Postprint: Breeding System and Pollination Biology of the Endangered Plant Plantago fengdouensis

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Abstract

Plantago fengdouensis is an endemic, rare and endangered plant species in the Three Gorges Reservoir Area, currently known only from a small population on Dazhongba near Tujia Village, Zhiping Town, Jiangjin District, Chongqing Municipality. Using both wild and transplanted populations as subjects, the pollination biology and breeding system of *P. fengdouensis* were investigated through field observations and artificial pollination experiments. The results showed that: (1) The individual flower duration of *P. fengdouensis* was approximately 4 days, the inflorescence flowering period was about 8 days, and the population flowering period lasted approximately 3 months. The flowering process of a single flower could be divided into six stages: bud stage, pistil elongation stage, initial stamen emergence stage, petal unfolding stage, petal reflexing stage, and withering and senescence stage. (2) Before petal unfolding, the stigma protruded from the corolla first, reaching maximum receptivity; subsequently, when petals unfolded, the stamens emerged, but by this time most stigmas had already withered, lost viability, and become non-receptive, with only a small portion remaining receptive. This exhibited characteristics of dichogamy, which to some extent prevents selfing. (3) Pollen viability began at the initial stamen emergence stage, reached its peak when petals unfolded and anthers dehisced, and remained viable until withering and senescence. The period of peak pollen viability avoided the optimal period of stigma receptivity, with only slight overlap. (4) Breeding system tests revealed a pollen-ovule ratio of 15373.29 and an outcrossing index of 3. Combined with bagging experiments, these results indicated that *P. fengdouensis* may possess both anemophilous and entomophilous pollination mechanisms, with *Apis cerana* and hoverflies (Syrphidae) as pollinators, albeit in low numbers. The species does not exhibit apomixis, is primarily outcrossing, partially self-compatible, and sometimes requires pollinators. (5) The flowering period avoided the flood inundation period at its distribution site, enabling successful completion of flowering, pollination,

and fruit set. In summary, the floral characteristics, flowering phenology, and breeding system of *P. fengdouensis* provide certain reproductive assurance for adapting to summer flood inundation stress at its distribution site, thereby promoting population persistence.

Full Text

Breeding System and Pollination Biology of the Endangered Plant *Plantago fengdouensis*

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Abstract

Plantago fengdouensis is a unique and endangered plant endemic to the Three Gorges Reservoir region, currently known only from a small population on a river island near Tujia Village, Zhiping Town, Jiangjin District, Chongqing. We investigated its pollination biology and breeding system through field observations and artificial pollination experiments on both wild and transplanted populations. The flowering span of a single flower, inflorescence, and population were approximately 4 days, 8 days, and 3 months, respectively. The single flower development process comprises six stages: bud stage, pistil elongation stage, early stamen showing stage, petal expansion stage, petal reversal stage, and withering stage. Before petal unfolding, stigmas first emerge from the corolla and reach peak receptivity. Stamens are exposed only after petal expansion, by which time most stigmas have withered, become inactive, and largely lost receptivity, with only a small portion remaining receptive. This dichogamy effectively prevents self-pollination to some extent. Pollen viability begins at the early stamen showing stage and reaches its maximum after petal expansion, maintaining viability until the withering stage. The peak pollen viability period avoids the optimal stigma receptivity period, though some overlap exists. The pollen-ovule ratio was approximately 15373.29, and the outcrossing index (OCI) was 3. Combined with bagging experiments, these results indicate that *P. fengdouensis* utilizes both wind and insect pollination. The primary pollinator was *Apis cerana*, though visitor numbers were low. The breeding system is predominantly outcrossing, partially self-compatible, sometimes requiring pollinators, with no apomixis observed. The flowering period avoids the flood season at the distribution site, enabling successful pollination and fruit set. The floral characteristics, flowering phenology, and breeding system provide reproductive assurance that facilitates adaptation to summer flooding stress in the Three Gorges Reservoir region, thereby promoting population persistence.

