2009 年臺灣國際科學展覽會

優勝作品專輯

編號: 050011

作品名稱

Anthropogenic Restoration of an Endangered Plant Induced the Initial Sympatric Divergence of a Butterfly

得獎獎項

動物學科大會獎第一名

美國正選代表:美國第60 屆國際科技展覽會

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關鍵字: Hygrophila pogonocalyx、host reference 、Junonia iphita iphita

作者簡介



我是譚文皓,目前就讀於台北市立建國高級中學三年級。從小就對生物世界 充滿好奇,很幸運的自國小至今,一直有機會在師長的指導下參與科展競賽,讓 我學習如何藉由科學的研究方法來探究生物世界的奧秘。做研究的過程是辛苦但 是充滿樂趣的,在進行實驗的這一年裡,來往奔波於學校、實驗室與野外調查樣 區之間的日子不計其數;在實驗設計與操作上遇到的挫折也不知有多少次;課業 的壓力一直伴隨,不僅僅培養出良好的時間利用能力,更重要的是學習如何面對 壓力。做生物科展的一路過程帶給我許多成長與體會,成為我珍貴的回憶與經驗。

學習的事永無止境,一路上有許多人給我協助與指導,我心存感激,最後僅 在此謝謝所有曾教導與幫助我的教授、老師與學長們,感謝科教館的輔導計畫, 也感謝家人的鼓勵支持。 大安水蓑衣(Hygrophila pogonocalyx)為局限於臺中沿海溼地之稀有植物, 大量境外復育後,造成黑擬蛺蝶(Junonia iphita iphita)利用此種新寄主植物,而且比 例逐年增加。本實驗比較黑擬蛺蝶在原寄主植物臺灣馬藍(Strobilanthes formosanus) 及新寄主植物上之生長環境遮蔽度、雌蝶產卵偏好、幼蟲生長發育及雄蝶領域的 差異,探討大安水蓑衣復育對黑擬蛺蝶族群可能造成的影響。

結果顯示雌蝶可能存在兩種產卵偏好,且其子代的偏好與親代一致,不受幼 蟲期取食植物影響。雄蝶領域行為與雌蝶偏好相似,並與其親代偏好一致。偏好 大安水蓑衣的個體子代在新寄主植物上有較好的生長表現;兩偏好雜交之子代幼 蟲生長發育顯著下降。本研究認為大安水蓑衣的復育,可能造成黑擬蛺蝶族群在 共域的情況下,因為利用新的寄主植物而產生初步分化的現象。

Abstract

Over the past ten years, *Hygrophila pogonocalyx*, a rare plant species with an original narrow distribution in wetlands along the west coast of central Taiwan, has been purposely cultivated cross Taiwan for off-site restoration. However, extensive anthropogenic planting of certain plant species may cause sympatric divergence of herbivore insects. Here, I show that a nymphalid butterfly *Junonia iphita iphita*, which originally relied mainly on the hostplant Strobilanthes formosanus, can now recognize *H. pogonocalyx* as a new hostplant. The potential effects of *H. pogonocalyx* restoration on *J. i. iphita* are analyzed and discussed.

J. i. iphita collected from a site with both *S. formosanus* and *H. pogonocalyx* showed distinct female oviposition preference for one or the other species, a preference that was heritable for three generations tested. Their respective preference for *S. formosanus* or *H. pogonocalyx* was also revealed in male territoriality. The male territorial behavior together with female egg-laying preference could increase the opportunity for assortative mating, which reduces the gene flow between individuals with different preference. Offspring also had better growth performance on the hostplant which their parents preferred. Moreover, the survival rate of hybrid offspring was decreased, reducing the fitness of hybrid individuals. Genetic differences among these populations were compared by analyzing microsatellite and RAPD markers. Taken together, the behavioral and physiological differences suggest that divergence has occurred between these populations. The choice in host plant usage of *J. i. iphita* may represent an early stage of sympatric speciation via host shifting.

