INTRODUCTION

In the production of greenhouse vegetables, aphids such as the green peach aphid Myzus persicae (Sulzer) and the cotton aphid Aphis gossypii Glover are very serious pests. They reproduce very rapidly and are too small for growers to detect in the early stages of colonization. Thus, growers are at risk of introducing natural enemies too late. In order to overcome this risk, introductions can be made by means of a banker plant system, or an open-rearing system (Hansen, 1983; van Lenteren and Woets, 1988; Yano, 2006). Prior to pest occurrence, banker plants serve as a reservoir of control agents in the greenhouse by providing them with an alternative, non-pest food source. For the control of aphids, the aphid parasitoid Aphidius colemani Viereck is one of the most powerful agents (van Steenis, 1995a). Ever since the banker plant system using A. colemani on bird cherry-oat aphid Rhopalosiphum padi (Linnaeus) was developed for cucumber protection against the cotton aphid ( Bennison and Corless, 1993), techniques using banker plants have become commonplace in protected crops in the UK (Walters and Hardwick, 2000).

In the early 21st century in Japan, the banker plant system was attempted in several regions producing greenhouse-raised eggplant and sweet peppers (Yano, 2006). In 2003, successful control using this technique was achieved in more than 50 commercial greenhouses in Kochi prefecture (Nagasaka and Oya, 2003), which is one of the most productive regions for greenhouse-raised eggplant and sweet pepper in Japan. However, in 2003–2005, aphid control in ca. 30% of greenhouses using the banker plant system failed, to the extent that blanket insecticide application was required (Nagasaka et al., 2010).

Secondary parasitism is very common in aphid-parasitoid communities. Numerous cases of high-
level secondary parasitism in agro-ecosystems have been reported (e.g., Horn, 1989; Höller et al., 1993; Mackauer and Völkl, 1993; van Veen et al., 2002). Although there are few reports on secondary parasitism in cultivated fields in Japan (e.g., Takada, 1976a; Sato et al., 1998; Senoo et al., 2002; Tatsumi et al., 2003), high levels of secondary parasitism have also been recognized. Because secondary parasitoids disrupt the short-term regulation of hosts by primary parasitoids, they are generally assumed to be detrimental to pest control (May and Hassell, 1981; Sullivan, 1987; Rosenheim, 1998).

Even in greenhouses, *A. colemani* populations in the banker plant system can be disrupted by secondary parasitoids. It was reported that the failure of the banker plant system to control aphids on cucumbers in an experimental greenhouse was likely caused by secondary parasitoids in addition to a high temperature (van Steenis, 1995b); however, the occurrence of secondary parasitoids in commercial greenhouses using the banker plant system and aphid-control results has not been demonstrated. In order to develop an effective banker plant system adapted for the production of greenhouse vegetables, we focused on secondary parasitism on banker plants in commercial greenhouses in Kochi prefecture, Japan. We evaluated the impact of secondary parasitism on the control of pest aphids by comparing greenhouses using the banker plant system that achieved success and those that did not.

**MATERIALS AND METHODS**

**Commercial greenhouses in the study area.** The areas of the greenhouses surveyed in Kochi prefecture ranged from 500 to 3,800 m², most being more than 1,000 m². Crop seedlings, such as eggplant, sweet pepper and paprika, are transplanted in September. The main harvesting season is February through May. During the growing season, the air temperatures in greenhouses are kept at more than 12°C for eggplant and 15°C for sweet pepper. These greenhouses are equipped with insect screens with 0.8×0.8 mm² or 1.0×1.0 mm² mesh over the side ventilators.

In ordinary years, the infestation of aphids starts in February or March. In more than 80% of greenhouses where the banker plant system was introduced, pest aphids were observed by growers during the main harvesting season each year from 2002 to 2005 (Nagasaka et al., 2010). In greenhouses where no aphid parasitoids were introduced, overall insecticide application against pest aphids was required twice on average during the main harvesting season in 2002 and 2003 (Nagasaka et al., 2010).

