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Effects of host stages and temperature on population parameters of *Oomyzus sokolowskii*, a larval-pupal parasitoid of *Plutella xylostella*

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Abstract. *Oomyzus sokolowskii* is a larval-pupal parasitoid of diamondback moth, *Plutella xylostella*. In a host stage preference test, the parasitoid parasitised all larval and pupal stages, but exhibited a strong preference for larvae over prepupae or pupae, and did not show a preference among the larval instars. At 25 °C, the developmental time, number and sex ratio of offspring per host pupa, and successful parasitism did not differ significantly among parasitoids reared from host larvae of different instars, indicating similar host suitability between larvae of different instars. Mean developmental times from egg to adult at 20, 22.5, 25, 30, 32.5, and 35 °C were 26.5, 21.0, 16.0, 12.7, 11.9 and 13.4 days, respectively. The favourable temperature range for development, survival, and reproduction of the parasitoid was 20–30 °C. However, wasps that developed and emerged at a favourable temperature could parasitise effectively at 32–35 °C for 24 hours. Life-fertility table studies at 20, 25, and 30 °C showed that each female wasp on average parasitised 3.1, 13.2, 6.8 larvae of diamondback moth and produced 20.5, 92.1, 50.4 offspring, respectively, during her lifetime. The highest intrinsic rate of natural increase (r_m) of 0.263 female/day was reached at 30 °C as a result of the short mean generation time at this temperature compared to that at 20 and 25 °C, suggesting that the parasitoid had the highest potential for population growth at relatively high temperatures.

Key words: host stage preference, host suitability, temperature effects

Introduction

Diamondback moth (DBM), *Plutella xylostella* (L.), is the most destructive pest on crucifer crops worldwide; the annual cost for managing this pest was estimated to be US $ 1 billion in 1992 (Talekar and Shelton, 1993). High reliance on insecticides in the last two decades has led to resistance of DBM to almost all types of insecticides, including the bacterial insecticide *Bacillus thuringiensis* Berliner, particularly in tropical and subtropical areas in the

world (Tabasknik et al., 1990; Talekar and Shelton, 1993). Therefore, it is increasingly important to develop biologically-based integrated pest management of DBM in such areas, where effective native natural enemies of DBM are lacking.

More than 40 hymenopterous parasitoids are known to be associated with DBM larvae (Talekar and Shelton, 1993). *Oomyzus sokolowskii* (Kurdj.) (junior synonym: *Tetrastichus sokolowskii*) is one of the major parasitoids of DBM in most Asian countries, including India (Chelliah and Srinivasan, 1986), Pakistan (Mushtaque, 1990), Japan (Noda et al., 1996), and China (Liu et al., 1997). The parasitoid has also been recorded in the USA (Ru and Workman, 1979), Brazil (Ferronatto and Becker, 1984), Leeward Island, Russia, Zambia (Waterhouse and Norris, 1987), Jamaica and some other Caribbean Islands (Alam, 1990), and South Africa (Kfir, 1998). It has been successfully introduced to several countries including Trinidad (Yaseen, 1978), Cape Verde Islands (Lima and van Harten, 1985) and Malaysia (Ooi, 1988).

O. sokolowskii is a gregarious larval-pupal parasitoid of DBM, and parasitises all the different stages of DBM larvae (Ooi, 1988). In Hangzhou, China, the parasitoid was found to be active from May to October, entered into a quiescent state in the pupal stage in October–November to overwinter, and did not emerge until April–May of the next year (Liu et al., 1997). Talekar and Hu (1996) reported that the parasitoid preferred to parasitise larvae of the 3rd and 4th instars and failed to parasitise pupae, and that its rate of parasitism was positively correlated with temperature over the range of 10 to 35 °C. They suggested that this parasitoid was suitable for the control of DBM in hot tropical lowlands. However, the high parasitism at high temperatures reported by Talekar and Hu (1996) was obtained under unusual experimental conditions, in which wasps reared from a favourable temperature of 25 °C were used to parasitise hosts at high temperatures and the parasitised hosts were returned to 25 °C for parasitoid development. To determine the potential of parasitism and population growth of *O. sokolowskii* at high temperatures, data on the effects of temperature on its survival, developmental time, and reproduction are necessary. The purpose of this study was to further investigate the host stage preference of *O. sokolowskii*, and to determine host stage suitability and the effects of temperature on population increase.