Anthropogenic Restoration of an Endangered Plant Induced the Initial Sympatric Divergence of a Butterfly

A. Introduction

(A) Motivation

Alteration in host species usage patterns of insect herbivores may be originated from the time when an insect species encounters a new combination of host plant species, and this phenomenon could arise from a plant species invading a locality where an insect herbivore population is already present (Thomas *et al.*, 1987). *Hygrophila pogonocalyx* (Figure 1.), belonging to the family Acanthaceae, is an endangered and endemic aquatic plants species originally distributed in wetlands along seashore of Taichung County in Taiwan. It has been widely cultivated all over Taiwan due to the off site restoration practices since 1997. The insect species whichI am interested in, *Junonia iphita iphita* (Figure 2.), is a common nymphalid butterfly originally associated with *Strobilanthes formosanus* (Figure 3.) and several other host plant species in Acanthaceae. I have studied about life history and larval survival strategies of this butterfly, and found that it has recognized *H. pogonocalyx*, a recently introduced plant in its habitat, as a new larval host plant through the field observation and experiments.



Figure 1. Hygrophila pogonocalyx

The findings mentioned above and ability to utilize the new host plant would seem more reasonable if the new host plant species is related to existing host, and indeed shifts between more closely related plants have been reported to happen more frequently, at several taxonomical levels (Janz and Nylin, 1998). The tendency of utilizing the new plant as a host plant by this butterfly seems to have increased over time (Tan, 2007). Therefore, the present study is to investigate whether the restoration practice of *H. pogonocalyx*, which has brought about sympatry of *H. pogonocalyx and S. formosanus*, has led to novel adaptations of this butterfly due to host shift to this new host plant.



Figure 2. Junonia iphita iphita



Figure 3. Strobilanthes formosanus

If a novel host plant is similar to a previously used host, sufficient behavioral and physiological preadaptations may be present, and the plant may be included in the diet without substantial evolutionary change. This process may be responsible for the rapid accumulation of some herbivores on recently introduced plants (Strong, 1974; Southwood and Kennedy, 1983). Both behavioral (preference) and physiological (performance) traits are important components of the ability of phytophagous insects to use particular plant species as hosts (Futuyma and Peterson, 1985; Singer, 1986; Via, 1986). A behavioral change in host preference (followed by larval adaptation) may be implicated in the sympatric divergence of phytophagous insect lineages (e.g. Feder, 1998). Host races in plant-feeding insects, in particular, have often been used as evidence for the probability of sympatric speciation (Drès and Mallet, 2002). Sympatric speciation is the splitting of one evolutionary lineage into two without the occurrence of geographic isolation (Berlocher and Feder, 2002). During much of the twentieth century, sympatric speciation was viewed as much less plausible than geographic (allopatric) speciation (Berlocher and Feder, 2002). Only in the past two decades, with evidence for host races in insects and ecological divergence in fish, has sympatric speciation gained wider acceptance (Berlocher and Feder, 2002). New models of sympatric speciation have largely overcome objections to the possibility of sympatric speciation via host shift (Via 2001).

Host plant use in butterflies can conveniently be divided into the two complex traits namely female oviposition preference and larval performance (Thompson 1988). The tests of female oviposition preference and larval growth performance on two host plants were conducted in this study with the aim of finding out if the host plant preference of adults has changed or diverged and comparing larval growth performance on the native and the new host plant. These tests were to evaluate if a new host race of *J. iphita iphita* had been evolved due to the restoration practices of *H. pogonocalyx*. Oviposition preference and larval performance were chosen for these conditions because a positive correlation between these traits is generally considered to be indicative of host-associated adaptation, and because preference and performance may be important ecological factors generating reproductive isolation in phytophagous insects (Forister, 2004). To find out the factors influencing oviposition preference and growth performance, not only the preference of ovipositing females captured in the study site for testing hosts and the performance of larvae reared on both host plants was

measured, but also their offsprings were used and interbreeding individuals of these two groups.