**Maintenance of banker plants.** In order to control aphids, the growers prepared a banker plant system in their respective greenhouses by the end of December. Specifically, barley or wheat was sown in November as banker plants in four to six patches per 1,000 m². Each banker plant patch had ca. 100 plants, growing in a planter or as part of a ridge. Two to three weeks later, a barley pot with ca. 1,000 bird cherry-oat aphids as alternative hosts of the control agent was placed in each banker plant unit. By the end of December, ca. 500 adult *A. colemani* as the control agent were released in each greenhouse. Every three or four months, the banker plants were reseeded. Alternative host aphids were reintroduced to banker plants when their numbers became low due to parasitism. The banker plants were maintained by the growers. Control agents were also purchased from commercial suppliers by growers, whereas alternative host aphids were provided by National Agricultural Research Center for Western Region.

**Evaluation of the banker plant system based on the growers’ observation of aphid occurrences.** The results of the banker plant system in each greenhouse were classified into three categories: complete success, partial success and failure. Because the purpose of introducing the banker plant system into the IPM program was to conserve the natural enemy of harmful thrips, *Thrips palmi* Karny, during the main harvesting season (Oka-bayashi, 2003), the specific goal of reducing the use of chemical insecticide against aphids to less than 1/10th of the area of each greenhouse throughout the main harvesting season was established (Nagasaka and Oya, 2003). Thus, the occurrences of pest aphids less than 1/10th of the area throughout the main harvesting season could be categorized as a success, either complete or partial. Specifically, when the occurrences of pest aphids were at a low density and restricted to small areas (less than 1/10th of the area) without insecticide treatment throughout the main harvesting season,
the banker plant system was recognized as a ‘complete success’. If growing populations of pest aphids were observed in less than 1/10th of the area and insecticides applied with knapsack-type sprayers were necessary to control them, the banker plant system was evaluated as a ‘partial success’. On the other hand, cases in which pest aphids occupied more than 1/10th of the area of greenhouses were categorized as a ‘failure’. In such greenhouses, overall insecticide treatment using a power sprayer was applied by the growers.

**Monthly census for the primary and secondary parasitoids on banker and crop plants.** In order to survey primary and secondary parasitoids on alternative host aphids on banker plants and those on pest aphids on crop plants every month during the growing seasons of 2002 through 2005, we visited 9 to 25 greenhouses, mainly in Aki city, and also Nangoku city, Kochi city and Tosa city in Kochi prefecture. Because our aim was to discover the regional tendencies of secondary parasitism, the greenhouses surveyed each month were not fixed. At the end of the growing season, the records of aphid occurrence and insecticide application were collected, and then the success or failure of aphid control by means of the banker plant system was determined for the respective greenhouses.

To examine the ratio of secondary parasitism in each greenhouse, 10 to 20 shoots with living aphids or mummified aphids were collected from banker plants. If there were colonies of pest aphids on crop plants, 5 to 20 leaves with aphid colonies were also collected. The pest aphids collected from crop plants were mostly green peach aphid and cotton aphid, although small numbers of glasshouse potato aphid *Aulacorthum solani* (Kaltenbach), which cannot be parasitized by *A. colemani*, were also included. The shoots of banker plants or leaves of crop plants from the respective greenhouses were placed in 1.5-l plastic containers without lids, and then sealed in bags made of fine cloth. They were kept in a chamber at 25°C until all the parasitoids had emerged (more than one month). In this condition, the shoots or leaves wilted gradually and accordingly, aphids could not live for more than one week. In this period, some primary parasitoids could grow inside the aphids, whereas some of the parasitized aphids or mummified aphids might be able to be parasitized by secondary parasitoids which emerged immediately after sampling; however, the appropriate timing for secondary parasitoids to oviposit is restricted to the short period before or after mummification of the host aphids (Sullivan, 1987; Takada and Tatsumi, 2002). Although only mummified aphids should be collected and placed individually in small capsules (e.g., Takada, 1976a; Senoo et al., 2002; van Veen et al., 2002) in order to evaluate secondary parasitism precisely at a particular moment, the method mentioned above is valid to compare the rates of secondary parasitism among years, seasons and the three types of greenhouse categorized by aphid-control results.

