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BIOLOGICAL CONTROL IN DISTURBED AGRICULTURAL SYSTEMS AND THE RAPID RECOVERY OF PARASITOID POPULATIONS

KIMBERLY S. RAUWALD AND ANTHONY R. IVES[1]

Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706 USA

Abstract. In annual or periodically harvested crops, biological control of pests is aided if natural enemy populations rapidly recover within fields following disturbances. Here, we show that the life history of parasitoids may facilitate their recovery within fields. Because many parasitoids live within their still-living hosts, recovery of parasitoid populations can occur simultaneously with the recovery of their host populations. In alfalfa, periodic harvesting causes crashes in the populations of pea aphids, *Acyrthosiphon pisum*, and their parasitoid *Aphidius ervi.* Using laboratory experiments, we showed that the survival of parasitized aphids (before parasitoid-caused death) is little different from the survival of unparasitized aphids. In field experiments, by erecting exclosure cages immediately following harvesting we showed that both aphid and *A. ervi* populations can recover in the absence of immigration. Furthermore, successful *A. ervi* recovery suppresses aphid population growth over the ensuing harvesting cycle in the absence of other natural enemies. Therefore, the persistence of parasitoids within their hosts may be a key factor leading to successful biological control by specialist parasitoids in disturbed systems.

Key words: Acyrthosiphon pisum; *alfalfa crop system;* Aphidius ervi; *biological control of pests in disturbed crops; disturbance; generalist predators; parasitoid, recovery after harvest; pest control in agricultural systems; specialist natural enemies.*

INTRODUCTION

Biological control is more frequently successful in stable systems, such as orchards and forests, than in annual crops, presumably because harvesting is a disturbance that disrupts biological control (DeBach 1964, Watt 1965, Southwood 1977, Ehler and Miller 1978, Waage and Greathead 1988, Smith et al. 1997). In the face of frequent disturbances, generalist natural enemies are often thought to provide better biological control than specialist natural enemies (Doutt and DeBach 1964, Miller 1977, Ehler and Miller 1978, Miller and Ehler 1978, Riechert and Lockley 1984, Riechert and Bishop 1990, Settle et al. 1996). As argued by Doutt and Debach (1964:132), ''if a host population is periodically depressed by other factors, a specific natural enemy will suffer most, whereas a more general feeder will maintain itself on other hosts during adverse periods'' (see also DeBach and Rosen 1991). Because the dynamics of specialist natural enemies will be coupled to those of the pest, the pest population must recover following a disturbance to a sufficient density before the population of any specialist natural enemy can grow (Rochat 1997). Thus, the specialist natural enemies introduced for classical biological control may be ill suited for controlling pests in frequently disturbed agricultural systems.

For successful biological control in frequently disturbed systems, the speed of recovery of the natural-enemy population relative to the recovery of the pest is critically important (Doutt and DeBach 1964, Force 1972, Wallner 1987). High dispersal ability of the natural enemy may reduce the time lag in recovery between natural-enemy and pest populations, and thereby lead to more continuous biological control (Force 1972, Ives and Settle 1997, Wissinger 1997). In addition to immigration, natural-enemy populations may also recover from the individuals that survive the disturbances within fields (Nyrop et al. 1998). Although survival during disturbances is generally thought to be a characteristic of generalist rather than specialist natural enemies, specialist parasitoids have a mode of survival unavailable to generalist natural enemies. Because parasitoids spend much of their life cycle within living hosts, if some hosts survive disturbances, then so too will some parasitoids. Thus, even though a disturbance could cause a huge decline in pest densities within fields, the relative number of parasitoids to pests (i.e., the percentage parasitism) may be little changed, thereby reducing the time lag in recovery of the parasitoid population relative to its host.

Here, we investigate the recovery dynamics of the pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae) and its parasitoid *Aphidius ervi* Haliday (Hymenoptera: Braconidae) following disturbances to determine the importance of survival within fields for continued biological control. The pea aphid is a common pest of alfalfa (lucerne) in Wisconsin, USA, and *A. ervi* is its dominant primary parasitoid, attacking mainly the juvenile stages of aphids. Alfalfa is har-

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[1] Author to whom correspondence should be addressed. E-mail: arives@facstaff.wisc.edu

vested 2–3 times per year, and harvesting causes 2–3 orders of magnitude crashes in pea aphid abundance within a field. The recovery of pea aphid populations can occur either by alates (winged adults) immigrating into a field, or by a few aphids surviving in the field during harvesting. Similarly, *A. ervi* populations can recover either through immigration of adults, or survival within fields either as larvae within aphids or as pupae. Adult parasitoids do not remain within fields, but appear to emigrate or die during harvesting.

To investigate the recovery of pea aphid and *A. ervi* populations following alfalfa harvesting, we performed four types of experiment. First, we monitored aphid and parasitoid abundances over the course of the summer in two alfalfa fields in order to quantify the magnitude of aphid and parasitoid population crashes at harvesting. Second, we performed laboratory experiments to compare the survival of parasitized and unparasitized aphids. Survival of parasitoids within fields requires that parasitized aphids survive through to pupal formation of the parasitoid. The experiments were designed to determine whether the survival of parasitized aphids relative to unparasitized aphids is sufficiently high to maintain levels of percentage parasitism during harvesting. Third, we performed field experiments using large exclosure cages to eliminate immigration of both aphids and parasitoids. By eliminating immigration, these experiments give a direct measure of the importance of survival within fields for the recovery of both aphid and parasitoid populations. Furthermore, these experiments reveal the impact of parasitism on control of the aphid population. Finally, we conducted experiments on the ability of parasitized alate aphids to fly. In addition to recolonizing fields by immigrating adults, parasitoids could potentially recolonize via the immigration of parasitized aphids. This type of ''hitchhiking'' is a potentially novel mode of population recovery of parasitoids that generalist natural enemies do not have.