Theoretical and empirical work on host-associated divergence has dealt almost exclusively with sympatric populations, which has allowed researchers to focus on ecological (as opposed to geographic) mechanisms producing reproductive isolation (Via, 2001). The chances of speciation improve sharply when an individual's choice of habitat enhances the probability of mating with other individuals having the same choice (Colwell, 1986; Butlin, 1990; Rice & Hostert, 1993; Bush, 1994; Dieckmann & Doebeli, 1999). To compare the host plant preference of male and female, male territorial behavior was also tested in order to know which host plant males choose to defend. Defended encounter sites are frequently defined by landscape features that reliably bring the sexes together (Parker, 1978). The environmental condition that they adapted to can also be a factor for ecological divergence. Lee & Chang (1988) indicated that *J. iphita iphita* dwells in humid habitats such as those along forest trails and by the edge of forests, where its native host plant, *S. formosanus*, grows abundantly. However, the novel host plant, *H. pogonocalyx*, grows in a more open and brighter environment.

(B) Goal

The purpose of this research is to investigate whether the off-site restoration practice of *H. pogonocalyx* has led to new adaptations of a native butterfly on a new larval host plant due to novel host plant usage caused by the anthropogenic expansion of *H. pogonocalyx*.

B. Materials and Methods

(A) Materials

1. Insect and plants:

Larvae and adults of J. iphita iphita, sprigs and leaves of S. formosanus and H. pogonocalyx.

2. Equipments:

Multi-thermo growth chamber(Chang-Kuang , CK-68S), T6 full spectrum sun light tube (18W520mm, luminous flux: 1350Lm -18W*75Lm/w), wood and wire mesh cages, forceps, plastic boxes, and small green houses.

(B) Methods

1. Study site

The study site is located at An-Kang Butterfly Ecological Education Park in Sindian City of Taipei County. Several kinds of native host plants of *J. iphita iphita* were growing there, with *S. formosanus* and *H. pogonocalyx* both abundant. *S. formosanus* - and *H. pogonocalyx* -feeding individuals of *J. iphita iphita* were both commonly found at the study site. *H. pogonocalyx* was introduced to the region from Kau-Mei damp area in Taichung County about 15 years ago.

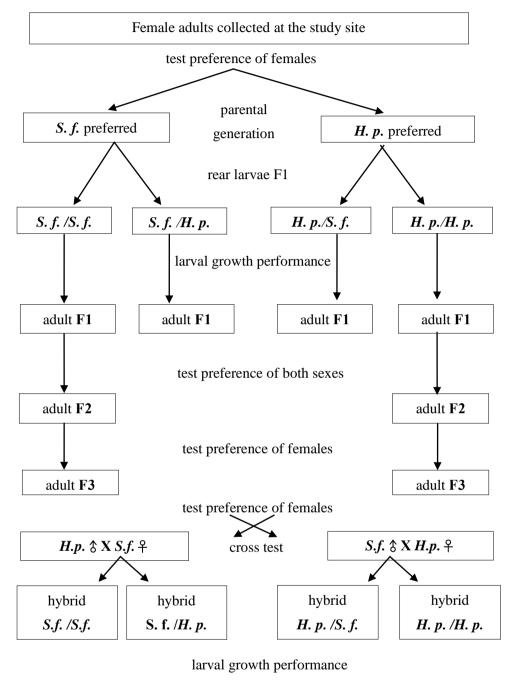
2. Oviposition preference

(1) Experimental design

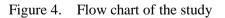
a. Female adults were collected at the study site, and their oviposition preference was tested. They were subsequently divided into two groups, namely *S. formosanus* preferred and *H. pogonocalyx* preferred. Adults with stronger preference from each group were then picked up as the parental generation, and their eggs were then used for the rest of the experiments.

