DOI:10.6661/TESFE.2005012 台灣昆蟲Formosan Entomol. 25: 119-125 (2005) 科學短訊 Scientific note

Formosan Entomologist
Journal Homepage: entsocjournal.yabee.com.tw

A Revision of the Pathway from Monoecious Species to Dioecious Species in Ficus (Moraceae) - Based on Pollinators' Relative Ovipositor Lengths and Seed/Pollinator Production 【Scientific note】

由授粉蜂的相對產卵管長度及其子代與種子比例來推導榕樹雌雄同株至雌雄異株之演化【科學短訊】

Ying-Ru Chen
陳穎儒

*通訊作者E-mail : yrchen@mail2000.url.com.tw

Received: 2004/08/20 Accepted: 2005/08/19 Available online: 2005/06/01

Abstract

In this study, the author attempted to deduce the evolutionary direction between monoecious and dioecious species in Ficus by the relative ovipositor lengths of pollinators and seed/pollinator production. Since the relative ovipositor lengths of pollinators become longer from dioecy to monoecy, the benefits of seed production in dioecy is not greater than that in monoecy, and the fitness of pollinators in monoecy is also no better. That is, the evolutionary pathway from dioecy to monoecy was not beneficial for either figs or fig wasps. Hence this hypothetical evolutionary process is energetically expensive and yet not beneficial, so we infer that the monoecious species are not the evolutionary descendants of dioecious species in Ficus.

摘要

假設雌雄異株是原始種類，而雌雄同株是進化種類，亦即榕樹是由雌雄異株演化至雌雄同株，則與其共生的授粉雌蜂也應一起協同演化，在雌雄異株上的授粉雌蜂應是原始的，而在雌雄同株上的授粉蜂是進化的。依據前人對於十幾種榕樹上的授粉雌蜂進行測量，授粉雌蜂產卵管的相對長度在雌雄異株上較短，而在雌雄同株上較長，若以上的假設為正確，則授粉雌蜂產卵管的長度從相對較短演化成相對較長，而授粉雌蜂的產卵管這樣演化，應可獲得較大的適存值，亦即子代數應該增加。但是事實上授粉雌蜂的產卵管雖可達到50～99% 的雌花，子代數卻只有20～30%。另外，在雌雄同株的榕果產子率也沒有比雌雄異株的產子率來得高，因此授粉雌蜂產卵管的長度從相對較短演化成相對較長，對授粉蜂與榕樹而言，皆不能獲得任何的好處，此演化路徑花費了能量但卻沒有得到相對的好處，從演化的觀點來看是不正確的。這個結果推翻了原先的假設，因此榕樹的演化路徑應是由雌雄同株演化至雌雄異株。

Key words: evolution, Ficus, fig wasp, ovule, ovipositor length
關鍵詞: 演化、榕樹、榕果小蜂、小花、產卵管長度

Full Text: PDF(0.27 MB)

台灣昆蟲 25: 119-125 (2005)
Formosan Entomol. 25: 119-125 (2005)

A Revision of the Pathway from Monoecious Species to Dioecious Species in *Ficus* (Moraceae) - Based on Pollinators' Relative Ovipositor Lengths and Seed/Pollinator Production

Ying-Ru Chen 3Fl., No.6, Lane 244, Rui-Ann St., Taipei, Taiwan

ABSTRACT

In this study, the author attempted to deduce the evolutionary direction between monoecious and dioecious species in *Ficus* by the relative ovipositor lengths of pollinators and seed/pollinator production. Since the relative ovipositor lengths of pollinators become longer from dioecy to monoecy, the benefits of seed production in dioecy is not greater than that in monoecy, and the fitness of pollinators in monoecy is also no better. That is, the evolutionary pathway from dioecy to monoecy was not beneficial for either figs or fig wasps. Hence this hypothetical evolutionary process is energetically expensive and yet not beneficial, so we infer that the monoecious species are not the evolutionary descendants of dioecious species in *Ficus*.