Materials and methods

Insects

DBM were originally collected from crucifer crop fields on the suburbs of Hangzhou, China in 1996. *O. sokolowskii* was obtained from parasitised

larvae and pupae of DBM from these collections. Laboratory cultures of DBM and *O. sokolowskii* were maintained in an insectary at 25–30 °C with a photoperiod of 14:10 (L:D) and 60–80% RH.

DBM were reared on potted common cabbage, *Brassica oleracea*. An easy and effective method was used to collect DBM eggs and to rear DBM larvae: a cabbage leaf was wrapped in a transparent plastic bag which was fastened around the petiole with a rubber band. The petiole was inserted in a small bottle (100 ml) containing water to maintain leaf freshness. The bottle was then put inside the DBM oviposition cage, and small holes were made in the plastic bag using an insect pin so that DBM adults would be attracted by both the visual and olfactory stimuli emitted from the cabbage leaf. Moths oviposited on the plastic bag, and eggs were collected daily. Before the eggs hatched, the plastic bag was placed over a potted cabbage or was cut into pieces and pinned onto the leaves for subsequent larval development.

O. sokolowskii were reared on larvae of DBM in a 500-ml bottle, and have been reared for 2–3 generations prior to the experiments. The opening of the bottle was covered with a fine nylon mesh. Five mated *O. sokolowskii* females were held in the bottle for 24 hours with twenty 2nd to 4th instar larva of DBM on a piece of cabbage leaf. Parasitised larvae were then transferred to a fresh bottle and reared on cabbage leaves. Prior to emergence of the parasitoids, parasitised host pupae were individually transferred to small vials (2 cm × 7 cm), and maintained until the adults emerged.

Experimental container

A cylindrical plastic box measuring 14.5 cm in height with 9 cm top diameter and 13 cm base diameter was used as an experimental container throughout the study. The top was covered with a fine mesh gauze to prevent the escape of host larvae and parasitoid adults. After a parasitoid was introduced into the box, a cabbage leaf carrying host larvae was fixed on the base. The box was placed onto a 500-ml glass bottle containing water, and the petiole of the cabbage leaf was plunged in water.

Host stage preference and suitability

Two-to-three-day-old, mated female wasps were used in this experiment. Five female wasps were provided with 24 hosts, consisting of four individuals of each of the four larval instars, prepupae and freshly formed pupae, in the experimental container for 24 hours, as preliminary observation had shown that one female usually parasitised on average 2–3 hosts per day at 25 °C. To allow the prepupae and pupae to distribute on the cabbage leaf, fourth instar DBM larvae were first placed on the leaf prior to the experiment until

enough prepupae and pupae were obtained (extra prepupae and pupae were removed), and then four individuals of each larval instar were placed on the leaf. Hosts were removed after 24 hours exposure, and reared separately in petri dishes (diameter 8 cm) until they pupated. Host pupae were then maintained individually in vials (2 cm × 7 cm) until the emergence of either DBM adults or parasitoid adults. There were 25 replicates, and the experiment was carried out in growth chambers at 25 °C with a photoperiod of 14:10 (L:D) and 60–80% RH.

The developmental time from egg to adult, and the number and sex of adult parasitoids that emerged per host pupa were checked twice daily. All dead hosts were dissected immediately to determine whether or not they were parasitised, and at the end of the experiment all the parasitised host pupae were dissected to count the number of immature parasitoids that failed to emerge. From these data, for each of the stages, the number of parasitised hosts, and the successful parasitism, which is defined as the proportion of parasitoid individuals developing successfully from egg to adult, were calculated. Data on percent parasitism of each of the stages were used to determine the host stage preference, and data on developmental time, number and sex ratio of offspring per host pupa, and successful parasitism, were used to compare the host suitability of the different host stages.

Temperature effects on development, parasitism and survivorship

Five 2nd to 3rd instar DBM larvae were transferred to a cabbage leaf, and the leaf was fixed inside an experimental container. A newly emerged female wasp and a male wasp which developed at 25 °C were mated in a vial (2 cm × 7 cm), and the female wasp was then introduced into the experimental containers placed respectively in growth chambers at each of 7 different temperatures (15, 20, 22.5, 25, 30, 32.5, 35 °C) with a photoperiod of 14:10 (L:D) and 60–80% RH. There were 20–30 replicates for each temperature treatment. After 24 hours exposure, the wasp was removed, and the host larvae in the experimental container were checked twice daily for development and survivorship. As in the above experiment, the data on number of host parasitised, developmental time, number and sex ratio of offspring per host pupa, and percent emergence of the parasitised hosts were recorded and calculated.