- b. "A/B" denotes "offspring of A host plant-preferring female / fed with B host plant".
 For example, S.f./S.f. indicates "offspring of S. *formosanus*-preferring female / fed with S. *formosanus*", and so forth.
- c. The larvae hatched from the eggs deposited in flow chart (Figure 4.) with S. formosanus and H. pogonocalyx respectively. Consequently "S.f./S.f.", "S.f./H.p.", "H.p./S.f." and "H.p./H.p." 4 were recognized.
- **d.** After eclosion, F1 adults were placed into a butterfly net house at the study site for mating. After one week, I tested the oviposition preference of F1 females.
- e. Repeated above procedure to the third generation offspring (F4).

The flow chart of oviposition preference test



test preference of female



"A/B" denotes "off spring of **A** host plant-preferring female / fed with **B** host plant". For example, **S.f./S.f.** indicates "off spring of *S. formosanus*-preferring female / fed with *S. formosanus*"

(2) Test methods

Testing oviposition preference of female adults:

Females were tested for oviposition preferences between H.p. and S.f. by placing them individually for 12 hours (from 8 a.m. to 8 p.m.) into plastic container ($36 \times 26 \times 18$ cm) in which two similarly sized sprigs of Hp and Sf were fastened to the opposite walls of the container. Two full spectrum sun light tubes (each 18w x75Lm/w) were hanged above the container as substitution of natural sun light. At the end of each trial, the females were removed and number of eggs on each plant sprig was recorded to estimate the percentage of eggs on each plant sprig. According to what I learned from the pretests, the sum of eggs that one *J. iphita iphita* female produced usually more than 60 eggs. To enhance the accuracy of the experiment, data from females that produced fewer than 30 eggs (less than 50% of usual sum) during the 12-h test were excluded from analyses of oviposition preference. The female was retested for oviposition preference in the following day, until it laid more than 30 eggs. The purpose of this experiment is to understand the host preference of the female adults.

Oviposition preference index (OPI) = 100% X $\frac{\# \text{ of eggs laid on } H. p.- \# \text{ laid on } S. f.}{\text{total eggs laid}}$

OPI range from -100 (complete aversion to H. p.) to 0 (equal, or no preference) to +100 (exclusive use of H. p.)

3. Larval growth performance

The larvae were reared individually in plastic boxes (12 x 8 x 5 cm) in the growth chamber. The survival rate of larvae was estimated and the pupal weight recorded. These data represent the larval growth performance and the fitness of the butterfly on alternative host plant.

(1) Pupa weight

The pupal weights between "S.f./S.f.", "S.f./H.p.", "H.p./S.f." and "H.p./H.p." was compared in order to detect the difference between these 4 groups.

(2) Larval survival rate

The survival rate of larva was recorded. The larval survival rate between "S.f./S.f.", "S.f./H.p.", "H.p./S.f." and "H.p./H.p." was compared in order to detect the difference between these 4 groups.

(3) Larval development time

The development time of larva was recorded. The larval development time between "S.f./S.f.", "S.f./H.p.", "H.p./S.f." and "H.p./H.p." was compared in order to detect the difference among these 4 groups.

4. Cross test

Male adults from "S.f./S.f." and female adults from "H.p./H.p." were allowed to interbreed, half of them on *S. formosanus*, the other half on *H. pogonocalyx*. The survival rate of hybrid offspring was recorded, and the oviposition preference of F1 female adults was tested in order to understand the oviposition preference of hybrid individuals, and the growth performance of their offsprings.

5. Territoriality of male adults

Male adults from each of "S.f./S.f.", "S.f./H.p.", "H.p./S.f." and "H.p./H.p." groups were caught and marked with different colors. They were subsequently released at the study site, and the male adults which displayed territorial defense were re-caught in its domain. The hostplant species found in the domain was recorded to find whether their preference was corresponded with their parental generation.

