

Reproductive Biology of *Ficus beipeiensis*

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Abstract

This paper uses morphological, anatomical and ecological methods to study the morphological characteristics and propagation mechanism of *Ficus beipeiensis* S.S Chang which is endemic to China, providing a scientific basis for the rare population of wild plants and repopulation. The following results were obtained. First, *F. beipeiensis* with pollinating fig wasps was highly adapted in morphological structure and behavior. Second, a monoclinal flower period existed during the developmental phase of male flowers. *F. beipeiensis* had one to four stamens and one pistil. The pistil in the stigma of syconium flowers was similar to that of gall flowers, but no pollinating fig wasps that laid eggs in the ovary were found. Third, wild individual specimens were found to be rare. The investigation found only one male and four female individuals among them. However, only two female plants can bear fruits. The remaining 9 female plants were cultivated, among which only four grew syconia. No fruit, seed germination, and seeding were found under natural conditions. Several possible reasons for the growth of rare wild plants can be found as following: 1) An imbalance between male and female plants reduces breeding efficiency; 2) *Ceratosolen* sp. is a species-specific pollinator of *F. beipeiensis*, so the gall rate is lower; 3) The high mortality of *Ceratosolen* sp. results in low pollination rate; 4) The seed rate [25.64% ± 54.13% (N = 50)] is lower, ranging from 2% to 70%; 5) Seed germination is difficult under natural conditions.

Keywords

F. beipeiensis, Morphological Structure, Reproductive, Wild Individual Were Rare

1. Introduction

Ficus spp. (Moraceae) pollinated by highly specific fig wasps has long been held as an example of coevolution with their highly specialized pollination mutualism [1]. Previous studies investigated the morphological structure, physiological ecology, and biological behavior of these wasps and revealed a complex and precise pollination relationship with syconia [2]-[5]. In monoecious species, each syconium carries male flowers and female

flowers with styles of varying lengths. Pollen-loaded female wasps enter a syconium to pollinate the female flowers and spawn in ovaries [6] [7]. In dioecious species, male and female plant syconiums release similar chemicals through mutual simulation to attract pollinators [8]-[10]. However, non-pollinating fig wasps disturb pollinating fig wasps in the syconium. Pollinating and non-pollinating fig wasps compete to gain more resources for their offspring. Research on fig pollination biology has greatly progressed around the world. The present study aims to contribute further templates and experience.

F. beipeiensis is a dioecious and narrow field distribution species found on limestone soil in Jinyun Mountain, Chongqing, China. Site survey revealed that the wild plants found comprised one male and four females. Only two female wild plants can fruit. Differences in leaf and fig shape were found between the male and female plants. The distance between the male and female plants was approximately 500 m (linear distance). The quantity of male individual was less than that of individual quantity, but the female can fruit. The fig wasp pollination was also found to adapt to each other based on morphological structure. In this paper, we addressed the following to study the reproductive characteristics of *F. beipeiensis*: 1) the possible special syconium composition of the species; 2) the cause of the rarity of the wild plants. The results of this study may serve as a scientific basis for recovering the wild population of *F. beipeiensis*.

2. Materials and Methods

2.1. Materials

F. beipeiensis (Moraceae: *Ficus* subgen. *Sycomorus*) is dioecious. The male plant has the following characteristics: 4 - 5 m, diameter of 12.6 cm, oval leaf blade, 21 cm to 31 cm × 14 cm to 18 cm, papery, acute or mucronate apex, irregular and sparsely toothed margins. The figs pendulous on specialized leafless branchlets of the main branches have a diameter of 3.90 cm. They have a top depression and are densely covered with short rust-colored pubescence (Figure 1).

The female plant has the following characteristics: 7 - 12 m, diameter of 27.8 cm, oblong-elliptical leaf blade, 22 cm to 28 cm × 8 cm to 12 cm, papery, cuneate base, irregularly and sparsely toothed margins on the upper 2/3. The figs pendulous on specialized leafless branchlets of the main branches are pear shaped and 1 cm to 2 cm in diameter (Figure 2).

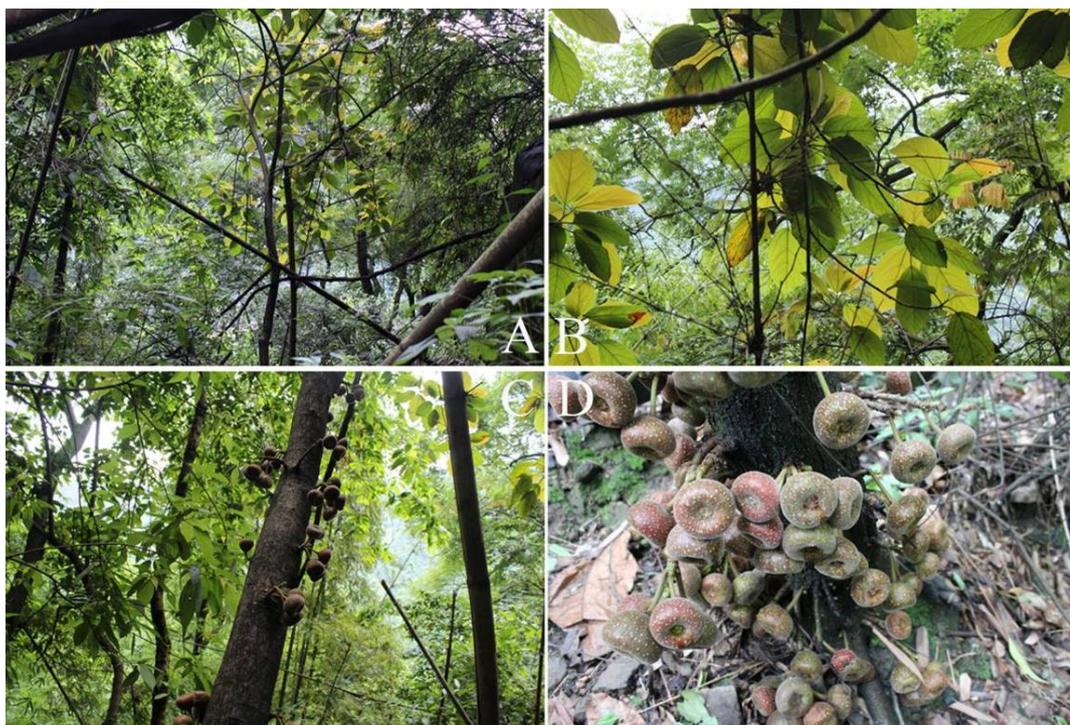


Figure 1. Male plants characteristics. (A): male plant; (B): leaf; (C)-(D): syconium.