Keywords: *Plantago fengdouensis*; pollination biology; breeding system; flow-

ering characteristics

Introduction

Plantago fengdouensis is a biennial herb belonging to the Plantaginaceae family and represents a unique endangered plant endemic to the Three Gorges Reservoir region [1-2]. Its wild distribution is extremely narrow, with few individuals historically recorded on several isolated islands in the Yangtze River within Fengdu County and Banan District [3]. Following the Three Gorges Project construction, the original habitats of many islands were destroyed, and *P. fengdouensis* was once considered the only species whose natural populations became extinct due to habitat loss from this project. However, a small remnant population was later discovered on a seasonal flood island at the confluence of the Yangtze and Qijiang Rivers near Tujia Village, Zhiping Town, Jiangjin District, Chongqing. Repeated surveys revealed this island experiences seasonal flooding during summer flood seasons, with water level rises causing inundation. Agricultural development poses a severe threat to this wild population. Previous conservation efforts for *P. fengdouensis* have focused primarily on taxonomy, while studies on reproductive organ characteristics, pollination habits, and adaptation to seasonal flooding remain unreported. Using both the extant wild population and a transplanted population as materials, this study comprehensively analyzes the flowering characteristics to provide theoretical foundations for exploring endangerment mechanisms, effective conservation of this rare and endangered plant in the Three Gorges Reservoir region, and improved propagation applications.

The wild population is located on a river island at the confluence of the Yangtze and Qijiang Rivers near Tujia Village, Zhiping Town, Jiangjin District. The transplanted population was established by relocating individuals from the wild population to the ecological garden at Southwest University (29°16 56 N, 106°23 12 E, 202 m). Wild plants have lanceolate to linear-lanceolate leaves with pinnatifid margins, short hairs at sinus bases, and narrowly triangular lobes. Anthers are reddish-yellow. These key characteristics significantly distinguish *P. fengdouensis* from related species such as *P. udicola* and *P. erosa*. Seeds have hammer-shaped elliptical ventral surfaces.

Materials and Methods

1.1 Experimental Materials Research materials were collected from two sources: (1) the wild population in Jiangjin District, and (2) a transplanted population derived from the wild population and cultivated in the ecological garden at Southwest University during 2016 and 2017.

1.2 Floral Morphology and Flowering Dynamics Observation When *P. fengdouensis* entered reproductive growth, we observed flowering dynamics in the wild population from the opening of the first flower until all flowers in the population had withered. The population flowering period was recorded as

the time interval from first to last flower opening [4]. Daily weather conditions were documented. Inflorescences with minimal human disturbance were tagged and measured for floral morphology and single flower development progression between 7:00 and 18:00. We recorded floral composition and morphological changes of pistils and stamens. The early stamen showing stage (when filaments become visible at the petal opening) was designated as the flowering marker, and anther yellowing or withering indicated flowering completion.

1.3 Pollen Viability and Stigma Receptivity We used the method of Rodriguez-Riano and Dafni [5-6] to detect pollen viability and stigma receptivity at different developmental stages in the wild population. Viable pollen and receptive stigmas stained blue, while non-viable/non-receptive structures remained unstained. Pollen viability percentage was calculated as: (number of stained pollen grains / total pollen grains measured) × 100%.

1.4 Pollen-Ovule Ratio and Outcrossing Index To determine the pollen-ovule ratio (P/O), we randomly selected pre-opening flowers from the wild population. All anthers were removed with forceps and placed in a 1.5 mL centrifuge tube with 5 mol/L NaOH solution. After 30 minutes, anthers were crushed with a dissecting needle, distilled water was added to 1.5 mL, and the tube was placed in an ultrasonic cleaner for 10 minutes to separate and evenly disperse pollen. The suspension was placed on a slide, and pollen grains were counted under a dissecting microscope at high magnification. The corresponding ovary was dissected to count ovules per flower. The P/O ratio was calculated by dividing the average pollen number per flower by the average ovule number per flower. According to Cruden [7], higher P/O ratios indicate greater outcrossing degrees.