**Identification of primary and secondary parasitoids.** Primary and secondary parasitoids were identified with reference to Takada (1998, 2002) and Takada and Tatsumi (2002). In addition, a key to the three species of Charipinae (Cynipoidea: Figitidae) that are hyperparasitic on *Myzus persicae* and *Aphis gossypii* on cruciferous crops and potatoes was provided by Takada (unpublished document). The primary and secondary parasitoids in this study were solitary parasitoids.

**Data analysis.** For the comparison of secondary parasitism among months, trial years and the three types of greenhouse categorized by aphid-control results, the ratios of secondary parasitoids to total parasitoids on alternative host aphids on banker plants, those on pest aphids on crop plants, and those of each secondary parasitoid species were calculated for each sample with more than 15 specimens per greenhouse. The values were arcsine-transformed for the following analyses. The data from November 2002 to May 2005 were used, but those from February to May 2002 were not used for the analysis, because the banker plant system was introduced in January of that year.

**Seasonal changes in secondary parasitism on banker plants and crop plants.** In order to describe the general trends in years and seasons, overall variations in secondary parasitism among trial years and months were analyzed using the SAS GLM procedure (SAS® statistical software package, version 9.2). We included one factor (trial years), one covariate (number of months after November) and their interaction in the general linear model. Non-significant interaction was then eliminated from the model (Snedecor and Cochran, 1967). In addition, the correlation between the ratios of secondary parasitism on banker and crop
plants in the same greenhouse were tested using 25 available pairs of data.

**Difference in seasonal changes in secondary parasitism among the three types of greenhouse categorized by aphid-control results.** The seasonal changes in secondary parasitism were compared among the three types of greenhouse. During the three trial years, 76, 69 and 65 greenhouses were evaluated as complete success, partial success and failure in aphid control, respectively (Nagasaka et al., 2010). Analysis was performed with the SAS GLM procedure. One factor (three categories of greenhouses), one covariate (number of months after November) and their interaction were included in a general linear model. In addition, for greenhouses with failed aphid control, where a full insecticide spray was applied, the data consisted of the number of months before the insecticide spray. The model had one factor (banker/crop plants), one covariate (number of months before insecticide spray) and their interaction. Non-significant interaction was eliminated subsequently from the models.

**Influence of secondary parasitism on aphid-control results.** In order to detect the influence of secondary parasitism on aphid-control results, ordinal logistic regression analyses were performed using the SAS GENMOD procedure. The model includes one factor (trial year) and one covariate (arcsine-transformed ratio of secondary parasitoids) as explanatory variables, and three ranks of control results (complete success = 1, partial success = 2 and failure = 3) as the dependent variable. The model was separately tested for each of the four stages (November–December, January–February, March–April and May–June) because we could not include a saturated model for the existence of missing cells. In a few greenhouses where there were data for both months, the average ratios of secondary parasitism were used. For analyses in the later season, data from the same greenhouses as those appearing in the preceding stage were included to some degree.

**RESULTS**

**Secondary parasitoids appeared in the banker plant system**

Eight species of secondary parasitoids were recognized on the aphids on banker and crop plants (Table 1). Among them, four species were endophagous hyperparasitoids, which directly attack

### Table 1. Species composition (%) of parasitic Hymenoptera from the alternative host aphids (R. padi) on banker plants (barley or wheat) and pest aphids (M. persicae and A. gossypii) on crop plants (eggplant and sweet peppers) in each trial year