6. Comparison

In this study, I compared the differences between these groups:

- 1. Oviposition preference of female individuals in the study site: to examine if some individuals have developed preference of the new host plant.
- Oviposition preference between parental generation and F1: to study whether their preference corresponds with parental generation, or it varies by what they eat as immature.
- 3. Oviposition preference from parental generation to F3: to investigate whether the preference maintains over generations or not.
- 4. Larvae growth performance of the four groups: to study the relationship between larval growth and oviposition preference.
- 5. The difference between 'S.f./S.f.', 'H.p./H.p.' and F1 hybrid: to investigate if there are any difference in larval growth performance between the colony from original host and hybrid offspring.
- 6. Oviposition preference between the colony from original host and hybrid F1 oviposition preference: to exame the oviposition preference is controlled by both

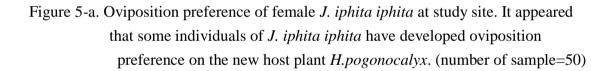
male and female or controlled by single sex.

7. Territoriality of male adults and oviposition preference of female adults: to study whether similar host plant preference was demonstrated in both sexes.

C. Results

(A) Oviposition preference of female

- 100% 80% 60% 40% 20% -20% -20% -40% -60% -80% -100%
- 1. Oviposition preference of female J. iphita iphita. (Figure 5.)



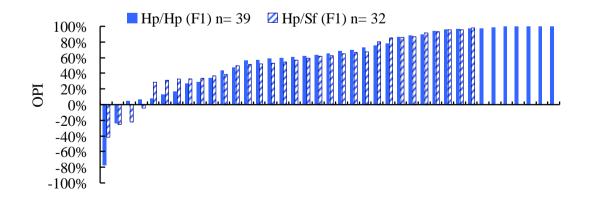


Figure 5-b. Oviposition preference of offsprings of *H. pogonocalyx*-preferring females fed with *H. pogonocalyx* and *S. formosanus* (Hp/H p and Hp/Sf).

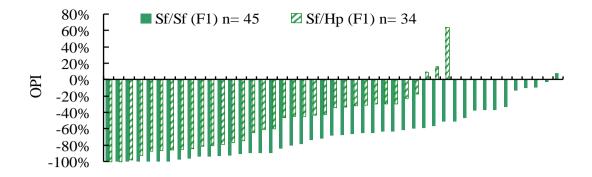


Figure 5-c. Oviposition preference of offsprings of *S. formosanus*-preferring females fed with *H. pogonocalyx* and *S. formosanus* (Sf/Sf and Sf/Hp). It shows that nearly all of the females preferred the same host plant as their parental generation, no matter which host plant the offsprings were fed.

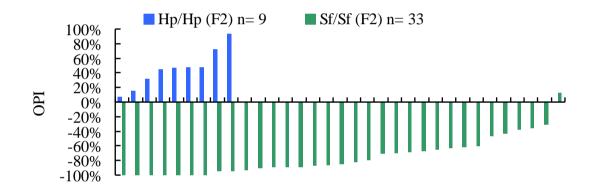


Figure 5-d. Oviposition preference of F2 females of H. p./H. p. and S. f./S. f.

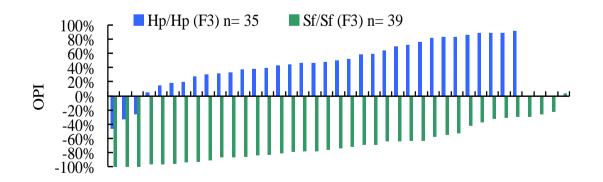


Figure 5-e. Oviposition preference of F3 females of H.p./H.p. and S.f./S.f. It shows that nearly all of the females preferred the same host plant as their parental generation; no matter which host plant the offsprings were fed.