Key words: evolution, *Ficus*, fig wasp, ovule, ovipositor length

Introduction

Ficus species can be classified into two categories: monoecious and dioecious species. Generally, each species of *Ficus* is specifically associated with a single pollinating chalcid wasp (Wiebes 1963, 1986). In the literature, many people have discussed the evolutionary path of *Ficus* or fig wasps (Murray, 1987; Kjellberg and Rasplus, 1989; Kerdelhue and Rasplus, 1996; Machado *et al.*, 2001; Wieblen, 2002; Harrison and Yamamura, 2003). The evolution of *Ficus* was often discussed according to climate, latitude, geography, and phenology before 1990 (Murray, 1987; Kjellberg and Rasplus, 1989). There are surely effects from these environmental differences. However, in addition, determining whether figs are capable of surviving with their pollinators is the relation of mutualism. After 1990, few papers discussed the evolutionary path of *Ficus* from the proportion of seeds and gall-makers (Kerdelhue and Rasplus, 1996; Harrison and Yamamura, 2003).

In this article, the author provides a new point of view that leads to an argument for the evolutionary path from

*Correspondence address
e-mail: yrchen@mail2000.url.com.tw

monoecy to dioecy. The author describes for the first time how the ovipositor lengths of pollinators can be used as a viewpoint to look at the evolution of *Ficus* species, and as direct evidence, obviously without other subsidiary factors from outside the core system, to the evolutionary path from monoecy to dioecy.

Before 1996, florets in B-phase figs of monoecious species were divided into two to several ovarian layers based on different lengths of the styles (Galil and Eisikowitch, 1968, 1977; West and Herre, 1994; Kerdelhue and Rasplus, 1996; West *et al*., 1996; Jousselin *et al*., 2001). Galil and Eisikowitch (1968) proposed that two types of florets appear in monoecious figs, namely, long- and short-styled florets. In their hypothesis, it is believed that in mature figs, the galls of pollinators are all located on short-styled florets, while the seeds are almost exclusively located on long-styled florets. According to their argument, this is due to the ovipositor lengths of the pollinators. Since pollinator ovipositors are longer than short-styled florets but shorter than long-styled florets, pollinators can only oviposit their eggs in short-styled florets. The pollen carried by pollinators thus falls on the stigma of long-styled florets as pollinators crawl about during oviposition, thereby pollinating the stigma leading to seed development. This hypothesis, in agreement with experimental data, describes the mutualistic phenomenon between figs and fig wasps. The morphological division in the length of the floret style restricts pollinators to oviposit on long-styled florets, which in turn allows the separate development of galls and seeds in the figs. Contrarily, the ovarian layers of florets in each dioecious fig are almost uniform, only that those in male figs are higher than those in female figs (Berg, 1984). Male and female figs of dioecious species release the same chemical smell to attract pollinators into the B-phase. Because pollinators' ovipositors can reach all florets of male figs but only a few of the female figs, pollinators entering male figs can oviposit all florets but those entering female figs are unable to oviposit on any floret. Therefore, florets in male figs become galls, while those in female figs become seeds.

This hypothesis was not questioned until 20 years later when Bronstein (1988) reexamined the style lengths of florets, in measurements done on *Ficus pertusa*, a monoecious species. Bronstein found that the style length in fact had a left-polarized normal distribution which cannot be simply categorized into two types. Moreover, the ovipositor length of pollinators, on average, is actually longer that 82% of the floret styles. However, curiously enough, only 23% of the florets ultimately become galls. Although Bronstein did not successfully explain this seemingly contradictory discovery, her research indeed revealed the weakness of the previous hypothesis.

Nefdt and Compton (1996) performed a similar investigation on up to 11 *Ficus* species (10 monoecious and 1 dioecious species). Their large amount of data further comfirmed inconsistencies in the application of Galil and Eisikowitch's hypothesis. As to measurements for dioecious species in comparison to those for monoecious species, florets in both male and female figs are obviously either long or short. In male figs, pollinators can lay their eggs on all florets, while in female figs, only 8% of florets are accessible to pollinators. As for monoecious species, style lengths of florets are normally distributed. Amazingly enough, there are five monoecious species in their data for which the average ovipositor lengths of their pollinators are sufficient to reach 90% of florets, as shown in table 1.