<table>
<thead>
<tr>
<th>Species</th>
<th>Alternative host aphids on banker plants [%]</th>
<th>Pest aphids on crop plants [%]</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2002</td>
<td>2003</td>
</tr>
<tr>
<td>Primary parasitoids</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Aphidius colemani</em></td>
<td>52.9</td>
<td>57.8</td>
</tr>
<tr>
<td><em>A. gifuensis</em></td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Other Aphidiinae</td>
<td>0.0</td>
<td>0.2</td>
</tr>
<tr>
<td><em>Aphelinus</em> spp.</td>
<td>0.5</td>
<td>0.1</td>
</tr>
<tr>
<td>Endophagus hyperparasitoids</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Phaenoglyphis villosa</em></td>
<td>2.6</td>
<td>6.1</td>
</tr>
<tr>
<td><em>Alloxysta</em> sp. nr victrix</td>
<td>11.9</td>
<td>9.4</td>
</tr>
<tr>
<td><em>Alloxysta</em> sp. nr brevis</td>
<td>1.4</td>
<td>0.9</td>
</tr>
<tr>
<td><em>Syrophagus</em> spp.</td>
<td>1.7</td>
<td>4.6</td>
</tr>
<tr>
<td>Ectophagus hyperparasitoids</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dendrocerus laticeps</em></td>
<td>6.4</td>
<td>18.9</td>
</tr>
<tr>
<td><em>D. carpenieri</em></td>
<td>0.5</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Asaphes suspensus</em></td>
<td>20.5</td>
<td>1.9</td>
</tr>
<tr>
<td><em>Pachyneuron aphidis</em></td>
<td>1.7</td>
<td>0.2</td>
</tr>
</tbody>
</table>

Total number of specimens 420 2,587 5,260 2,887 11,154 624 2,668 1,952 628 5,872

As other Aphidiinae, there were *Ephedrus nacheri* (5) on banker plants in 2003, *Diaeretiella rapae* (1) on crop plants in 2003, and *Lipolexis gracilis* (5) on crop plants in 2005. *Phaenoglyphis villosa*, *Alloxysta* sp. nr *victrix* and *Alloxysta* sp. nr *brevis* are identical to *Alloxysta* sp. a, *Caripis* sp. b and *Caripis* sp. c in Takada (1976b), respectively.
parasitoid larva in live and mummified aphids by ovipositing in them (Sullivan, 1987; Takada and Tatsumi, 2002). There were three species of Charipinae (Figitidae), including *Phaenoglyphis* and *Alloxysta*, and one species of Encyrtidae, *Syrphophagus*. Although there are species that have not been completely identified yet (Takada and Tatsumi, 2002), *Phaenoglyphis villosa* (Hartig) [= *Phaenoglyphis* sp. a in Takada and Tatsumi (2002); = *Alloxysta* sp. a in Takada (1976b)], *Alloxysta* sp. nr *victrix* [= *Alloxysta* sp. b in Takada and Tatsumi (2002); = *Charips* sp. b in Takada (1976b)], *Alloxysta* sp. nr *brevis* [= *Alloxysta* sp. c in Takada and Tatsumi (2002); = *Charips* sp. c in Takada (1976b)] and *Syrphophagus* sp. [= *Aphi-dencyrtus tachikawai* Hoffer in Takada (1976b)] were recognized in our samples (Takada, personal communication). The other four species were ectophasic hyperparasitoids, which attack larva or pupa of the primary parasitoid after it has killed the aphid and a mummy is formed (Sullivan, 1987). There were two species of Megaspilidae; *Dendrocerus laticeps* (Hedicke) and *D. carpenteri* (Curtis), and two species of Pteromalidae; *Asaphes suspensus* (Nees) and *Pachyneuron aphidis* (Bouché). All of these eight species are obligate secondary parasitoids (Takada and Tatsumi, 2002).

**Seasonal changes in secondary parasitism on banker plants**

The most prevalent primary parasitoid of *R. padi* on banker plants was *A. colemani* (Table 1). Although other primary parasitoids, such as *Ephedrus nacheri* Quilis and *Aphelinus* spp., were found, their abundance was less than 1% of that of *A. colemani*.