(B) Larval growth performance

1. Pupa weight (Figure 6.)

The data on pupal weights was analyzed using T-test. Hp/Hp is significantly heavier than Hp/Sf (t=4.559, p<0.05); Hp/Hp is significantly heavier than Sf /Hp (t=3.443, p<0.05); Sf / Sf is significantly heavier than Sf /Hp (t=-3.227, p<0.05); there was no significant difference between Sf / Sf and Sf / Hp (t=-1.853, p=0.07). (Sample size: Sf/Sf=47, Sf/Hp=40, Hp/Sf=53, Hp/Hp=38)

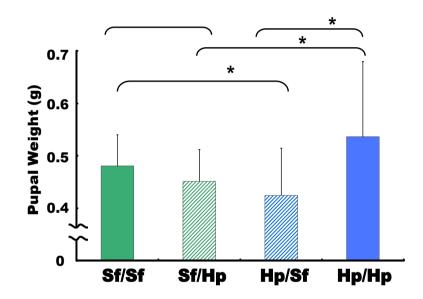


Figure 6. Analysis of variance on pupal weights of *J. iphita iphita*. (* p<0.05)

2. Larval survival ship (Table 1.)

The data on the larval survival rate was analyzed using chi-square test, the larval survival rate was significantly higher on "H.p. /H.p.", compared with "H.p. /S.f."; there was no significant difference between "S.f./S.f." and " S.f./H.p.".

Table 1. larval survival rate.

	survival rate	df	р	χ2
Hp/Hp	84.4%	44	< 0.05	0.123
Hp/Sf	57.8%			
Sf/Sf	80.0%	44	>0.05	0.010
Sf/Hp	71.1%			

(C) Cross test

1. Larvae growth performance of hybrid offspring (Table 2.)

Hp \bigcirc **X Sf** \bigcirc **:** The data on the larval survival rate was analyzed using chi-square test; the larval survival rate of "H.p. /H.p." was significantly higher than "hybrid /H.p."; whereas "S.f. /S.f." was significantly higher than "hybrid /S.f.".

Table 2-A. Larval survival rate of hybrid offspring (Hp \bigcirc X Sf \bigcirc).

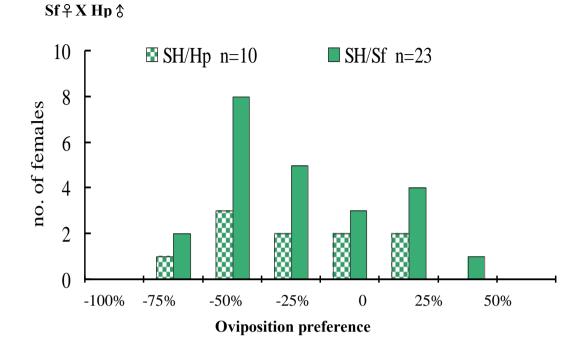
	survival rate	df	р	χ2
H. p. /H. p.	84.4%	44	< 0.001	0.259
Hybrid /H. p.	48.9%			
S. f. /S. f.	80.0%	44	< 0.001	0.284
Hybrid /S. f.	44.5%			

Sf Υ X Hp \Im : The data on the larval survival rate was analyzed using chi-square test, the larval survival rate of "H.p. /H.p." was significantly higher than "hybrid /H.p."; whereas "S.f. /S.f." was significantly higher than "hybrid /S.f.".

Table 2-B. Larval survival rate of hybrid offspring (Sf \bigcirc X Hp \bigcirc).

	survival rate	df	р	χ2
H. p. /H. p.	46.8%	119	< 0.001	0.233
Hybrid /H. p.	23.3%			
S. f. /S. f.	79.2%	119	< 0.001	0.296
Hybrid /S. f.	43.3%			