Temperature effects on adult longevity and reproduction

A newly emerged female wasp and a male wasp reared respectively at each of three constant temperatures (20, 25, 30 °C) were mated in a vial as above, and the female wasp was then provided daily with five 2nd to 3rd instar DBM lar-

vae on a fresh cabbage leaf in an experimental container, and kept in a growth chamber at the corresponding temperature, with a photoperiod of 14:10 (L:D) and 60–80% RH. Adults were supplied with 20% honey solution smeared on a cotton pad till the female died. Adult survival was checked twice daily. The DBM larvae were removed daily and reared individually on cabbage leaves in small plastic containers (3 cm $\times$ 4 cm) till they pupated and developed into DBM or parasitoid adults. All dead individuals were dissected immediately to determine parasitism. The number, sex and developmental time from egg to adults of each offspring produced daily per female were recorded. From these data, the life-fertility table parameters were calculated, including net reproductive rate (R_o), intrinsic rate of natural increase (r_m) and its variance, mean generation time (T), pre-ovipostional period and post-ovipositional period. There were 20 replicates for each temperature.

Data analysis

All proportional data were transformed by arcsin square root before analysis of variance, and were back-transformed to proportions for presentation. All data were tested against the ANOVA assumption: nonhomogeneity of variance and non-normality. Data which met the above assumptions were analysed using ANOVA (JMP, Version 3.1, SAS Institute 1995). Where significant differences were detected, means were compared using Tukey-Kramer HSD. Life-fertility table parameters were calculated using the Jacknife method described by Hulting et al. (1990), and the difference in these parameters between temperatures were also compared using ANOVA, except that the comparison of differences between r_m was tested using the Newman-Keul Sequential Test (see Hulting et al., 1990 for details).

Results

Host stage preference

O. sokolowskii parasitised all larval and pupal stages of DBM, but strongly preferred to oviposit into host larvae, seldom ovipositing into prepupae and pupae ($F = 55.1$, df = 5, 149; $P < 0.05$). A few prepupae and pupae were parasitised in only 8 and 2 replicates, respectively. There was no significant difference in the percent parasitism by *O. sokolowskii* between the larval instars of DBM (Table 1), indicating no preference for a particular larval instar of DBM.

Table 1. Parasitism of instars and pupal stages of *P. xylostella* by *O. sokolowskii* in choice test of host stage preference

Developmental stage	Parasitism (%) (Mean ± SD)[a] (N = 4)	Replicates with parasitised DBM (%) (N = 25)
1st instar	52.1 ± 4.94 a	100
2nd instar	45.3 ± 4.69 a	91.7
3rd instar	55.1 ± 4.69 a	92.0
4th instar	57.2 ± 4.18 a	96.0
Prepupae	9.0 ± 2.84 b	32.0
Pupae	2.0 ± 1.38 b	8.0

[a]Means followed by the same letter are not significantly different ($P > 0.05$, Tukey-Kramer HSD test).

Host stage suitability

Parasitoids reared from different larval instars did not exhibit significant differences in developmental time from egg to adult (Table 2, F = 1.88, df = 3, 140; $P > 0.05$), number of offspring per host pupa (F = 0.91, df = 3, 134; $P > 0.05$), sex ratio of offspring per host pupa (F = 1.58, df = 3, 134; $P > 0.05$), and successful parasitism (F = 2.13, df = 3, 134; $P > 0.05$). But individual variation in developmental time within a clutch of wasps was significantly lower in wasps reared from first instar than those reared from other instars (Table 2, F = 5.79, df = 3,138; $P < 0.05$). When data for all host instars were combined, the mean number of offspring per host pupa was 8.6 ± 3.6, of which about 14% were male.

Temperature effects on development, parasitism and survivorship

The developmental time of *O. sokolowskii* decreased significantly with an increase in temperature up to 32.5 °C and then increased at 35 °C (Table 3, F = 26.5, df = 6, 181; $P < 0.05$). Based on the relationship between developmental rate and temperature within the range of 20 to 32.5 °C, the estimated developmental threshold temperature and thermal requirements for *O. sokolowskii* were 10.7 °C and 240.0 day-degree, respectively.