Figure 2. Female plants characteristics. (A) Female plant; (B): leaf; (C)-(D): syconium.

2.2. Methods

Investigation on the morphological characteristics, pollination biology, and other factors was conducted from May 2010 to November 2012.

2.3. The Characteristics of Syconium

One male plant and one female plant in the young flowering phase were selected. A total of 20 and 50 syconia were selected from the male and female strains, respectively. The selection of syconia was performed every 7 d. The diameters of the syconia were measured using vernier gauges until maturity.

2.4. Measure Length of the Flower and Style

A total of 20 and 60 male and female syconia in the female phase were collected. The lengths of gall flowers, female flowers, and styles were measured using a biological micrometer in stereoscopic microscope.

2.5. Collection of Statistical Flower

Male and female syconia in the female, inter-floral, and male phases were separated and collected. The numbers of gall flowers, male flowers, female flowers, and galls and seeds were recorded. Gall and seed rates were calculated as $\text{gall rate} = \text{gall number}/\text{gall flower number}$ and $\text{seed rate} = \text{seed number}/\text{female flower number}$, respectively. The number of syconia was at least 20.

2.6. Research of Pollination and Mating Behavior of Pollinator

Male syconia (D-Phase) were selected and divided. Then, the mating behavior of the pollinator was observed. Female syconia (B-Phase) were also selected and divided. The pollination behavior of the pollinator was observed. The syconium number was less than 10 in each observation.

2.7. Research of Morphological Characteristics of Seed

Seeds were collected from the female and were observed the morphological characteristics by longitudinal

anatomy from August to October 2012.

2.8. Data Analysis

Statistical analyses were performed using SPSS (ver. 13.0). The results were presented as mean \pm SD. Statistical significance between groups and variables was considered at $p < 0.01$.

3. Results

3.1. The Growth Cycle of *F. beipeiensis* Syconium

The growth cycle of *F. beipeiensis* syconium is continuous. The growth cycle of male syconium is divided into five phases: pre-female, female, inter-floral, male, and post-floral. The growth cycle of female syconium is divided into four phases: pre-female, female, inter-floral, and post-floral. These divisions were made to better describe and explain the internal development of syconium. The divisions are consistent with the standard of Galil and Eisikowitch [11].

Pre-female phase: Male figs (N = 40) 0 cm to 2.91 cm \pm 0.72 cm in diameter are fascicular on leafless old branches or main branches. They appear green or reddish and are covered with pubescences and white projections. Female figs (N = 40) 0.62 cm \pm 0.15 cm in diameter are fascicular and round. They appear red and covered with pubescences and projections. In addition, bracts are raised at the top of figs. Gall and female flowers begin to develop and are raised. Tight bracts fill the syconium cavity.

Female phase: Male figs (N = 40) 3.89 cm \pm 0.29 cm in diameter change from green to red. When gall flowers fill the whole syconium cavity, male flowers begin to develop and are surrounded by petals. Female figs (N = 40) 1.72 cm \pm 0.18 cm in diameter and female flowers fill the syconium cavity. Then the bracts blossom and form a channel directed outside.

Inter-floral phase: Male figs (N = 40) 4.26 \pm 0.32 cm in diameter appear red with tightly arranged bracts. Spawned gall flowers variably and gradually grow. The stigma fades, and the peduncle stretches to 1.50 mm \pm 0.32 mm (N = 168). By contrast, un-spawned flowers fade. Male flowers gathering in front of the bracts have hermaphrodite characteristics. Male figs (N = 50) 2.15 cm \pm 0.20 cm in diameter have tightly gathered bracts. Pollinated female flowers develop into fruits, whereas un-pollinated female flowers fade. These figs appear dark red at the bottom of the branches. This characteristic distinguishes them from the female phase.

Male phase: Male figs (N = 40) 4.31 cm \pm 0.37 cm in diameter turn soft. Female pollinating fig wasps fly out when the bracts open. When male flowers mature, another flower splits and grows with bracts. No male flower exists in female figs, so the male phase does not exist.

Post-floral phase: After pollinating fig wasps fly out, male figs (N = 40) and female figs (N = 50) become 4.12 cm \pm 0.53 cm and 2.18 cm \pm 0.40 cm in diameter, respectively. Fertilized female flowers develop into fruits. Figs fade when the life cycle is complete.

3.2. Characteristics of Male, Gall, and Female Flowers

F. beipeiensis is a dioecious plant. Male figs have both male and gall flowers; however, gall flowers cannot reproduce. They simply offer pollinating fig wasps a place to spawn. Female figs only have female flowers.

A male flower (N = 100) growing at the top of figs has two stamens (3.09 mm \pm 0.54 mm in length), a peduncle, and two cracks in anthers. Four connate, obovate, and yellow tepals are found, with a style remaining on the pistil on the base (**Figure 3**). Gall flowers are distributed in the cavity, and male flowers during the development stage appear to be at the hermaphroditic flower stage (female phase to male phase). Hermaphroditic flowers have complete stamens (1 - 4) and pistils (1) (**Figure 4**). Gall flowers are 1.37 mm \pm 0.22 mm (N = 223) in length and may or may not have a peduncle. The style is 0.34 mm \pm 0.11 mm (N = 223) and of the terminal type. The stigma is trumpet shaped. The ovary is obovate and white. Three to four pale red or pink and oval or obovate tepals with base joint tightly surround the ovary (**Figure 5**).