2. Oviposition preference of F1 hybrid (Figure 7)



Hp♀X Sf

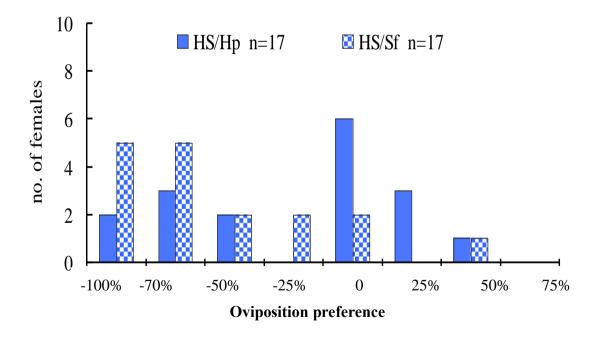


Figure 7. Oviposition preference of F1 hybrid. It shows that the oviposition preference is not apparent, so it means that the preference might not be decided by single sex.("HS/Hp" denotes "hybrid of Hp-preferring mother x Sf-preferring father fed with Hp", and so no.)

(D) Territoriality of male adults

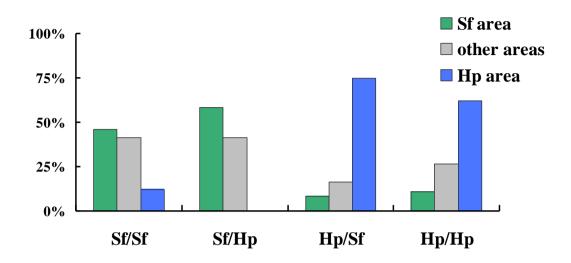


Figure 8. Territoriality behavior of "S.f./S.f.", "S.f./H.p.", "H.p./S.f.", "H.p./H.p." male adults. It shows that most of the males preferred the same host plant as their parental generation, no matter which host plant the offspring were fed with. (sample size: Sf/Sf = 41, Sf/Hp = 12, Hp/Sf = 12, Hp/Hp = 41)

D. Discussion

(A) Oviposition preference of female adults and larval growth performance

Genetic variation of host preference is largely responsible for interpopulation variation of diet.(Radtkey and Singer, 1995) My study showed that two types of host plant preferences seem to exist in the population of *J. iphita iphita* at the study site. It turned out that no matter which host plant the larvae were fed with, the female adults produced still maintained the oviposition preference of their parental generations. Therefore, it turned out that oviposition preference may be heritable.

Larval performance refers to a measurable trait or set of traits that adequately approximate, or correlate well with, offspring fitness on a given host plant. (Thompson, 1988; Nylin et al., 1996) Larval growth performance of offspring from H.p.-preferring and S.f.-preferring parental generation showed that pupal weight of "H.p./H.p." was significantly heavier than that of the other treatments. However, pupal weight of "S.f./H.p." was not as heavy. Based on such results, the preference of choosing *H. pogonocalyx* by some individuals of *J. iphita iphita* may have a genetic basis. These host-specific differences may involve adaptations in larval physiology, including the ability to utilize hosts with toxic secondary compounds (Zangerl & Berenbaum, 2003). Since pupal weight of "H.p./S.f." was significantly lighter than the others, and the larval survival rate also significantly lower on "H.p. /S.f." compared with "H.p./H.p.". Suggesting that host switching to *H. pogonocalyx* may have some disadvantages to development on the native host plant.

Oviposition preference toward a new host plant as demonstrated in the present study, regardless larval exhibiting better growing performance on the new host plant or losing their fitness to the native host plant, oviposition preference toward a new host plant demonstrated in this study could be the mechanism of initial divergence for insect populations. Moreover, the behavior of ovipositing females in relation to the fitness of their offspring has a number of important ecological and evolutionary implications. (Forister, 2004)

(B) The association between territoriality of male adults and oviposition preference of female adults

According to the results of cross test, host plant preference might be controlled by both male and female adults. The result of territoriality of male adults showed that, the male adults preferred to choose the area growing with the host plant that their parental generation preferred as their territories. Butterfly territories may occur along flyways (Baker, 1972, Bitzer & Shaw, 1980), oviposition sites frequented by gravid females (Baker1972), and female emergence sites (Dennis, 1982), etc. For the phytophagous insects that mate on or near host plants, patterns of host use may directly influence mate choice and the timing of mating (Diehl & Bush, 1989; Feder, 1998).