The mean number of hosts parasitised per day by *O. sokolowskii* females was positively correlated with temperature within a range of 15 °C to 35 °C (Figure 1, F = 29.7, df = 6, 227; $P < 0.05$).

Although the parasitoid effectively parasitised hosts at high temperatures within 24 hours, the percent emergence decreased sharply above 32.5 °C (Table 3). The parasitoids failed to emerge at 15 °C. The mean number of parasitoids emerging per host pupa at 35 °C was significantly higher than that at other temperatures (Table 3, F = 4.43, df = 169; $P < 0.05$). There were no

Table 2. Developmental time from egg to adult, number of offspring per host pupa, sex ratio (% female) and successful parasitism of *O. sokolowskii* parasitising different instars of *P. xylostella*

Instar	Developmental time (days)			No. of offspring per host pupa			
	N	Mean ± SD[a]	Variation[b]	N	Mean ± SD	Sex ratio	SP[c]
1st	36	16.5 ± 0.25 a	0.72 ± 0.15 a	36	8.8 ± 0.53 a	85.0 ± 1.9 a	93.7 ± 1.6 a
2nd	21	17.1 ± 0.30 a	1.33 ± 0.25 ab	21	7.6 ± 0.50 a	87.0 ± 2.3 a	92.6 ± 2.2 a
3rd	45	17.0 ± 0.25 a	1.26 ± 0.17 ab	39	8.0 ± 0.48 a	85.7 ± 2.1 a	86.5 ± 2.9 a
4th	42	17.3 ± 0.28 a	1.76 ± 0.19 bc	39	9.5 ± 0.50 a	86.1 ± 1.8 a	88.5 ± 1.9a

[a]Means followed by the same letter are not significantly different ($P > 0.05$, Tukey-Kramer HSD test).
[b]Variation refers to the time between the first and last emergence within a clutch.
[c]SP refers to successful parasitism.

Table 3. Developmental time from egg to adult, number of offspring per host pupa, emergence and sex ratio of *O. sokolowskii* at different temperatures

Temp. (°C)	N	Developmental time (days) (Mean ± SD)[a]	N	No. of offspring per host pupa (Mean ± SD)	Emergence (%)	N	Sex Ratio (Mean ± SD)
20	20	26.5 ± 0.71 a	10	9.1 ± 0.43 a	66.7	10	84.9 ± 0.89 a
22.5	18	20.9 ± 0.09 b	15	9.3 ± 0.41 a	71.4	30	88.6 ± 1.16 a
25	53	15.6 ± 0.18 c	53	9.4 ± 0.24 a	82.4	55	85.9 ± 1.31 a
30	46	12.7 ± 0.15 d	46	8.5 ± 0.28 a	77.6	40	87.3 ± 1.11 a
32.5	14	11.0 ± 0.13 e	14	9.6 ± 0.53 a	39.4	14	85.7 ± 2.05 a
35	32	13.4 ± 0.15 f	32	11.2 ± 0.42 b	8.6	32	84.6 ± 1.15 a

[a]Means followed by the same letter are not significantly different ($P > 0.05$, Tukey-Kramer HSD test). No statistics are given for the 15 °C treatment because *O. sokolowskii* failed to develop and only 2 hosts were parasitised.

significant differences in sex ratio among the different temperatures (Table 3, F = 1.68, df = 6,180; $P > 0.05$).

Temperature effects on adult longevity and reproduction

Because *O. sokolowskii* appeared to be more suited to the temperature range of 20 to 30 °C, we only investigated the effects of three constant temperatures (20, 25, 30 °C) on the population parameters. Adult longevity was significantly reduced when temperatures increased from 20 to 30 °C (Table 4). Adults mated immediately after emergence and the number of offspring produced per day decreased with increasing adult age (Figure 2). The highest

