

Reproductive Isolation between Japanese and Myanmar Populations of *Cotesia vestalis* (= *plutellae*) (Hymenoptera: Braconidae), a Larval Parasitoid of *Plutella xylostella* (Lepidoptera: Plutellidae)

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**Reproductive Isolation between Japanese and Myanmar Populations of
Cotesia vestalis (= *plutellae*) (Hymenoptera: Braconidae),
a Larval Parasitoid of *Plutella xylostella*
(Lepidoptera: Plutellidae)**

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Cotesia vestalis (Hymenoptera: Braconidae) has been widely used in many parts of the world as a major biocontrol agent of the diamondback moth, *Plutella xylostella*. The rate of parasitism and the rate of control exerted on the pests are highly variable geographically as well as not all introduction and augmentations were successful. Populations from different geographic regions often display various levels of reproductive incompatibility because they have been geographically isolated, experienced different selection pressures and/or adapted to various local environments. Experiment were conducted to compare reproductive compatibility between two geographic populations of *C. vestalis* one from Fukuoka, Japan (Temperate population) and the other from Mandalay, Myanmar (Tropical population). Results indicated that there was partial incompatibility between the two populations.

INTRODUCTION

Populations from different geographic regions often display various levels of reproductive incompatibility and exhibit different biological traits and genetic variability because they have been geographically isolated, experienced different selection pressures and/or adapted to various local environments (Diehl and Bush, 1984; Hopper *et al.*, 1993). *Cotesia vestalis* Haliday (= *C. plutellae*) (Hymenoptera: Braconidae) is a solitary endo-larval parasitoid of diamondback moth (DBM), *Plutella xylostella* (Talekar and Yang, 1993; Noda *et al.*, 1996; Kawaguchi and Tanaka, 1999), a serious pest of cruciferous crops worldwide (Abro *et al.*, 1992; Talekar and Shelton, 1993; Reddy *et al.*, 2004; Shelton, 2004). This parasitoid is distributed worldwide (Lim, 1986; Waterhouse and Norris, 1987; Talekar and Shelton, 1993; Talekar and Yang, 1993) and has been used in biological control programs of DBM in several countries because of its resistance against insecticides (Waterhouse and Norris, 1987; Fitton and Walker, 1992). This parasitoid has been widely used as a biological control agent for DBM and it is one of the most important agents of diamondback moth control in Southeast Asia (Lim, 1992; Talekar, 2004).

Although *C. vestalis* distributed world wide, it is currently reintroduced in already colonized areas, because a number of attempts to introduce and reintroduce failed (Waterhouse and Norris, 1987; Waterhouse, 1992). Major factors of these failures may have been a lack of knowledge of the biology and ecology of the introduced popula-

tions, and reproductive incompatibilities between local and introduced (or among introduced) populations (Rincon *et al.*, 2006). Wang and Keller (2002) categorized *C. vestalis* a generalist parasitoid and there was highly variable in rates of parasitism of the population of *C. vestalis* and the level of control exerted on the pest geographically (Goudegnon *et al.*, 2004; Guilloux *et al.*, 2003; Kfir, 1997; Waladde *et al.*, 1999).

The possible reproductive isolation between populations of natural enemies has not received much attention from researchers in the context of classical biological control (Rincon *et al.*, 2006). The effect of releasing a non-native species might not have much of an influence on biological control if no interspecific mating occurs between the released and native population (Stouthamer *et al.*, 2000). The introduction of reproductively incompatible biological control agents may have severe negative effect on the outcome of biological control operations, even leading to the extinction of the local populations of natural enemies (Rincon *et al.*, 2006). Partial reproductive isolation can potentially reduce fertility due to post-mating incompatibilities and/or reduce progeny viability by hybrid depression (Turelli *et al.*, 2001).

