the number of flowers remaining after treatment increased with increasing percentages of flower removal, but not with the initial number of flowers. This result indicated that a fruit set does not change despite changes in floral mortality. Our result seems to support the "*ovary reserve hypothesis*".According to this hypothesis, the plant can maintain a relatively stable fruit/flower ratio under selective pressure, even if there is unpredictable mortality (Ehrlen, 1991).

The "*male function hypothesis*" states that pollen donation should increase more quickly than seed production when the number of flowers increases (Campbell, 1989; Queller, 1983). These results were validated in some plant species. However, in our experiments, hand-pollination increased the fruit set of *D. cercidifolius* var. *longipes*, and the validity of pollen strictly limited the fruit set—an indication that the "*male function hypothesis*" is also somewhat true in this species.

Field results from 1998 indicate that *D. cercidifolius* var. *longipes* always had low fruit sets in the natural population, jointly with a striking phenomena of "fruit set alternately with year", which shows that different factors may interact and cause these low levels of fruit set. The joint adoption of "*selective abortion hypothesis*", "*ovary reserve hypothesis*", and "*male function hypothesis*" seems to be the most likely explanation for the production of "excess flower with low fruit set" in *D. cercidifolius* var. *longipes*.

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