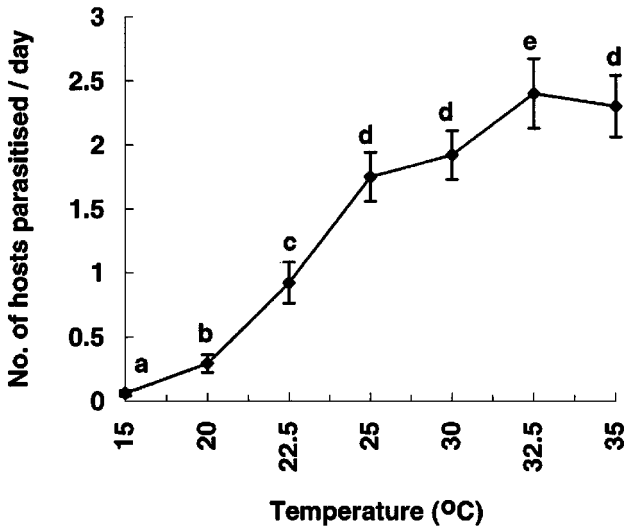

Figure 1. Mean number (± SD) of *P. xylostella* parasitised by *O. sokolowskii* per day at different temperatures. The different letters indicate significant difference ($P > 0.05$, Tukey-Kramer HSD test).

Table 4. Longevity, number of hosts parasitised per lifetime, and number of offspring produced per lifetime of *O. sokolowskii* females at 3 temperatures

Temp. (°C)	Longevity (days) (Mean ± SD)[a]	No. of hosts parasitised/ lifetime (Mean ± SD)	No. of offspring produced/ life time (Mean ± SD)
20 °C	28.3 ± 1.79 a	3.1 ± 0.43 a	20.5 ± 2.9 a
25 °C	12.4 ± 0.79 b	13.2 ± 0.85 b	92.1 ± 8.4 b
30 °C	6.6 ± 0.49 c	6.8 ± 0.42 c	50.4 ± 3.8 c

[a]Means followed by the same letter are not significantly different ($P > 0.05$, Tukey-Kramer HSD test).

number of larvae parasitised per female (19), and the highest mean number of offspring (162 females, 26 males) were observed at 25 °C. Female wasps reared at 25 °C parasitised the highest number of hosts and had the highest lifetime fecundity of the three temperatures (Table 4).

Temperature effects on population growth

Table 5 summarises the life-fertility table parameters of *O. sokolowskii* estimated by the Jacknife methods at the three temperatures (20, 25, 30 °C). The parasitoid had the highest net reproductive rate (R_o) at 25 °C. However, the highest r_m was reached at 30 °C, mainly because of the relatively shorter

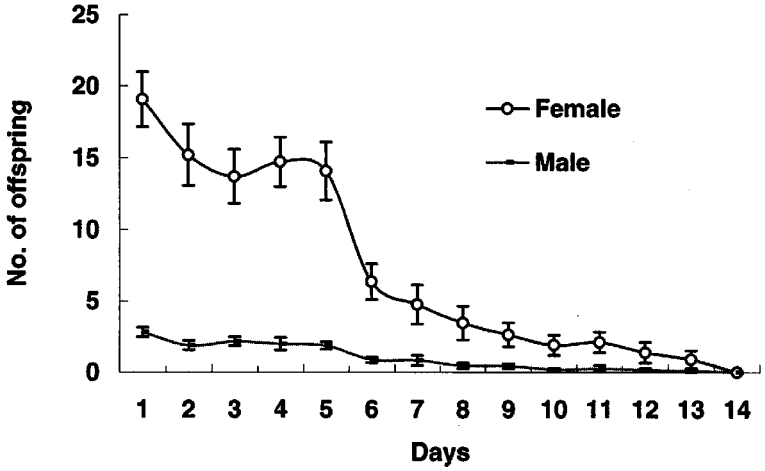

Figure 2. Mean number (± SD) of offspring produced daily per female *O. sokolowskii* at 25 °C.

Table 5. Life-fertility table parameters of *O. sokolowskii* parasitising *P. xylostella* at three temperatures[a]

Temp. (°C)	r_m[b]	T (days)	R_o	Pre-oviposition period (days)	Post-oviposition period (days)
20	0.082 ± 0.004 a	35.4	18.3 ± 2.6 a	5.0 ± 1.0 a	14.2 ± 1.7a
25	0.240 ± 0.004 b	18.3	80.4 ± 7.5 b	0.1 ± 0.1 b	4.3 ± 0.6 b
30	0.263 ± 0.004 c	14.5	44.9 ± 3.4 c	0.2 ± 0.1 b	1.8 ± 0.3 c

[a]Means followed by the same letter are not significantly different ($P > 0.05$, Tukey-Kramer HSD test). T = mean generation time; R_o = net reproduction rate.
[b]r_m = intrinsic rate of natural increase. Means followed by the same letter are not significantly different ($P > 0.05$, Newman-Kuel Sequential Test).

mean generation time at this temperature than at 25 °C. Female longevity, pre-oviposition period and post-oviposition period decreased with increasing temperature.