For the outcrossing index (OCI), we observed and measured the flowering process and flower diameter in the wild population following Dafni' s [8] criteria: (1) flower diameter <1 mm = 0, 1-2 mm = 1, 2-6 mm = 2, >6 mm = 3; (2) temporal separation: synchronous anther dehiscence and stigma receptivity or protogyny = 0, protandry = 1; (3) spatial separation: same height = 0, spatial separation = 1. The sum of these three values gives the OCI.

1.5 Single Flower Pollen Dispersal We randomly marked flowers at the same developmental stage before opening in the wild population to measure temporal changes in pollen dispersal. Flowers were collected at 4 h, 1 d, and 2 d after anthesis. Remaining pollen quantities were measured using the method described above, and the difference between consecutive time periods represented pollen dispersal during that interval.

1.6 Artificial Pollination Experiments Using healthy inflorescences from the transplanted population, we conducted six pollination treatments: (1) Natural pollination (no treatment) to determine natural fruit set; (2) Emascu-

lated and bagged to test for apomixis; (3) Bagged to detect autonomous self-pollination; (4) Cross-pollination within the same plant (emasculated before anther dehiscence, then pollinated with pollen from a different flower on the same plant when stigmas became receptive); (5) Cross-pollination between different plants (emasculated before anther dehiscence, then pollinated with pollen from another plant); (6) Emasculated and not bagged to test for wind pollination in ventilated indoor conditions. Fruit set rate = (fruit number / flower number) × 100%.

1.7 Flower Visitor Observation During the peak flowering season in 2016 and 2017, we conducted continuous observations at the wild population site on sunny days. Flower visitors were photographed and captured for specimen preparation. Visitor behavior and visitation frequency were recorded.

1.8 Water Level Changes at Distribution Site Hydrological variation patterns at the distribution site were determined based on studies of the Three Gorges Reservoir region by Shen Qian [9] and Yuan Shenhong [10], combined with field survey data.

Results

2.1 Flowering Characteristics and Floral Traits of *P. fengdouensis* The spicate inflorescence of *P. fengdouensis* contains numerous flowers that open sequentially from bottom to top. Individual inflorescences flower for 5-8 days, while the population flowering period lasts approximately 3 months, occurring from late May to August. This period coincides with the drawdown phase of the current water level regulation in the Three Gorges Reservoir region, when water levels remain below the site's elevation, allowing flowering and pollination to proceed without inundation.

Referencing the classification standards for single flower opening processes in *Terminalia franchetii* [11] and *Orchidantha chinensis* longisepala [12], and considering the changes in pistils and stamens during *P. fengdouensis* flowering, the process can be divided into six stages: (1) Bud stage: flower buds are wrapped by greenish sepals (Fig. 1A, B); (2) Pistil elongation stage: the pistil emerges from the corolla and elongates (Fig. 1C); (3) Early stamen showing stage: four anthers connected to curved filaments converge inward, with sepal edges turning from greenish-white to light reddish-purple (Fig. 1D-F); (4) Petal expansion stage: petals expand in a cross shape, anthers turn from bright reddish-purple to withered light brown, and filaments extend with anthers popping out of the corolla mouth and dehiscing longitudinally (Fig. 1G-I); (5) Petal reversal stage: petals gradually reflex backward, some even wrapping around the corolla mouth, with filaments continuing to wither (Fig. 1J, K); (6) Withering stage: filaments wither completely, anthers become lower than the stigma, and the flower senesces (Fig. 1L, M).

Floral morphological characteristics are shown in Table 1 and Figure 1 (N1, N2). The flower opening diameter is approximately 3.25 mm. Each flower has bracts that are triangular-ovate. The corolla tube is about equal in length to the sepals, with narrowly triangular corolla lobes that reflex after anthesis. Anthers are narrowly ovate, turning light brown when dry, and are basifixed. In most flowers, the pistil has dried and withered by anthesis, while in a small portion it withers gradually after flower opening.