Reproductive incompatibility in arrhenotokous Hymenoptera is measured using the production of females in inter-population crosses (Pinto *et al.*, 1991; Stouthamer *et al.*, 1996) because only females result from fertilized eggs, whereas males originate from unfertilized eggs. The lack of females in between-species crosses can have several causes: (1) no insemination takes place in the between-species crosses, (2) insemination takes place but males develop from fertilized eggs, (3) fertilized eggs die and the all-male offspring produced from unfertilized eggs. These various outcomes can have profound effects on biological control when one species is released in the native area of another (Stouthamer *et al.*, 2000).

Rinconon *et al.* (2006) studied the reproductive com-

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patibility between 5 populations of *C. vestalis* from (South Africa, Benin, Martinique, Reunion and Taiwan). They found that the five populations represent two geographically widespread reproductive groups that are partially incompatible with one another and concluded that *C. vestalis* is a single species composed of at least two partially incompatible population aggregates. Comparative studies between its geographic population would help to reveal intraspecific variation which, if exist, should be considered in the introduction of this parasitoid for the biological control. Here we examined the reproductive compatibility of two geographic populations of *C. vestalis*, one from Japan and the other from Myanmar.

MATERIALS AND METHODS

Cotesia vestalis culture

Two geographic populations of *C. vestalis* were used in this study: one originating from Hisayama, Fukuoka Prefecture, Japan in April 2007 and the other from TadarOo City, Mandalay Township, Myanmar in May 2006. Both parasitoid populations were collected from DBM larvae on farmers' cabbage field. Myanmar population was started with about 200–300 cocoons and Japanese population was started with about 100 cocoons and 100 parasitized *P. xylostella* larvae. The identification of *C. vestalis* both Japanese and Myanmar populations were taxonomically confirmed by Dr. Kaoru Maeto (Laboratory of Insect Science, Faculty of Agriculture, Kobe University, Japan). Parasitoids were maintained on *P. xylostella* larvae fed on artificial diet in laboratory. DBM larvae were obtained from a stock culture maintained at Kyushu University, Japan. The laboratory colony of DBM was originated from field collected (about 200–300) larvae and pupae from farmers' cabbage field in Hisayama, Fukuoka Prefecture, Japan at April 2004 and maintained on artificial diet (Htwe *et al.*, in preparation). Two populations of the parasitoid were reared in separate room at 25 °C and 16L: 8D.

Crossing experiments

To obtain virgin females and males from the two populations of *C. vestalis*, DBM larvae were exposed to adult wasps for 24hr for oviposition. The parasitized larvae were reared at 25 °C for parasitoid development and the parasitoid cocoons were singly placed in 1.5 ml centrifuge tube after pupation until adult emergence. We set up a total of 25 crosses for each combination. The crossing experiment consisted of homogamic control crosses (intra-population crosses) and heterogamic crosses (inter-population crosses). The two intra-population crosses and two inter-population crosses were conducted concurrently at 25 °C with a 16L: 8 D photoperiod. Newly emerged male and female wasps less than 6hr old were used in crossing experiments. One virgin female and two virgin males from the corresponding strains were enclosed in a glass tube (7.5 cm height × 1.5 cm diameter) for 24 hr providing with honey streak. The parasitoid couples were then each provided with 50 early third instar DBM larvae for 24 hr. Parasitized larvae were maintained

on artificial diet until the production of pupae and adults of *C. vestalis* or until caterpillar pupation. Parasitized larvae were monitored daily and newly developed cocoons were collected and held singly in 1.5ml centrifuge tube until adult emergence. The numbers of offspring and their sex were determined. Due to their haplodiploid sex determination system, a cross was considered incompatible in the absence of female in the progeny. Reproductive compatibility was calculated as the proportion of couples that produced at least one female, in each direction. The number and sex ratio of progeny from different combinations were compared to estimate the levels of reproductive compatibility between the two populations.