Discussion

Our study demonstrated that the larval-pupal parasitoid *O. sokolowskii* preferred to parasitise larvae of DBM, but could also attack prepupae and pupae of DBM. There were no significant differences in host stage preference and host suitability between larvae of different instars. These results differed from

the previous report of Talekar and Hu (1996), who reported that *O. sokolowskii* preferred to parasitise 3rd and 4th instar larvae and failed to parasitise pupae. Such differences might result from different experimental methods. Talekar and Hu (1996) used a much higher ratio of parasitoid to host (2.0), and the mean number of hosts parasitised per wasp per day was much lower (about 0.2) than our result. It is also possible that the difference resulted from use of a different strain of wasps.

O. sokolowskii showed a wider preference for host stages than the other two major larval parasitoids of DBM, *Cotesia plutellae* and *Diadegma semiclausum*. *D. semiclausum* has been reported to parasitise all four larval stages, whereas *C. plutellae* parasitised only the first three instars, and both wasps preferred 2nd and 3rd instars (Talekar and Yang, 1991).

Parasitism of DBM by *O. sokolowskii* over the temperature range of 10 to 35 °C was positively correlated with temperature. This result was consistent with the report of Talekar and Hu (1996), who suggested that *O. sokolowskii* was also suitable for the control of DBM at temperatures of 30 to 35 °C. However, our results further showed that, although wasps which developed and emerged at the favourable temperature of 25 °C could parasitise effectively at temperatures above 32.5 °C for a short period of 24 hours, the percent emergence of *O. sokolowskii* decreased dramatically at temperatures above 32.5 °C. Thus, a temperature range of 20 to 30 °C appeared to be most suitable for *O. sokolowskii* both for parasitization and survivorship. Liu et al. (1997) reported that in Hangzhou, China, *O. sokolowskii* was active only from May to October, and entered into a quiescent state in the pupal stage in October–November to overwinter. The mean daily temperature range is 20 to 30 °C during the seasons when *O. sokolowskii* is active in the fields in Hangzhou. Thus, this laboratory result was consistent with field observations.

In terms of rate of survival and intrinsic rate of natural increase, *O. sokolowskii* and *C. plutellae* had similar temperature requirements. Shi and Liu (1999) reported that a temperature range of 15 to 30 °C was suitable for *C. plutellae*, and that its rate of survival sharply decreased at temperatures above 30 °C. By contrast, *D. semiclausum* preferred a relatively low temperature range of 15 to 25 °C (Talekar and Yang, 1991).

The differences in host stage preference and temperature requirements between the three larval parasitoids of DBM may reduce to some extent the competition for hosts and result in niche segregation between the three species, and thus may potentially contribute to the overall biological control of DBM. *C. plutellae* and *D. semiclausum* have been successfully introduced from Europe into many subtropical and tropical countries to reduce DBM populations (Waterhouse and Norris, 1987; Talekar and Shelton, 1993). *D. semiclausum* has been established only in the cooler highlands in some Asian

countries, and its effective suppression of DBM in the highlands has been consistently high (Talekar and Shelton, 1993). However, in hot lowlands, where *C. plutellae* usually occurs, it appears unlikely that it could achieve the desired level of DBM control alone. Introduction of *O. sokolowskii* may improve the overall control of DBM because of its relatively wider host preference and the different temperature requirement between *D. semiclausum* and *O. sokolowskii.* In most tropical or subtropical areas, cruciferous crops are usually grown throughout the year, even in hot summers, and some crucifer species are grown in the highlands where temperatures are much lower. In the field, although some competition may occur when the three parasitoids coexist under suitable temperature conditions, the overall impact of a complex of the three parasitoids on DBM may be of great benefit, by providing control of DBM throughout the year. For example, in Jamaica the combination of *C. plutellae* and *O. sokolowskii* provides significant control of DBM (Alam, 1990). However, because of the similar temperature requirement between *O. sokolowskii* and *C. plutellae,* competition between these two parasitoids may be expected.

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