The ratios of secondary parasitoids to all parasitoids on banker plants varied significantly among months (result of the general linear model: $F_{1,140}=45.98$, $p<0.0001$), while the variation among trial years was not significant ($F_{2,140}=0.89$, $p=0.4123$). In the early season (November to December) in every trial year, secondary parasitism was low, less than 35% (Fig. 1). As the seasons progressed, secondary parasitism increased. The mean rate of secondary parasitoids exceeded 40% in March–April, and surpassed 70% by the late season.

![Figure 1](image_url)

**Fig. 1.** Monthly changes in the proportion of each parasitoid species on bird cherry-oat aphids on banker plants. $N=$ total number of specimens in each month. The variation of the ratio of secondary parasitism among months was significant (MS=9.96, $F_{1,140}=45.98$, $p<0.0001$), whereas the variation among trial years was not significant (MS=0.19, $F_{2,140}=0.89$, $p=0.4123$). There were also significant variations among months in the ratio of *Alloxysta* sp. nr *victrix* and *D. laticeps* (MS=0.97, $F_{1,140}=11.12$, $p=0.0011$; MS=5.45, $F_{1,140}=47.03$, $p<0.0001$, respectively).
The main species of secondary parasitoids were *Alloxysta* sp. *nr victrix*, *Syrphophagus* sp., and *D. laticeps* (Table 1), which occurred throughout the growing season (Fig. 1). *Alloxysta* sp. *nr victrix* and *D. laticeps* increased as the season progressed ($F_{1,140}=11.12, p=0.0011; F_{1,140}=47.03, p<0.0001$, respectively), while *Syrphophagus* sp. showed no seasonal tendency ($F_{1,143}=1.13, p=0.2889$). *A. suspensus* and *P. aphidis* were present only in the later season (Fig. 1). The occurrence of *P. villosa* varied among trial years (Table 1). *Alloxysta* sp. *nr brevis* and *D. carpenteri* were only present in small numbers.

**Seasonal changes in secondary parasitism on crop plants**

The most prevalent primary parasitoid of green peach aphid and cotton aphid on crop plants was also *A. colemani* (Table 1). Another primary parasitoid, *Aphidius gifuensis* Ashmead, also occurred on green peach aphid, at an abundance about 12% of that of *A. colemani*. *Diaeretiella rapae* (M’Intosh), *Lipolexis gracilis* Föster and *Aphelinus* spp. also occurred, but the abundance was less than 1% of that of *A. colemani*.

The three main species of secondary parasitoids on crop plants were *Alloxysta* sp. *nr victrix*, *Syrphophagus* sp. and *D. laticeps*, as well as those on banker plants (Table 1). The seasonal change in secondary parasitism on crop plants was also similar to that on banker plants (Fig. 2). The total ratio of secondary parasitism increased during each growing season ($F_{1,53}=4.83, p=0.0323$). In addition, the ratios of *Alloxysta* sp. *nr victrix* and *D. laticeps* increased as the season progressed ($F_{1,53}=7.62, p=0.0079; F_{1,53}=9.02, p=0.0041$, respectively); however, that of *Syrphophagus* sp. did not increase ($F_{1,53}=2.32, p=0.1340$). *A. suspensus* and *P. aphidis* occurred in the later season (Fig. 2).

The ratios of secondary parasitism on crop plants were significantly correlated to those on banker plants in the respective greenhouses (Fig. 3; $r=0.6372, p=0.0004$). The ratios of *Alloxysta* sp. *nr victrix*, *Syrphophagus* sp. and *D. laticeps* on crop plants were also significantly correlated to those on banker plants, respectively ($p<0.05$).