Statistical analysis: Data for total numbers of progeny were analyzed using one way analysis of variance (ANOVA) and means were separated by Tukey's HSD test. Sex ratios were transformed by arcsine square root and analyze by Bonferroni test. Data for compatibility rate between and within population crosses were analyzed by Fisher's Exact Probability test by using R 2. 8. 1 (R Development Core Team 2008). Statistical analyses were done using the statistical software package, Stat View (SAS Institute, 1998).

RESULTS

Reproductive compatibility between Japanese and Myanmar *C. vestalis* population was estimated from reciprocal crossing experiments. Table 1 showed the compatibility rate, number of female progeny, number of total progeny and sex ratio of progeny obtained for all crosses. Compatibility rates were higher in homogamic crosses (intra-population crosses) than in heterogamic crosses (inter-population crosses). The highest compatibility rate was observed in Myanmar ♀ × Myanmar ♂ (homogamic cross) (92%) which was not significantly low ($P=0.84$) and the compatibility rate in Japanese ♀ × Japanese ♂ (homogamic cross) was 80%. There was only 12% compatibility in both (Myanmar ♀ × Japanese ♂) and (Japanese ♀ × Myanmar ♂) heterogamic crosses. Sex ratio was significantly male biased for females mated with males of the different population (inter-populations) ($p<0.01$) than for female mated with males of the same population (intra-population) ($p<0.01$) (Table 1). For compatible couples, the sex ratio of the progeny was nearly (1:1) for both intra- and inter-population crosses except in (Myanmar ♀ × Japanese ♂) heterogamic cross.

Total number of progeny was higher in (Myanmar ♀ × Myanmar ♂) homogamic cross than (Japanese ♀ × Japanese ♂) homogamic cross (ANOVA, $F_{3,96}=2.77$, $P=0.046$), however, no significant differences were observed for number of total progeny between intra- and inter-populations crosses (Table 1). Although total number of progeny was not significantly difference between intra- and inter-populations cross, both inter-population crosses resulted in very few female than intra-population crosses (ANOVA, $F_{3,96}=15.26$, $P<0.01$).

Table 1. Reproductive compatibility between Japanese and Myanmar populations of *C. vestalis*

Cross ^a	Number of crosses (n1, n2) ^b	Compatibility rate ^c	Number of Total progeny ^d	Number of female Progeny ^e	sex ratio ($\frac{\text{♀}}{\text{♀}+\text{♂}}$) ^f (overall) ^g	sex ratio ($\frac{\text{♀}}{\text{♀}+\text{♂}}$) (compatible couples) ^g
MM ♀ × MM ♂	25, 23	0.92a	32.32 ± 2.39a	14.56 ± 1.93a	0.45 ± 0.04a	0.48 ± 0.04b
MM ♀ × JP ♂	25, 3	0.12b	25.52 ± 2.66ab	3.04 ± 1.87bc	0.11 ± 0.06b	0.81 ± 0.01a
JP ♀ × JP ♂	25, 20	0.80a	22.88 ± 2.39b	7.12 ± 1.30b	0.35 ± 0.05a	0.43 ± 0.05b
JP ♀ × MM ♂	25, 3	0.12b	26.32 ± 2.12ab	1.00 ± 0.71c	0.04 ± 0.01b	0.31 ± 0.14b

^a MM, Myanmar population and JP, Japanese population.^b n1 = total numbers of crosses, n2 = numbers of cross that produce both female and male progeny.^c Means followed by the same letter do not differ significantly from each other by Fisher's Exact Probability test, $P < 0.01$.^{d,e} Means followed by the same letter do not differ significantly from each other by Tukey's HSD test after one way ANOVA, $P < 0.05$.^{f,g} Means followed by the same letters within the same column do not differ significantly from each other by Bonferroni test $P < 0.01$.