According to the results of territoriality of male adults and oviposition preference of female adults, it appeared that both sexes behaved similar preference, and corresponded with their parental generations. Therefore, it suggested that this phenomenon may not only increase the proportion for individuals with same preference to mate by enhancing the opportunity for encounter and decreasing the proportion for individuals with different preference to mate, but also reduce the number of preference-hybrid J. iphita iphita individuals in the population. Moreover, the initial change in host preference may facilitate a host switch and provide a partial behavioral barrier to gene flow, allowing for the build-up of further host-specific differences (Dethier, 1952; Maynard, 1966; Diehl and Bush, 1989; Kawecki, 1996; Fry, 2003). These differences in preference were correlated with differences with respect to the butterfly movements to and from patches of the two host species. Females were likely to leave areas without preferred hosts and stay where preferred hosts were present. This association between preference and movement increases the correlation between oviposition preference and host use, and increases the likelihood of host race formation (Thomas and Singer, 1987).

(C) The growth performance of hybrid F1

The cross test showed that, the survival rate of F1 hybrid was significant lower than the the colony from original host offsprings no matter they were fed on the native host plant or the new host plant. It appeared that there may be some disadvantages on growth performance among the offspring of different-preference hybrid individuals possibly by decreasing their fitness to both host plants. According to these experiments, the host plant preference of both male and female will reduce the opportunity for individuals with different host plant preference to reproduce. And even if the interbreeding does occur, the survival rate of these offsprings was also low, no matter they were grown on the native or the new host plant.

Claridge (1997) defined host races as populations that show no clear-cut diagnostic differences in morphology, but do show some differences in survival and development on a particular host. The present study showed that a new host race of *J. iphita iphita* may have been evolved with the adaption to *H. pogonocalyx* in the study site. Host races represent the hypothesized incipient stage of sympatric speciation (Berlocher and Feder, 2002). Furthermore, there are reasons supporting that ecological differences will evolve much more rapidly in sympatry, as strong selection driven by competition between close relatives can cause rapid ecological divergence (Jiggins, 2006). Insect biotypes feeding on different species of host plants are particularly well documented and also represent the category most strongly associated with controversial theories of sympatric speciation (Bush, 1969; Diehl and Bush 1984; Via, 2001). The present study offered an example to suggest that the anthropogenic expansion of a plant species in distribution might cause the initial differentiation of another species.

E. Conclusions

1. This study suggested that the restoration practices of *H. pogonocalyx* may have brought about a sympatric condition of this plant with *S. formosanus*, a host plant of *J. iphita iphita*, and this sympatry may have caused the population of *J. iphita iphita* to explore this new host plant and developed new adaptations associated with this novel host usage. This may have created a possibility of a tendency toward sympatric speciation via host shifting. It is worthwhile to make a persisting study on this subject in the future.

2. These results demonstrate the possible effects on *J. iphita iphita* by restoration of *H. pogonocalyx*, including changes on their host plant preference and larval growth performance. This study may serve as an example to show that restoration practice of a species may create ecological and evolutional influences upon another species. The results of this study may be used as a caution or reference when establishing restoration plan for the other species in the further.

F. References

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G. Acknowledgements

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Dr. Yi-Fang Tsay

Taipei Municipal Chien Kuo High School, Taipei, Taiwan

Biology Teacher: Tsui-Hua Liu

All other seniors and friends who had generously helped me in any aspects.

評語

作者長期觀察黑擬蛺蝶之生態,並探討寄主之間之轉換是極有創新之想法且 嘗試。

作者之產卵實驗有重複且重複數 10 個以上,可見注意到統計是可喜之處。若 能用 cage 實驗進行 preference 觀測則更多,此外建議 cage 的 size 會影響蝶類的產 卵行為,宜考慮。

寄主植物的轉移及 adaptation,可從 entyme 方面(代謝)去考慮。可使本作品 更完美。