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**Fig. 2.** Monthly changes in the proportion of each parasitoid species on pest aphids on crop plants. $N$=total number of specimens in each month. The variation of the ratio of secondary parasitism among months was significant (MS\(=1.38, F_{1,53}=4.83, p=0.0323$), whereas the variation among trial years was not significant (MS\(=0.23, F_{2,53}=0.79, p=0.4580$). There were also significant variations among months in the ratio of *Alloxysta* sp. *nr victrix* and *D. laticeps* (MS\(=0.78, F_{1,53}=7.62, p=0.0079; MS=0.58, F_{1,53}=9.02, p=0.0041$, respectively).
Difference in seasonal changes in secondary parasitism among the three types of greenhouse categorized by aphid-control results

Among the three types of greenhouse categorized by aphid-control results, there was a significant difference in the manner of increase in secondary parasitism on banker plants (interaction of month and category: $F_{2,102}/H_{11005}^{2,102}=3.42$, $p=0.0364$). In greenhouses with failed aphid control, secondary parasitism increased more sharply than in those with complete success in aphid control (Fig. 4A). In March, the mean rate of secondary parasitism surpassed 70% in those greenhouses. On the other hand, in greenhouses with complete success, it was around 50%.

In greenhouses with failed aphid control, a blanket insecticide spray was applied, the grand mean ratios of secondary parasitism increased linearly with the seasonal progress ($F_{1,45}=22.23$, $p<0.0001$) when the data consisted of the number of months before the insecticide spray. The mean rates reached more than 60% one month before blanket insecticide treatment (Fig. 5).

On crop plants, the secondary parasitism varied among the three types of greenhouse categorized by aphid-control results ($F_{2,34}=4.55$, $p=0.0177$). In greenhouses with failed aphid control, the mean ratio of secondary parasitism, except in April, was higher than in greenhouses with successful control using the banker plant system (Fig. 4B).

Influence of secondary parasitism on the aphid-control results

In the March–April stage, secondary parasitism on banker plants has a significant influence on the results of aphid control during the main harvesting season (Table 2), although those in former seasons were not significantly related. This suggests that higher ratios of secondary parasitism on banker plants in March and April tend to cause a failure of aphid control. On crop plants, higher ratios of secondary parasitism in any season tend to induce the failure of aphid control (Table 2).

DISCUSSION

The results presented in this study clearly
showed the negative impact of secondary parasitism on aphid control by means of a banker plant system using A. colemani. Higher ratios of secondary parasitism on banker plants in March and April, when outbreaks of pest aphids occur in ordinary years, had a significant influence on failure of aphid control (Table 2). Although such a negative influence has been suggested theoretically, and has also been supported through some trials of the banker plant system in small greenhouses (e.g., May and Hassell, 1981; Sullivan, 1987; van Steenis, 1995b), no study has previously demonstrated the relationship between secondary parasitism and aphid-control results in commercial greenhouses using the banker plant system.

The secondary parasitoids, as well as primary parasitoids, were assumed to move between banker plants and crop plants in the banker plant system, because similarities were shown in the seasonal occurrences of main secondary parasitoid species in both the banker plants and crop plants (Table 1; Figs. 1 and 2), in addition to the positive correlations of both total and respective ratios of secondary parasitism (Fig. 3). Thus, higher ratios of secondary parasitism on banker plants affected aphid-control results through higher secondary parasitism on crop plants. This means that the observation of secondary parasitoids on banker plants in a greenhouse may predict the decreased effectiveness of the banker plant system, and growers in Kochi can discriminate between the adults of beneficial primary parasitoids and harmful secondary parasitoids (Nagasaka et al., 2010). At one or two months after secondary parasitism exceeded 50%, the growers recognized that the banker plant system could not depress pest aphids on crop plants (Fig. 5); therefore, when there are more secondary parasitoids than primary parasitoids on banker plants, growers should adopt additional control methods, such as partial chemical insecticide spraying and the release of aphid predators.