Female flowers (N = 435) 2.28 mm \pm 0.29 mm in length have four tepals and may or may not have a peduncle. These flowers are obovate lanceolate and red. They have a lateral style and a rod-shaped white stigma. The piligerous style is 1.43 mm \pm 0.57 mm in length (N = 435), and the ovary is spherical. The stigma joint forms a Syn-stigma, which increases pollination chances (**Figure 6**).

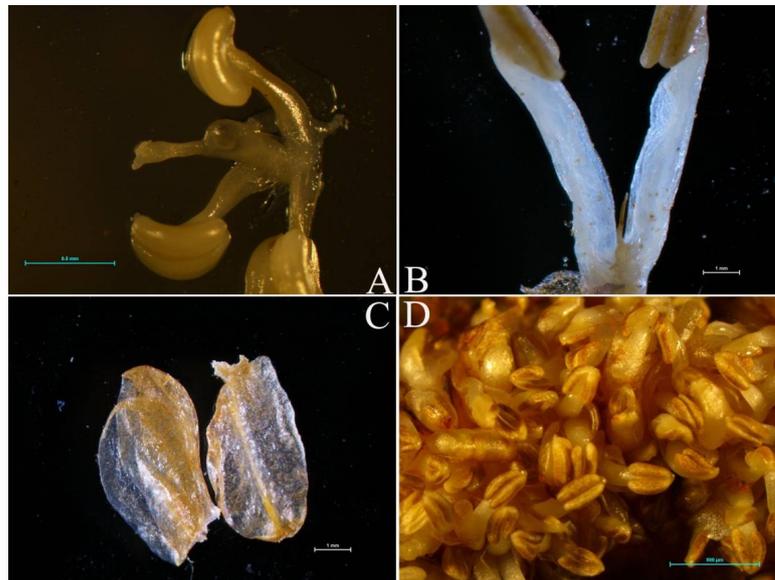


Figure 3. Male flower morphological characteristics. (A): Developmental male flowers (Fig wasps lay eggs in the pistil); (B): Mature male flowers (pistillode in bottom of the male flower); (C): Bracts; (D): Male flowers around the bracts.



Figure 4. Hermaphrodite flower morphological characteristics. (A)-(D): Developmental male flowers had hermaphrodite flower characteristics 1 (1 - 4 stamens and 1 pistil); (E): Rudimental pistil in the bottom of mature male flowers; (F): Hermaphrodite flowers around the bract.

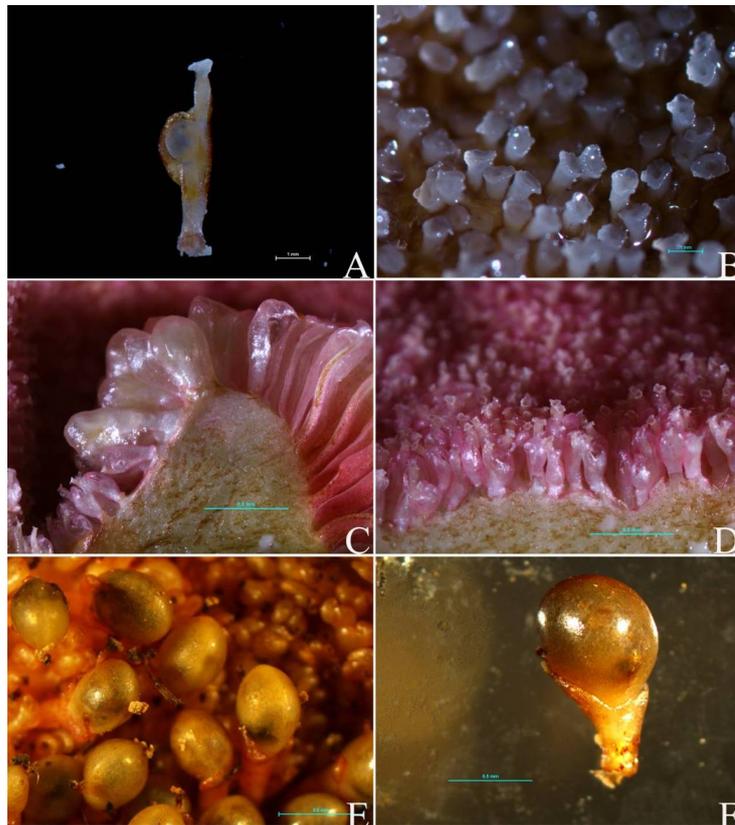


Figure 5. Gall flowers morphological characteristics. (A): Gall flower; (B): Trumpet chapter; (C): Bract in top of syconus; (D): The location of gall flowers; (E)-(F): Galls.



Figure 6. Female flowers morphological characteristics. (A)-(B): The location of female flower; (C): Syn-stigma; (D): Ovary and stigma and tepal of female flower.

3.3. Phenological Characteristics of *F. beipeiensis*

The growth of figs is a continuous process (Figure 7). From August to September, the number of female figs