However, despite the fact that their experiments effectively questioned the

Table 1. Percentages of florets in nine monoecious and one dioecious species estimated to be accessible as indicated in Nefdt and Compton (1996)

	Ficus species	Percentages of florets estimated to be accessible
Monoecious	*F. salicifolia*	99%
	F. verruculosa	60%
	F. lutea	93%
	F. thonningii	95%
	F. sycomorus	98%
	F. abutilifolia	79%
	F. ottoniifolia	76%
	F. sur	55%
	F. sansibarica	91%
Dioecious	*F. capreifolia*	54%

Table 2. Predicted percentages of florets estimated to be accessible by pollinators and observed mean foundresses and percentage of galls in two monoecious species in two papers (Bronstein 1988, Nefdt and Compton 1996)

Ficus species	Percentages of florets estimated to be accessible	Actual galls	Mean no. of foundresses
F. pertusa	82%	23%	1.94
F. burtt-davyi	83%	41%	1.37

hypothesis of Galil and Eisikowitch, they still did not provide a reasonable explanation to account for the curious fact that only a low percentage of florets finally become galls in monoecious species (Table 2). Many hypotheses and probabilities were suggested by them, but none have actually been proven (Nefdt and Compton, 1996). Even after 2000, a lot of scientists have focused on finding the mechanism controlling seed/pollinator composition (Jousselin *et al*., 2001, 2003; Kjellberg *et al*., 2001; Yu *et al*., 2004), but they still have not found the answer.

This hypothesis does not focus on discussing the mechanism of determining pollinator offspring by figs. The author tries to deduce the evolutionary path of *Ficus* according to the relative ovipositor lengths of the pollinators. From measurement information in past papers, the author organizes some important results as follows.

(1) Generally speaking, relative ovipositor lengths of pollinators of monoecious species are longer than those of dioecious species. According to past data (Bronstein, 1988; Nefdt and Compton, 1996), the ovipositors of pollinators of monoecious figs can reach over 60%, and even up to 99%, of florets style, but those of dioecious species can only reach 50-54% of floret styles (Table 1). Therefore, pollinators' ovipositors in monoecy can reach more of the florets than in dioecy.

(2) Comparing the offspring number of pollinators, about 20-40% of florets become pollinators in monoecy (Table 2), while about 30-45% do so in dioecy (Nefdt and Compton, 1996; Jousselin *et al*., 2003), and there were no significant differences between two groups of *Ficus*. Although pollinators in monoecy can

reach more florets, they do not obtain greater benefits to their fitness than in dioecy.

(3) From information on seed production, monoecy only produces 17-25% of seeds (Bronstein, 1998; Nefdt and Compton, 1996). However, almost all florets of female figs in dioecy are pollinated and become seeds, that is, 50% of florets produce seeds in dioecy, so the percentage of seed production in dioecy is higher than that in monoecy.

According to the actual information, the author proposes an argument for the evolutionary direction between monoecious and dioecious species from the relative ovipositor lengths of *Ficus* pollinators and seed/pollinator production. The author found this is a good point from which to discuss the evolutionary path of *Ficus*. It is a general deduction, but exceptions probably exist.

Hypothetical inference

Let us first assume that dioecious species are the evolutionary origin of monoecious species. Pollinators of dioecious species should correspondingly then be the evolutionary origin of those of monoecious species. According to Nefdt and Compton (1996), the relative ovipositor lengths of pollinators of monoecious species are longer than those of dioecious species. Following the assumption, one may conclude that longer ovipositors evolved from shorter ovipositors, and that pollinators should benefit from this evolutionary process. That is, the number of offspring of pollinators should increase, or at least reach 50%. However, the fitness of pollinators of monoecious species is only 20-40% offspring. Hence this hypothetical evolutionary process is energetically expensive and yet not beneficial, which is therefore incorrect (Fig. 1).

On the other hand, the author has several arguments which support the opposite hypothesis, i.e., dioecious species are evolutionary descendents of monoecious species. Seed production is 17-25% in monoecy, which is lower than the offspring number of pollinators. The efficiency of pollination is too low to obtain a lot of seeds. The population of dioecious trees is generally smaller than that of monoecious ones. In order to increase the pollination efficiency, the only way is to push pollinators to work harder. Therefore, it is reasonable to have evolution proceed towards longer styles of florets which suppresses the production rate of pollinators. Pollinators climb on to the long-style florets, fail to oviposit but pollinate a large proportion of the florets. In addition, the division into male and female figs still preserves the population of pollinators, since the styles of florets in male figs are uniformly short. The indistinguishable alluring chemical smell from male and female figs causes an equal possibility of entrance by pollinators (Hossaert-Mckey *et al.*, 1994), and therefore is beneficial for both figs and pollinators.