2.2 Pollen Viability and Stigma Receptivity Using the staining method [5-6], we detected pollen viability and stigma receptivity at different stages. Before anther dehiscence, pollen already showed high viability (80%), which increased to maximum strength within 0-3 h after dehiscence and was maintained until 1.5 d, after which viability declined sharply to near zero by 36 h. Stigma receptivity peaked before petal expansion, but most stigmas had withered and lost receptivity by the time petals expanded. Only a small portion remained weakly receptive after anther dehiscence. Thus, the peak pollen viability period lags behind the optimal stigma receptivity period, largely avoiding self-pollination that could lead to population decline, though some overlap provides opportunities for self-pollination and ensures reproductive success when environmental conditions change abruptly (Fig. 2 [Figure 2: see original paper], Fig. 3 [Figure 3: see original paper]).

2.3 Pollen Dispersal Dynamics As shown in Figure 4 [Figure 4: see original paper], anthers dehisce immediately after flower opening, with pollen continuously dispersing. Within 1 day, approximately half of the total pollen is dispersed, and after 2 days, about one-sixth remains. This pattern aligns with post-anthesis changes in pollen viability, ensuring timely pollination.

2.4 Pollen-Ovule Ratio The pollen-ovule ratio (P/O) represents the ratio of pollen grains to ovules per flower. Statistical calculations yielded a P/O ratio of 15373.29 for *P. fengdouensis* (Table 2).

2.5 Outcrossing Index According to Dafni' s [8] criteria, the outcrossing index (OCI) for *P. fengdouensis* is 3. Before anther dehiscence, the corolla diameter is 2.25 mm (scoring 2 for 2-6 mm). The stigma is already mature and receptive at this stage (protogyny, scoring 0). The four anthers are separated, and the spatial relationship between stigma and anthers changes continuously. When curved filaments are not extended, the stigma is higher than the anthers; when fully open, anthers exceed the stigma height and droop downward, indicating spatial separation (scoring 1). Therefore, the OCI is 3, indicating a breeding system that is partially self-compatible and sometimes requires pollinators.

2.6 Bagging Experiments Bagging experiment results show that *P. fengdouensis* can set fruit under natural conditions (fruit set rate 91.85%). Emasculated and bagged flowers showed 0% fruit set, confirming no apomixis. Di-

rect bagging yielded 31.54% fruit set, indicating autonomous self-pollination. Cross-pollination within the same plant produced 57.78% fruit set, while cross-pollination between different plants yielded 70.84% fruit set. Emasculated but unbagged flowers showed 92.23% fruit set, demonstrating that pollination is limited by pollinator availability. The natural outcrossing treatment produced 91.85% fruit set (Table 3).

2.7 Flower Visitors and Pollination Behavior The showy flowers of *P. fengdouensis* effectively attract insect visitors. Daily flowering peaks occur between 8:00-12:00, with most anthers dehiscing within 0.5 h. The main visitation peak for most pollinators is 9:30-12:30 on sunny days. The primary pollinator is *Apis cerana*, which prefers newly opened flowers, collects pollen on its hind legs and body, with an average visitation duration of (5.0±1.8) s and frequency of 8 visits/min. *Apis cerana* is the most effective pollinator, facilitating outcrossing through continuous flight between flowers. Two syrphid fly species, *Scaeva pyrastri*, prefer older flowers where stigmas are mostly non-receptive and pollen viability is low, making them less effective pollinators (Fig. 5 [Figure 5: see original paper]).

2.8 Water Level Changes Water level fluctuations at the Jiangjin distribution site show that June-August is the inundation period due to summer floods. During this time, *P. fengdouensis* completes leaf growth and successfully flowers and sets fruit. From September to the following May, water levels remain low. The average elevation of the distribution site (202 m) is above the maximum reservoir water level, ensuring that summer floods do not affect flowering and pollination. The flowering period is synchronized with the drawdown period, further ensuring population persistence (Fig. 6 [Figure 6: see original paper]).