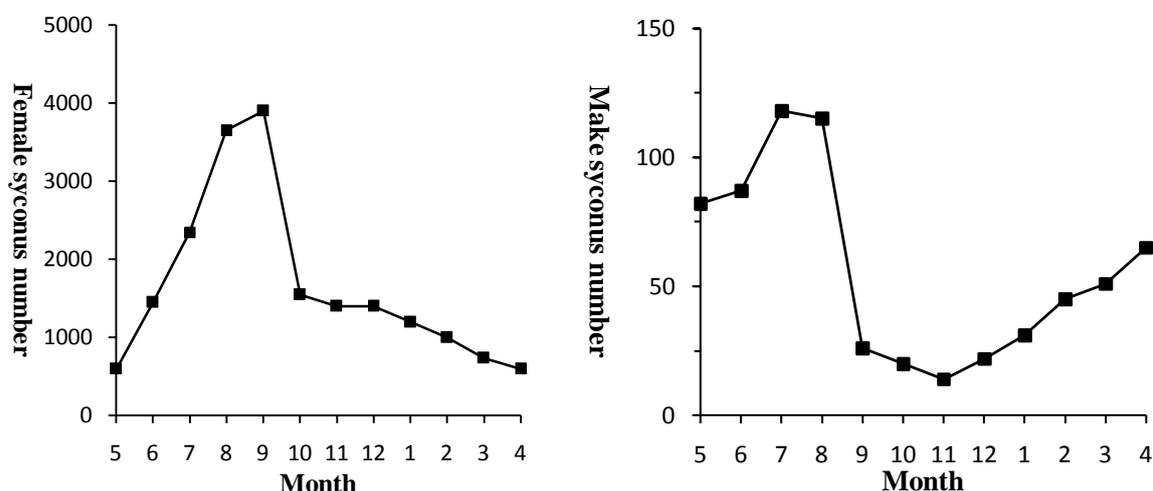


Figure 7. Phenological characteristics of *F. beipeiensis* (one year).

peaks (approximately 4000), and most of the figs (80.2%) are in the female phase waiting for pollinating wasps. If the figs succeed in pollination, fruits hang from the branches; otherwise, the figs fade. The number of figs shows a gradually decreasing trend after the peak, but the figs in the female phase are still found in other months. From July to August, the number of male figs peaks (approximately 130), and the male flowers of the figs (45.2%) in the male phase mature. At the same time, pollinating fig wasps crawl out after eclosion and maturity, bite the galls completely, mate, and then look for new figs to spawning. Some pollinating wasps in the process enter the female figs in the female phase, thereby completing the pollination for *F. beipeiensis*. The number of male figs sharply declines after the peak period. This number gradually increases again in the spring of the coming year. The number of figs generally reaches its peak from July to September when the pollinating fig wasps act relatively frequent.

3.4. Morphological Characteristics, Mating, and Pollination Behavior of *F. beipeiensis* Pollinating Fig Wasps

Only one type of pollinating fig wasp (*i.e.*, *Ceratosolen* sp.) is found in *F. beipeiensis* (Figure 8). Female wasps are dark brown and winged, whereas male wasps are tawny and wingless.

Mating behavior: After emergence and maturity, male wasps leave the galls and find new galls with mature female wasps in the male phase. After tearing the middle and lower parts of gall and inserting their genitals into the crack, male wasps finish mating with female wasps and then look for other female wasps. Male wasps can usually mate with several female wasps. According to statistic, the number of male wasps is 10% that of female wasps. Thus, male wasps have no competition in mating. Female wasps bite the top of galls and crawl out after mating, becoming active in syconium cavity. Male wasps gather at the top of the syconium to bite a channel leading outside. The channel is filled with male flowers, whose pollen adheres to female wasps when the females are out through the syconium. Females with pollen find a proper syconium to spawn. In this process, some female wasps enter female figs (in the female phase) and pollinate *F. beipeiensis*.

Pollination behavior: Pollination occurs during the female phase of female figs, *i.e.*, when the bracts are loose and form a channel. Female wasps stay on the surface of figs and test the tightness of bracts through continuous flapping. If the bracts are arranged tightly, female wasps fly away and search for a proper syconium to spawn by inserting their ovipositor into the stigma. In this state, female wasps have missed wings or broken paraeiopods. The ovipositor is shorter than the stigma. Thus, female wasps cannot spawn in the ovary, which finally dies in female syconium. However, the pollen adhering to female wasps falls on the chapter, thereby completing pollination.

The eclosion and maturity of pollinating fig wasps occur from July to August when the temperature in Beibei Chongqing reaches 39°C to 40°C. The lack of water causes the fading of many figs and the death of numerous pollinating fig wasps (Figure 9). The figs that faded are picked up and counted. Calculation results show that mortality can reach 70%.

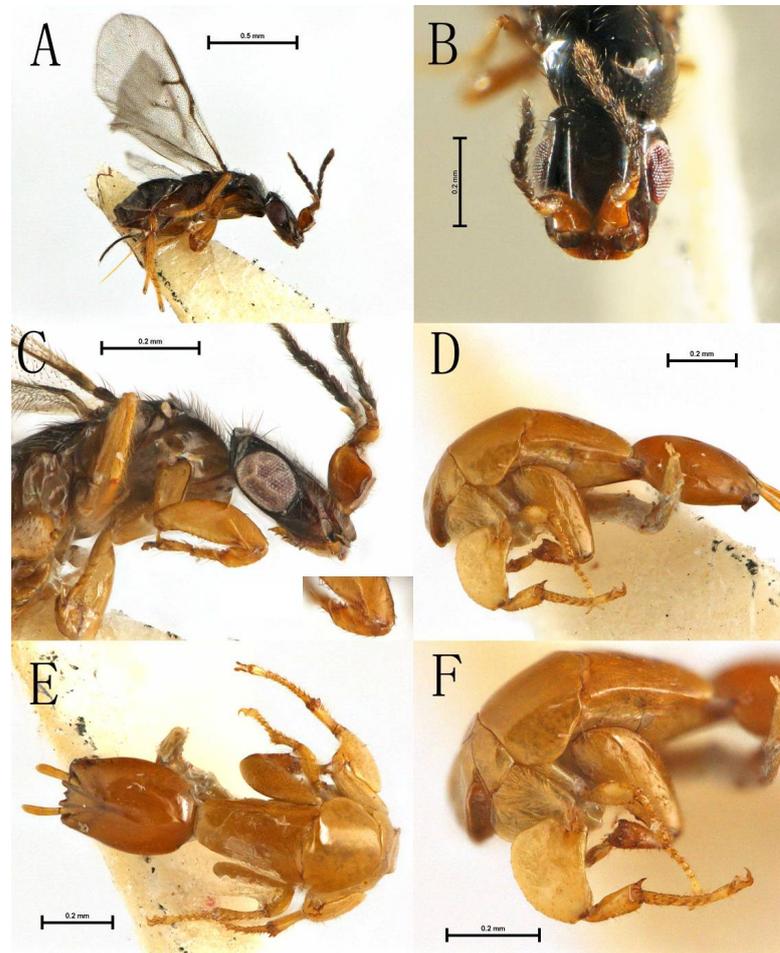


Figure 8. Morphological characteristics *F. beipeiensis* pollinating fig wasps. (A)-(C): Female pollinating fig wasps; (D)-(F): Male Pollinating fig wasps.