DISCUSSION

The results of crossing experiment clearly showed that reproductive isolation exists between Japanese and Myanmar populations of *C. vestalis*. The results of the present work rely on the estimation of reproductive incompatibility based on sex ratio data of a haplodiploid species. Heterogamic crosses between Japanese and Myanmar population produced only a few female offspring. In haplodiploid insect species, incompatibility in reproduction between strains results in skewed, highly male-biased sex ratios and reduced progeny production (Diel and Bush, 1984; Pinto *et al.*, 1991). Reciprocals crosses between Japanese and Myanmar populations resulted highly male-biased sex ratio in our experiment.

Many taxa used in biological control may be composed of several population units reproductively isolated to various degrees. In our experiment although, compatibility rate was higher in homogamic crosses, but both heterogamic crosses (Japanese ♀ × Myanmar ♂ and Myanmar ♀ × Japanese ♂) had very low compatibility rate. The introduction of a population reproductively incompatible with the local population may cause a long term reduction of the levels of control of the pest and result in a depression of intended biological control (Mochiah *et al.*, 2002; Stouthamer *et al.*, 2000). It is therefore important for any biological control attempt to determine the reproductive compatibility between local and introduced populations or between different source populations of the natural enemy selected. This is also important for the establishment of laboratory cultures because mixing of different populations could result in a severe reduction of population growth in the laboratory (Rincon *et al.*, 2006).

Populations of parasitoids collected from different host species or geographical regions can differ in host specificity. Host specificity surveys showed that *C. vestalis* can occasionally parasitise other species in the field, and laboratory studies in quarantine in New Zealand showed it has the ability to develop in several families of Lepidoptera (Cameron *et al.*, 1998). In our study, the population of *P. xylostella* from Japan was used as hosts for both populations of *C. vestalis*. As Japanese popula-

tion was collected from Japan, it would have had longer association with the host population than Myanmar Population. However, in crossing experiment *C. vestalis* from Myanmar population performed better than Japanese population in terms of total progeny as well as sex ratio. Therefore, it seems reasonable to assume that Myanmar population had better host suitability to *P. xylostella* than Japanese population. Furthermore, the larger wasp size in Myanmar population than Japanese population (Htwe *et al.*, unpublished) could be resulted in higher progeny production in Myanmar population because lifetime reproductive success is positively correlated with body size (Jervis *et al.*, 2001, 2003).

Rincon *et al.* (2006) stated that although multiple introductions of the same species of different origins seemed to be the best recipe for the successful introducing of biological control agents with the broadest genetic base possible is recommended but it can actually be a roadmap to failure. By the result of our experiment we agree with Rincon *et al.* (2006) statement that several introductions failures in the case of *C. vestalis* (Cordero and Cave, 1992; Waterhouse and Norris, 1987; Waterhouse, 1992) might be attributed to reproductive incompatibility of the strains selected for introduction or of the introduced strain with an already present one.

In some cases, cross mating incompatibility has been used to support cases where minor morphological, life history or allozymic differences have not been convincing enough to argue for species recognition (Pinto *et al.*, 1991). In others, it comprises the primary or even the sole source of evidence for the species (Nagarkatti, 1975), which have been justified by the role played by reproductive isolation in speciation (Pinto *et al.*, 1991) and the need to formally recognize distinct populations for biological control purposes. Lower reproductive compatibility between Japanese and Myanmar population in this study and smaller body size of Japanese population than Myanmar population (Htwe *et al.*, unpublished) showed us further investigation were needed to speciation process. The infection statuses of *Wolbachia* (a causative agent of various reproductive changes in arthropods, induces cytoplasmic incompatibility), as well as the possible ecological differentiation between the Japanese and

Myanmar populations of *C. vestalis* were needed to better understand the underlying mechanisms of reproductive isolation between the two populations.

The occurrence of reproductive isolation between the two geographically isolated populations of *C. vestalis* may have important consequences for the use of these species in inundative biological control. In Japanese and Myanmar strains of *C. vestalis* releasing both strains together could lead to a lower level of biological control than releasing either of the strains alone. It is importance to understand reproductive isolation between strains of biological control agents before their introduction (Stouthamer *et al.*, 2000; Mochiah *et al.*, 2002).

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