Among the predatory control agents commercially available in Japan, such as aphid midge, ladybird beetle and lacewing, the aphid midge Aphidoletes aphidimyza (Rondani) might be best able to compensate for the negative impact of secondary parasitism on A. colemani. The effectiveness of A. aphidimyza in banker plant systems has been confirmed in commercial greenhouses in Europe (e.g., Hansen, 1983; Bennison and Corless, 1993). Be-

![Fig. 5. Changes in secondary parasitism on banker and crop plants before full insecticide spray in greenhouses with failed aphid control using the banker plant system. Bars indicate standard errors of the means. The variation among the number of months until the insecticide spray was significant (MS=4.09, F_{1,45}=22.23, p<0.0001), whereas there was no significant difference between banker plants and crop plants (MS=0.03, F_{1,45}=0.16, p=0.6871).](head3.jpg)

Table 2. Ordinal logistic regression analysis of the two factors, trial year and secondary parasitism in each season, of the aphid-control results using the banker plant system (complete success, partial success and failure).
cause *A. aphidimyza* diapaus in winter (Hansen, 1983), it cannot be used as the primary control agent during the winter season in Japan; however, *A. aphidimyza* could colonize on banker plants in March (Nagasaka et al., 2010), when the average rate of secondary parasitism on *A. colemani* exceeded 50% on banker plants in greenhouses with failed aphid control (Fig. 4A). Therefore, it may be practical for *A. aphidimyza* to be introduced into greenhouses where more than 50% secondary parasitism is observed before March. In order to stabilize the control efficiency of this banker plant system in the Japanese greenhouse environment, the technique of using *A. colemani* with *A. aphidimyza* should be developed in the near future. In addition, to develop the technique, the interaction among the predator *A. aphidimyza*, the parasitoid *A. colemani* and secondary parasitoids in the banker plant system should be studied.

Greenhouses that suffer high levels of secondary parasitism on crop plants in late autumn tend to have failed aphid control during the main harvesting season (Fig. 4B; Table 2). Because secondary parasitoids move between banker pants and crop plants as mentioned above, those on crop plants in the early season can be the source of the population that colonize banker plants during the winter. Therefore, it is proposed that the timing of placing banker plants in greenhouses should be delayed until pest aphids have been controlled by another method in the case of outbreaks of pest aphids on crop plants in autumn. In cases of late-autumn outbreaks (November and December), banker plants should be abandoned and then reestablished in time for the main harvesting season.

To minimize the impact of secondary parasitism on banker plant systems, the life cycles of the respective species should be clarified. Such information enables us to predict the risk of a negative impact by each species, and thus is crucial for determining the proper timing to establish or reestablish the banker plant system. In Japan, however, there are only a few reports concerning secondary parasitoid life cycles (e.g., Takada, 1976a, b). In the culture system in Kochi (N33°E133°), secondary parasitoids immigrated into the greenhouses from the open field through the ventilators, even in winter, along with pest aphids, such as *M. perciae* and *A. gossypii*, and primary parasitoids, such as *A. gifuensis* (Fig. 2). Once the secondary parasitoids had invaded the greenhouses, the banker plant system allowed them to reproduce there (Fig. 1). Among the secondary parasitoid species, *Alloxysta* sp. nr *victrix* and *D. laticeps* increased, even in the winter, and *Syrphophagus* sp. showed a continuous presence, suggesting that part of the population of each of the three species did not diapause in the winter in heated greenhouses. On the other hand, *A. suspensus* and *P. aphidis* started to appear only in April, suggesting that they diapaused during the winter. The occurrences of *Alloxysta* sp. nr *victrix* and *P. aphidis* are in accordance with Takada's (1976b) open-field observation in Kyoto (N35°E135°). The data presented here represent the first research on secondary parasitoids in greenhouses throughout the winter season in Japan.

The aphid-primary parasitoid-secondary parasitoid system involves complicated relationships (e.g., Takada, 1976a; van den Bosch et al., 1982; Müller et al., 1999). The invasion of pest aphids and secondary parasitoids in greenhouses using the banker plant system, and the population dynamics of aphids, primary parasitoids and secondary parasitoids on both crop and banker plants are assumed to affect each other. In addition, this system includes multiple secondary parasitoid species, which have different life cycles and behaviors (Sullivan, 1987; Takada and Tatsumi, 2002). In order to develop a practical banker plant system adapted for the Japanese culture system, various aspects of these interactions still require research. The present study provides basic data about the phenomenon in commercial greenhouses in Japan.

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