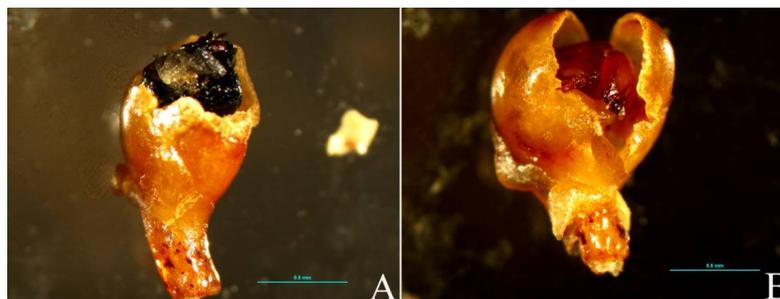


Figure 9. Pollinating fig wasps in gall. (A): Female pollinating fig wasp; (B): Male pollinating fig wasp.

3.5. Number of Pollinating Fig Wasps, Gall Formation, and Fruiting Rate

The male figs have 4323.37 ± 118.69 (N = 40) gall flowers and 716.87 ± 103.81 (N = 40) galls. The gall formation rate is $16.58\% \pm 14.75\%$ (N = 40), with a range of 6.20% to 31.20%. The number of pollinating fig wasps is 630.04 ± 121.81 (N = 40). The number of female wasps is more than that of male wasps, and the sex ratio is approximately 0.1168 ± 0.0239 (N = 40). The numbers of female flowers and fruits are 1541.45 ± 191.68 (N = 50) and 395.23 ± 103.77 (N = 50), respectively. The fruiting rate is approximately $25.64\% \pm 54.13\%$ (N = 50), with a range of 2% to 70%. The fruiting rate is positively correlated with the numbers of entering pollinating fig

wasps and pollen.

One to three wasps are found in a fig, which is more common in male syconium than in female syconium. The number of pollinating fig wasps that fly out of male figs is also presumed to be related to temperature. This factor was found to have an effect on the pollination of *F. beipeiensis* and the population of pollinating fig wasps. At high temperatures, wasps die before emergence and fly out of syconium.

3.6. Seed Morphology and Germination Results (Figure 10 and Figure 11)

F. beipeiensis seed is completely hard, yellow, and oval. For example, in *F. benjamina* var. *nuda*, seed germination under proper conditions is completed after 4.8 d to 34.7 d [12]. However, *F. beipeiensis* seed does not germinate until 35 d. In addition, *F. beipeiensis* seed testa is so hard that the seed cannot absorb water. The morphology of the seeds has no difference on the 35th day compared with the initial day. Dealing seeds with acid allows them to fully absorb water and to germinate on the 7th d when the germination rate is beyond 85%. Seeds can grow into seedlings. However, these seedlings are slender and weak, with slow growth.

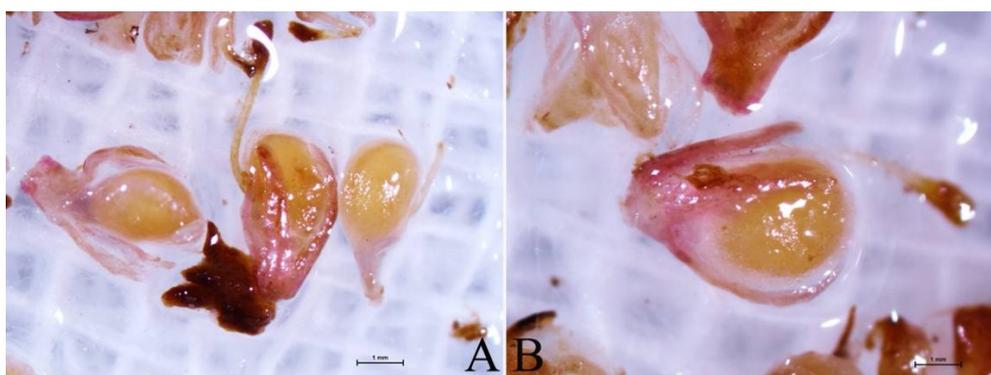


Figure 10. Seed morphology.