Discussion

3.1 Relationship Between Floral Characteristics and Breeding System Floral characteristics, including floral composition and display patterns, govern mating opportunities in flowering plants [13]. The floral traits of *P. fengdouensis* —showy anthers, long-persistent fresh sepals that increase inflorescence display area, and exserted pistils and stamens that enhance pollinator contact—effectively attract insect pollinators and increase pollination opportunities, demonstrating adaptation to entomophily. However, small flowers densely aggregated in spikes, dry pollen easily dispersed by wind, long slender filaments, loosely attached anthers, and elongated feathery stigmas also suit anemophily. Bagging experiments confirmed that wind also serves as a pollination vector, as ventilated indoor conditions produced some fruit set. The species lacks apomixis and shows no fruit set when emasculated and bagged, confirming sexual reproduction. Emasculated but unbagged flowers showed high fruit set, indicating predominant outcrossing with pollinator contribution, while bagged flowers showed some fruit set, indicating supplemental self-pollination.

Dichogamy is considered a mechanism to avoid intrafloral selfing and increase outcrossing rates [15-16]. *P. fengdouensis* shows clear protogyny: stigmas emerge from the corolla before anthesis, reaching peak receptivity, while stamens are exposed only after petal expansion. By this time, most stigmas have withered and lost receptivity, with only a small portion remaining receptive, thereby reducing self-pollination and increasing outcrossing opportunities. Some overlap in receptivity provides opportunities for self-pollination, which may benefit self-compatible species by ensuring reproductive success when pollinators are scarce [17-18]. The plant' s ability to produce new buds at the root collar base provides opportunities for geitonogamy.

According to Cruden [7], the P/O ratio of 15373.29 suggests obligate outcrossing, while Dafni' s [8] OCI of 3 indicates partial self-compatibility sometimes requiring pollinators. Thus, *P. fengdouensis* employs mixed wind-insect pollination, consistent with reports for other *Plantago* species such as *P. lanceolata* [19-20] and *P. maritima* [21-22]. Similar mixed pollination systems have been reported in *Chionanthus retusus* [23].

3.2 Flowering Characteristics and Pollination Different pollinators exhibit different visitation behaviors that affect pollination efficiency and plant reproductive success [24]. *Apis cerana*, the main pollinator of *P. fengdouensis*, prefers newly opened flowers when pollen dispersal is maximal and viability is strongest within the first day. This ensures timely and effective pollination. The bee' s thorax and abdomen contact both anthers and stigmas during visitation, carrying substantial pollen between flowers and promoting outcrossing. The two syrphid fly species prefer older flowers with mostly non-receptive stigmas and weaker pollen viability, making them less important pollinators. However, their visitation at different times coordinates with *A. cerana* activity, ensuring continuous pollination and avoiding competition for pollen, allowing effective pollinators to function optimally.

The high synchrony of flowering within single inflorescences and the mass-flowering pattern of multi-flowered spikes attract numerous visitors and encourage continuous visitation [26-28]. Extended flowering duration is an adaptation to variable environments or scarce pollinators [29-30]. The population-level flowering pattern, with continuous inflorescence development throughout the period, has been reported as an adaptive strategy in studies of two *Tamarix* species in Xinjiang [31].

3.3 Flowering Phenology and Pre-adaptation to the Drawdown Period Water stress is a primary limiting factor for vegetation in the Three Gorges Reservoir drawdown zone. The original distribution sites of *P. fengdouensis* were river islands that became completely submerged due to reservoir operation. The Jiangjin section of the reservoir is affected by both winter impoundment and summer floods. The studied population on Dazhongba Island is located at the reservoir tail where water fluctuation is moderate. Its flow-

ering period occurs during the drawdown phase when water levels are low, allowing completion of flowering and fruiting before summer flood arrival. This phenological timing avoids flood impacts on reproductive processes, consistent with findings by Yuan Shenhong [10]. The site' s average elevation (202 m) exceeds the maximum reservoir water level, further ensuring population persistence. Compared with observations at the Three Gorges Botanical Garden [33], the Jiangjin wild population shows earlier reproductive phenology, likely representing pre-adaptation to the new water level regime. Further research is needed on seed survival during inundation and seed viability.

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Note: Figure translations are in progress. See original paper for figures.