From the view of mutualistic relations, the purpose of the evolutionary direction of *Ficus* is to find a balance between figs and fig wasps. Regardless of how ovipositor length of pollinators has evolved or floret morphology has changed, both figs and pollinators evolve in directions beneficial to themselves. From actual data of relative ovipositor lengths of pollinators and seed/pollinator production, there is strong information telling us that there is meaning in the process of evolution. Maybe the results we are seeing are not the best, but surely they are the most suitable for the situation at this time. If the logic of our hypothesis is correct, the high probability that dioecious species evolved from monoecious species from the view of pollinators cannot be ignored.

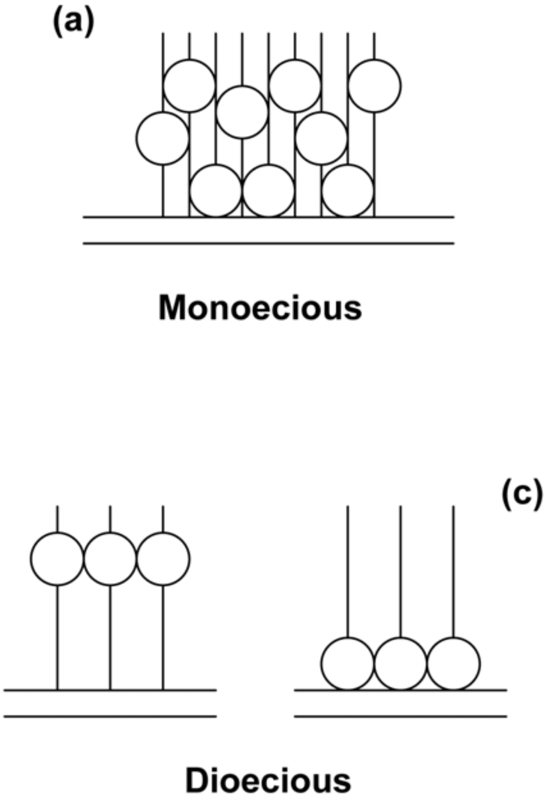

Fig. 1. Floret morphology of monoecious *Ficus* species (a), and male figs (b) and female figs (c) of dioecious *Ficus* species. Pollinators of monoecious species have the potential to oviposit over 70% of florets, while pollinators of dioecious species can reach all florets in male figs but almost no florets of females figs. On average, pollinators of dioecious species are estimated to oviposit 50% of both male and female florets. From the percentages, the relative ovipositor lengths of pollinators of monoecious species are longer than those of dioecious species. If dioecious species are more primitive than monoecious species in the evolutionary process, then the relative lengths of ovipositors of pollinators should have evolved from shorter to longer. Pollinators should have obtained greater benefits from this change. However, the result showed that only 23-40% of florets become galls, and the low percentage rejects the hypothesis.

References

Berg, C. C. 1984. Floral differentiation and dioecism in *Ficus* (Moraceae). pp. 15-25. *In*: F. Kjellberg, and G. Valdeyron, eds. Minisymposium on Fig and Fig Insects. CNRS, Montpellier.

Bronstein, J. L. 1988. Mutualism, antagonism, and the fig-pollinator interaction. Ecology 69: 1298-1302.

Galil, J. 1977. Fig biology. Endeavour (new series) 1: 52-56.

Galil, J., and D. Eisikowitch. 1968. Flowering cycles and fruit types of *Ficus sycomorus* in Israel. New Phytol. 67: 745-758.

Harrison, R. D., and N. Yamamura. 2003. A few more hypotheses for the evolution of dioecy in figs (*Ficus,* Moraceae). Oikos 100: 628-635.

Herre, E. A., C. A. Machado, E.

Bermingham, J. D. Nason, D. M. Windsor, S. S. McCafferty, W. V. Houten, and K. Bachmann.** 1996. Molecular phylogenies of figs and their pollinator wasps. J. Biogeogr. 23: 521-530.

Hossaert-Mckey, M., M. Gibernau, and J. E. Frey. 1994. Chemosensory attraction of fig wasps to sustances produced by receptive figs. Entomol. Exp. Appl. 70: 185-191.

Jousselin, E., M. Hossaert-Mckey, D. Vernet, and F. Kjellberg. 2001. Egg deposition pattern of fig pollinating wasps: implication for studies on the stability of mutualism. Ecol. Entomol. 26: 602-608.

Jousselin, E., M. Hossaert-Mckey, E. A. Herre, and F. Kjellberg. 2003. Why do fig wasps actively pollinate monoecious figs? Oecologia 134: 381-387.