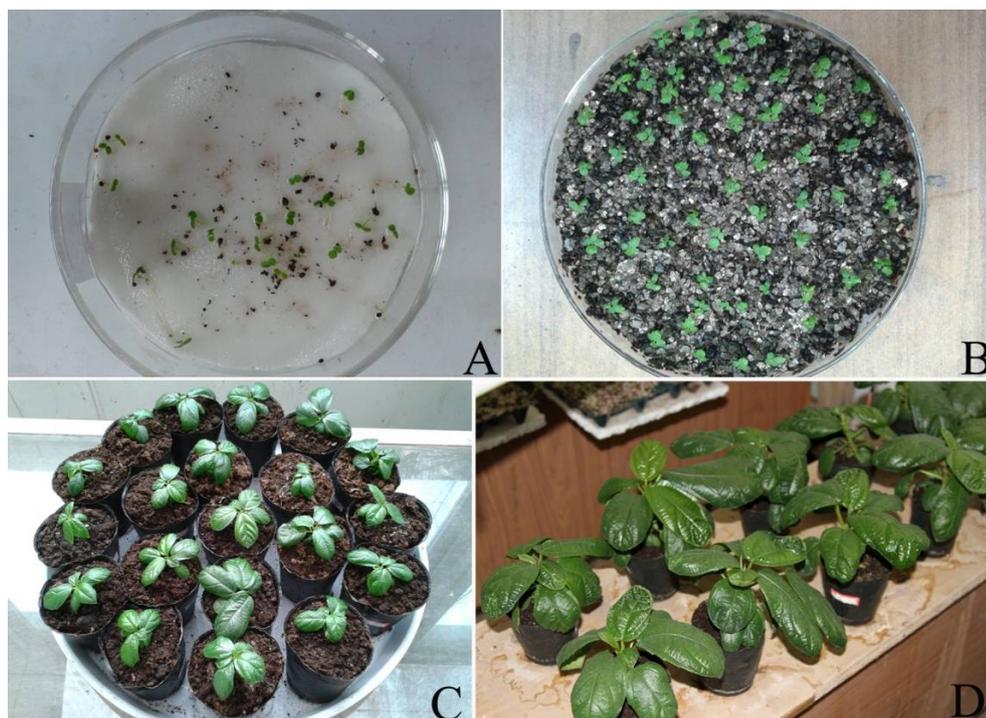


Figure 11. Seed Germination and different periods seeding. (A): Seed germination (10 d); (B): seedling (25 d); (C): seedling (77 d); (D): seedling (134 d).

4. Discussion

The development of male flowers includes a hermaphroditic flower stage (female phase to inter-floral phase) that has not been reported in *Ficus*. The structure and ovules of hermaphroditic flower are complete. The pistil stigma of male flowers is similar to that of female flowers in morphology and to that of gall flowers in length, a part of which is active. In male figs, several gall flowers in the development process have only one stamen and pistil. After completing development, the stamen turns into a unisexual gall flower. Therefore, *F. beipeiensis* hermaphroditic flowers are presumed to have developed from male flowers and some gall flowers. The syconium of *F. pumila* var. *awkeotsangs* has degenerate female flowers, indicating that unisexual flowers in *F. pumila* var. *awkeotsangs* syconium develop from hermaphroditic flowers. *F. hispida* also has hermaphroditic flowers, including a stamen, a pistil, and an ovary occupied by larvae of fig wasps [13]. However, fig wasps do not spawn in the ovary of the hermaphroditic flowers of *F. beipeiensis* because the pistil is wrapped so tightly by the perianth that the pistil cannot make contact with the wasps during their spawning period and during the hermaphroditic flower development stage.

F. vasculosa in Subgen. *Pharmacosycea* is monoecious with two male flowers, several 1 or 3. Degenerate pistils exist on the base of a male flower. In Sect. *Sycidium* of Subgen. *Ficus*, *F. tinctoria*, *F. subulata*, and *F. heteropleura* all have a stamen, whose base has a degenerate ovary (Flora of China). Only *F. cyrtophylla* has several hermaphroditic flowers in a few male figs, and *F. subulata* with abnormal female figs in a female plant have a few hermaphroditic flowers [14]. In the development process, *F. beipeiensis* undergoes a hermaphroditic flower stage when the hermaphroditic flowers are 86%, which has neither been discovered nor valued in the study of *Ficus*. The phenomenon directly proves that the male flowers in *F. beipeiensis* male syconium are developed from hermaphroditic flowers. *F. beipeiensis* retains the original development.

F. beipeiensis and pollinating fig wasps comprise the mutualistic symbiosis system by showing high adaptability to each other. The specific performance is as follows:

- 1) Male flowers are distributed near the bracts. Pollinating fig wasps have to pass through the male flowers to reach the outside world, thereby ensuring that pollen sticks on the wasps, which then fly out of the syconium. As a result, the success rate of pollination in different plants is increased.
- 2) After the gall flowers form galls, the peduncle gradually elongates and pushes the galls to the male flower, making the eclosion and mature pollinating wasps touch the anther while getting out of the galls.
- 3) Gall and female flowers are different in form and function. Gall flower styles are longer than the ovipositor of pollinating fig wasps, and the stigma is trumpet shaped, which improves the spawning efficiency of pollinating fig wasps. Female flower styles are longer than the ovipositor of pollinating fig wasps. The stigma is also clubbed, and the style is piligerous. The stigma joint forms a Syn-stigma, which increases the chances of pollination.
- 4) The development period of male flowers is consistent with the eclosion and maturity period of pollinating fig wasps. The late maturity of male flowers aids in avoiding pollination in the same syconium.
- 5) Male plants grow figs all year round. Male figs suitable for pollinating fig wasps pollinate in each phase to ensure that the life cycle of pollinating fig wasps can be completed smoothly and perfectly.
- 6) *F. beipeiensis* only has pollinating fig wasps, which reduce competition and allow the pollinating fig wasps to make full use of internal resources.

F. beipeiensis and pollinating fig wasps both show high adaptability. The late maturity of male flowers and the differentiation in the functions of female flowers are ubiquitous in dioecious species, which largely avoid inbreeding. This phenomenon is common in other *Ficus* and pollinating fig wasp symbiotic systems (*F. auriculata*, *F. cyrtophylla*, *F. subulata*, *F. semicordata*, and *F. hispida*). These phenomena fully prove that the *Ficus*-pollinating fig wasp symbiotic system is indispensable with closely related stages. However, male and female figs have fruit asynchrony, indicating that figs develop in different phases despite being part of the same plant. *F. beipeiensis* figs gradually develop from the base to the top of leafless branches, wherein the pre-female, female, inter-floral, and male phases simultaneously exist on the same branch. Some pollinating fig wasps choose figs in the female phase to spawn after flying out of figs. Pollinating fig wasps that maintain population in a single male plant were studied in *F. hirta*. A single male plant can maintain two to three generations of pollinating fig wasps depending on the development of the asynchrony of figs [13]. In the year cycle, male figs always exist in the female phase, which ensures that pollinating fig wasps spawn in nearby figs after eclosion and maturity. A similar phenomenon was reported in *F. hispida* and *F. cereicarpa* [15] [16]. However, fig wasps pollinating *F. bei-*

peiensis have the same behavior, which is presumed to maintain the population of pollinating fig wasps. This phenomenon is the key factor that retains the *F. beipeiensis*-pollinating fig wasp symbiotic system, especially in populations limited by plant number [17] [18].

Field investigation revealed that one male and four female *F. beipeiensis* were found behind the North Spring hill. Figs or seedlings were not found in two out of the four females. The ratio of male to female is 1:4; however, this ratio is 1:1 in other dioecious plants [19] [20]. The change in the population-to-sex ratio has an effect on population structure, development, and productivity. In dioecious plants, the females need to supply nutrition to the gamic ovule; therefore, the reproductive resource allocation model of female plants is higher than or equal to that of male plants [21]. Given the limitation in self factors of *F. beipeiensis*, a male plant may improve the reproductive structure, wherein male figs are 3 cm to 4 cm in diameter with 183.29 ± 31.39 flowers and an anther-to-ovule ratio of 0.08. By contrast, larger figs (e.g., *F. oligodon*) are 4 cm to 7 cm in diameter with 173.12 ± 2.92 male flowers and an anther-to-ovule ratio of 0.0421 ± 0.009 [22]. *F. beipeiensis* enlarges the diameter of figs and improves the ability of male flowers to adapt to bad conditions. However, the rarity of male plants greatly limits the syngamy process and seriously influences population. Mature *F. beipeiensis* figs are large in diameter and have 1541.45 ± 191.68 (N = 50) female flowers. The fruiting rate of *F. beipeiensis* is approximately $25.64\% \pm 54.13\%$ (N = 50), with a range of 2% to 70%. This rate is lower than that of other recently reported banyan trees, such as *F. Auriculata* (50.8%), *F. hispida* (73.8%), *F. semicordata* (28% to 81%), *F. pumila* (82%), and *F. pumila* var. *Awkeotsang* (83.5%) [23]-[26]. The fruiting rate may be related to the number of pollinating fig wasps and pollen in female figs. Research on the behaviors of pollinating fig wasps by dissecting female figs revealed that 80% of figs have only one pollinating fig wasp. However, the number of wasps per fig can reach 11.8 or even 27 for *F. racemosa* L. and *F. auriculata*. Only one wasp is found in *F. cyrtophylla*, but the figs are 12.27 and 10.87 mm in diameter for males and females, respectively. The ratio of *F. beipeiensis* wasps is low. The fruiting rate fluctuates largely. Approximately 10 to 30 fruits are found in some figs by dissecting the fruiting figs. In general, fruit distribution has two cases: 1) fruits disperse in the figs and 2) fruits gather near the top of the figs. These two cases conform to the place where pollinating fig wasps die. The cause for this phenomenon may be related to the amount of pollen that wasps carry and the action ability of wasps. The gall formation rate ($16.58\% \pm 14.75\%$) of *F. beipeiensis* is relatively low. Pollinating fig wasps are born in large scale in August. Numerous pollinating fig wasps are found dead when male figs are dissected. The mortality rate is rather high, which reduces the amount of pollen that wasps carry and influences the fig formation of *F. beipeiensis*. The high temperature may also cause the large number of deaths of pollinating fig wasps. Under natural conditions, seeds are difficult to germinate, and no sprouting or seedling can be found.

The absence of any seedling may be attributed to the hardness of seeds and the slenderness of seedlings. The conventional method of germinating the ripe and complete seeds of *F. beipeiensis* and *F. gasparriniana* miq. var. *laceratifolia* can make *F. gasparriniana* miq. var. *laceratifolia* seeds absorb water and germinate after 10 d. However, the same method is useless to *F. beipeiensis* seeds. *F. beipeiensis* seeds maintain their primary state and absorb a small amount of water after 30 d, which prevents germination. *F. beipeiensis* seeds dealt with acid can absorb water fully, and the testa softens. Hence, the germination rate increases. After seeds were gathered in different batches, the germination rate from September to October (over 85%) was found to be the highest, whereas that from November to December was low (approximately 30%). This phenomenon may be related to the quality of seeds.

In conclusion, the rarity of the wild *F. beipeiensis* has many causes. First, the male and female ratio is imbalanced, and the rarity of the male plant fundamentally reduces breeding efficiency. Second, only one type of pollinating fig wasp is found in *F. beipeiensis*. However, the rate of gall formation is low, and the pollinating fig wasps may be greatly influenced by temperature during eclosion and maturity. This factor decreases the probability of pollen being brought into the female figs. Third, the low fruiting rate of *F. beipeiensis*, the rarity of male plants, and the shortness of wasps may jointly lead to low fruiting rates of *F. beipeiensis*. Fourth, *F. beipeiensis* seeds have difficulty in germinating, and their seedlings are slender and weak.

Further research on the seed germination of *F. beipeiensis* should be conducted. The establishment of *F. beipeiensis* regeneration system can increase the population of *F. beipeiensis* and provide a quantitative basis for its population recovery. *F. beipeiensis* male and female plants greatly differ; thus, further research is needed to explore these differences. When figs are scarce, the pollinating fig wasps of *F. beipeiensis* maintain their population by completing their life cycle in a single male plant or by acting as non-pollinating fig wasps that breed other *Ficus* species. This phenomenon needs further studies for a more in-depth discussion.