Kjellberg, F., and S. Maurice. 1989. Seasonality in the reproductive phenology of *Ficus*: its evolution and consequences. Experientia 45: 647-660.

Kjellberg, F., E. Jousselin, J. L. Bronstein, A. Patel, J. Yokoyama, and J. Y. Rasplus. 2001. Pollination mode in fig wasps: the predictive power of correlated traits. Proc. R. Soc. Lond. B Biol. Sci. 268: 1113-1121.

Kerdelhue, C., and J. V. Rasplus. 1996. The evolution of dioecy among *Ficus* (Moraceae): an alternative hypothesis involving non-pollinating fig wasp pressure on the fig-pollinator mutualism. Oikos 77: 163-166.

Machado, C. A., E. A. Herre, S. McCafferty, and E. Bermingham. 1996. Molecular phylogenies of fig pollinating and non-pollinating wasps and the implications for the origin and evolution of the fig-fig wasp mutualism. J. Biogeogr. 23: 531-607.

Machado, C. A., E. Josselin, F. Kjellberg, S. G. Compton, and E. A. Herre. 2001. Phylogenetic relationships, historical biogeography and character evolution of fig-pollinating wasps. Proc. R. Soc. Lond. B Biol. Sci. 268: 685-694.

Murray, M. G. 1987. The closed environment of the fig receptable and its influnce on male conflict in the Old World fig wasp, *Philotrypesis pilosa*. Anim. Behav. 35: 488-506.

Nefdt, R. J. C., and S. G. Compton. 1996. Regulation of seed and pollinator production in the fig-fig wasp mutualism. J. Anim. Ecol. 65: 170-182.

West, S., and A. Herre. 1994. The ecology of the New World fig-parasiting wasps *Idarnes* and implications for the evolution of the fig-pollinator mutualism. Proc. R. Soc. Lond. B Biol. Sci. 258: 67-72.

West, S. A., E. A. Herre, D. M. Windsor, and P. R. S. Green. 1996. The ecology and evolution of the New World non-pollinating fig wasp communities. J. Biogeogr. 23: 447-458.

Wiebes, J. T. 1963. Taxonomy and host preferences of Indo-Australian fig wasps of the genus *Ceratosolen*. Tijdschr. Entomol. 106: 1-112.

Wiebes, J. T. 1986. The association of figs and fig-insects. Rev. Zool. Afr. 100: 63-71.

Wieblen, G. D. 2002. How to be a fig wasp? Annu. Rev. Entomol. 47: 299-330.

Yu, D. W., J. Ridley, E. Jousseline, E. A. Herre, S. G. Compton, J. M. Cook, J. C. Moore, and G. D. Wieblen. 2004. Oviposition strategies, host coercion and the stable exploitation of figs by wasps. Proc. R. Soc. Lond. B Biol. Sci. 271: 1185-1195.

Received: August 20, 2004
Accepted: August 19, 2005

由授粉蜂的相對產卵管長度及其子代與種子比例來推導榕樹雌雄同株至雌雄異株之演化

陳穎儒 台北市大安區瑞安街244巷6號3樓

摘　　要

假設雌雄異株是原始種類，而雌雄同株是進化種類，亦即榕樹是由雌雄異株演化至雌雄同株，則與其共生的授粉雌蜂也應一起協同演化，在雌雄異株上的授粉雌蜂應是原始的，而在雌雄同株上的授粉蜂是進化的。依據前人對於十幾種榕樹上的授粉雌蜂進行測量，授粉雌蜂產卵管的相對長度在雌雄異株上較短，而在雌雄同株上較長，若以上的假設爲正確，則授粉雌蜂產卵管的長度從相對較短演化成相對較長，而授粉雌蜂的產卵管這樣演化，應可獲得較大的適存值，亦即子代數應該增加。但是事實上授粉雌蜂的產卵管雖可達到 50～99% 的雌花，子代數卻只有 20～30%。另外，在雌雄同株的榕果產子率也沒有比雌雄異株的產子率來得高，因此授粉雌蜂產卵管的長度從相對較短演化成相對較長，對授粉蜂與榕樹而言，皆不能獲得任何的好處，此演化路徑花費了能量但卻沒有得到相對的好處，從演化的觀點來看是不正確的。這個結果推翻了原先的假設，因此榕樹的演化路徑應是由雌雄同株演化至雌雄異株。

關鍵詞：演化、榕樹、榕果小蜂、小花、產卵管長度。