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References

- [1] Janzen, D.H. (1979) How to Be a Fig. *Annual Review of Ecology and Systematics*, **10**, 13-51. <http://dx.doi.org/10.1146/annurev.es.10.110179.000305>
- [2] Wiebes, J.T. (1976) A Short History of Fig Wasp Research. *Garden's Bulletin of Straits Settlement*, **29**, 207-236.
- [3] Wiebes, J.T. (1979) Figs and Their Insect Pollinators. *Annual Review of Ecology and Systematics*, **10**, 1-12. <http://dx.doi.org/10.1146/annurev.es.10.110179.000245>
- [4] Herre, E.A. and Machado, C.A. (2008) Evolutionary Ecology of Figs and Their Associates: Recent Progress and Outstanding Puzzles. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 439-458. <http://dx.doi.org/10.1146/annurev.ecolsys.37.091305.110232>
- [5] Berg, C.C. (1989) Classification and Distribution of *Ficus*. *Experientia*, **45**, 605-611. <http://dx.doi.org/10.1007/BF01975677>
- [6] Galil, J. (1973) Pollination in Dioecious Figs: Pollination of *Ficus fistulosa* by *Ceratosolen bewitti*. *Gardens Bulletin Singapore*, **26**, 303-311.
- [7] Kjellberg, F.E., Jouselin, E., Bronstein, J.L., Patel, A., Yokoyama, J. and Rasplus, J.-Y. (2001) Pollination Mode in Fig Wasps: The Predictive Power of Correlated Traits. *Proceedings of the Royal Society of London B*, **268**, 1113-1121. <http://dx.doi.org/10.1098/rspb.2001.1633>
- [8] Ware, A.B., Kaye, P.T., Compton, S.G. and Van Noort, S. (1993) Fig Volatiles: Their Role in Attracting Pollinators and Maintaining Pollinator Specificity. *Plant Systematics and Evolution*, **186**, 147-156. <http://dx.doi.org/10.1007/BF00940794>
- [9] Grison-Pige, L., Bessi re, J.-M. and Hossaert-McKey, M. (2002) Specific Attraction of Fig-Pollinating Wasps: Role of Volatile Compounds Released by Tropical Figs. *Journal of Chemical Ecology*, **28**, 267-279. <http://dx.doi.org/10.1023/A:1017930023741>
- [10] Cook, J.M. and Lopez-Vaamonde, C. (2001) Fig Biology: Turning over New Leaves. *Trends in Ecology and Evolution*, **16**, 11-13. [http://dx.doi.org/10.1016/S0169-5347\(00\)02038-3](http://dx.doi.org/10.1016/S0169-5347(00)02038-3)
- [11] Galil, J. and Eisikowiteh, D. (1968) On the Pollination Ecology of *Ficus sycomorus* in East Africa. *Ecology*, **49**, 259-269. <http://dx.doi.org/10.2307/1934454>
- [12] Wang, X. and Song, S.-Q. (2006) Light-Sensitivity in Seed Germination of *Ficus benjamina* var. *nuda* (Moraceae) and Its Ecological Significance. *Acta Botanica Yunnanica*, **28**, 631-638.
- [13] Jia, X.-C., Dan, Y., Zhang, Y. and Chen, Y.-Z. (2007) Direct Evidence for the Cycling of Fig Wasps within One Male Fig Tree. *Nordic Journal of Botany*, **25**, 119-124. http://dx.doi.org/10.1111/j.0107-055X.2007.00021_23.x
- [14] Shi, Z.-H. and Yang, D.-R. (2006) The Reproductive Ecology of *Ficus cyrtophylla*, an Understory Fig Species in Xishuangbanna Tropical Rainforest, China. *Journal of Plant Ecology*, **30**, 610-616.
- [15] Patel, A. (1996) Variation in a Mutualism: Phenology and the Maintenance of Gynodioecy in Two Indian Fig Species. *Journal of Ecology*, **84**, 667-680. <http://dx.doi.org/10.2307/2261330>
- [16] Harrison, R.D. and Yamamura, N. (2003) A Few More Hypotheses for the Evolution of Dioecy in Figs (*Ficus*, Moraceae). *Oikos*, **100**, 628-635. <http://dx.doi.org/10.1034/j.1600-0706.2003.11829.x>
- [17] Anstett, M.C., Michaloud, G. and Kjellberg, F. (1995) Critical Population Size for Fig/Wasp Mutualism in a Seasonal Environment: Effect and Evolution of the Duration of Female Receptivity. *Oecologia*, **103**, 453-461. <http://dx.doi.org/10.1007/BF00328683>
- [18] Bronstein, J.L., Gouyon, P.-H., Gliddon, C., Kjellberg, F. and Michaloud, G. (1990) The Ecological Consequences of Flowering Asynchrony in Monoecious Figs: A Simulation Study. *Ecology*, **71**, 2145-2156. <http://dx.doi.org/10.2307/1938628>
- [19] Rottenberg, A. (1998) Sex Ratio and Gender Stability in the Dioecious Plants of Israel. *Botanical Journal of the Linnean Society*, **128**, 137-148.
- [20] Rottenberg, A. (2000) A Field Survey of Dioecious Plants in Israel Sex Ratio in Seven Rare Species. *Botanical Journal of the Linnean Society*, **134**, 439-442.
- [21] Delph, L.F. (1999) Sexual Dimorphism in Life History. In: Geber, M.A., Dawson, T.E. and Delph, L.F., Eds., *Gender*

and Sexual Dimorphism in Flowering Plants, Springer, Heidelberg, 149-173.

http://dx.doi.org/10.1007/978-3-662-03908-3_6

- [22] Yang, P. (2008) Comparison of Ecological Features of *Ficus auriculata*, *Ficus oligodon* and *Ficus sp.* in *Neomorpha*. Conference Article in Biological Diversity Conference of Province Yunnan.
- [23] Chen, Y., Li, Q.-H. and Ma, W.L. (2002) The Reproductive Character Of *Ficus Pumila* Var. *Pumilar*, *F. Pumila* Var. *Awkeotsang* AND Their Pollinators. *Acta Phytoecologica Sinica*, **26**, 58-63.
- [24] Yang, D.-R., Peng, Y.-Q., Song, S.-S., Zhang, G.M., Wang, R.-W., Zhao, T.-Z. and Wang, Q.-Y. (2002) Pollination Biology of *Ficus hispida* in the Tropical Rainforests of Xishuangbanna, China. *Acta Botanica Sinica*, **44**, 519-526.
- [25] Wang, Q.-Y., Yang, D.-R. and Peng, Y.-Q. (2003) Pollination Behaviour and Propagation of Pollinator Wasps on *Ficus semicordata* in Xishuangbanna, China. *Acta Entomologica Sinica*, **46**, 27-34.
- [26] Peng, Y.-Q. (2003) Pollination Biology of *Ficus auriculata* Lour. *Acta Phytoecologica Sinica*, **27**, 111-117.