Our work focuses on the recovery of parasitoid populations following disturbances via means other than immigration of adults. Immigration of adults certainly occurs. Nonetheless, we focus on other modes of recovery because the current view is that parasitoids, being specialists, have disadvantages as biological control agents in disturbed systems relative to generalist natural enemies. If in fact the recovery of *A. ervi* populations can occur from juvenile parasitoids within hosts, then this represents an unappreciated advantage of specialist parasitoids in disturbed systems not shared by generalist natural enemies.

Methods

Study organisms

The pea aphid, *Acyrthosiphon pisum*, is originally an Old World species that was introduced into North America in the 19th century. It feeds on peas, beans, alfalfa, and other agricultural crops throughout the United States, in some places reaching densities high enough to be a significant pest. During the summer, reproduction is asexual (Blackman and Eastop 1984). The parthenogenic females produce as many as 6 nymphs/d, and nymphs go through four subadult instars in approximately 145 degree-days, which is $\sim$ 5 d at normal summer temperatures (Hutchinson and Hogg 1984, 1985, Thiboldeaux 1986).

Aphidius ervi was introduced into the United States as a biological control agent for pea aphids in the 1960s (Gonzalez et al. 1978, Mackauer and Kambhampati 1986). It has now spread over much of North America (Thiboldeaux et al. 1987) and is regarded as a successful biological control agent in many areas. In Wisconsin alfalfa fields, percentage parasitism ranges from near zero to $>$95%, depending on the year and season (Hutchinson and Hogg 1985; A. R. Ives, *unpublished data*). A wasp parasitizes an aphid by laying a single egg through its exoskeleton (Stary 1988), and the larva develops in the aphid with a mummy forming in 6–10 d depending on temperature (Thiboldeaux 1986). Larvae spin a simple cocoon within the mummy to pupate, and then emerge in 5–7 d. The total time between oviposition and emergence is roughly 14 d.

In Wisconsin, alfalfa is normally harvested twice in the year of planting and 3 times per year subsequently. Harvesting involves first mowing, after which the alfalfa is allowed to lie on the ground for 1–4 d to dry before it is collected. Shoots grow from the cut alfalfa starting 2–6 d following mowing, with the rate of regrowth depending largely on soil moisture. Before the regrowth of shoots, the food quality of alfalfa for aphids is very low, and early-stage aphids are unlikely to be able to feed successfully on the dry, thick-walled stubble. Furthermore, mummies form towards the top of alfalfa stems (for *Aphidius nigripes*, see Brodeur and McNeil [1992], Brodeur and Vet [1994]) and are therefore frequently removed from a field when the alfalfa is collected.

Field observations

Detailed observations on aphid and parasitoid populations were conducted between 12 May and 1 September 1998 in two alfalfa fields located at the University of Wisconsin Arlington Agricultural Research Station. Field A was planted in 1997, and Field B was planted in 1998. In 1998, Field A was harvested 3 times while field B was harvested twice.

Aphids were sampled twice a week using sweep nets at four (12 May to 25 June) or two (29 June to 1 September) stations in the fields; fields were not sampled for 1–2 wk following harvesting, because alfalfa stubble cannot be sampled effectively using sweep nets. At each station 3, 6, 9, or 12 sets of 10 sweeps were conducted until a total of at least 200 aphids were found. Data on aphid abundance are presented as the number of aphids obtained per set of 10 sweeps.

Parasitoid abundance was measured by searching fields for mummies for a fixed time period. At the same stations used for the aphid samples, observers walked through unswept alfalfa for three (12 May to 2 July) or six (5 July to 1 September) sets of 3-min timed counts. *A. ervi* mummies are readily observed on the top surface of leaves towards the apex of the alfalfa. Data are presented as the number of mummies observed per 3-min observation period.

In four fields (Fields A and B, and two additional fields referred to as ''C'' and ''D'') we performed detailed measurements of aphid and mummy abundance immediately before and following harvesting; harvest dates for these samples were 28 June, 30 June, 7 July, and 25 June for fields A, B, C, and D, respectively. Immediately before mowing, aphid and mummy abundances were measured by counting the number of aphids and mummies on 400 stems of alfalfa in each field. After mowing we conducted a thorough ground search for aphids and mummies. A 90-cm-diameter circular ring (hula hoop) was tossed from each of four stations per field. The area within the ring was extensively searched for aphids (roughly 45 person-minutes per ring). If the ring contained mowed alfalfa, before searching the mowed alfalfa was shaken within the ring to dislodge any aphids and discarded to the side. All aphids found were returned to the laboratory and dissected to determine parasitism. In Field D, we collected additional aphids to obtain a more accurate estimate of parasitism. Sampling began the day after mowing and continued for three consecutive days.

To compare aphid and mummy abundances from stem counts before harvesting with the ring searches after harvesting, approximately a week after each field was mowed four rings were tossed at each of two stations per field. Each ring was divided into quarters, and within one randomly chosen quarter we counted the number of alfalfa stems. Using the average stem density in each field, we translated the data obtained from stem counts before harvesting into the number of aphids and mummies per square meter.

Survival experiments

We performed two sets of experiments in the laboratory to determine the survival of parasitized vs. unparasitized aphids over the period before the parasitized aphids were killed by the parasitoid larvae. The first set of experiments measured survival on host plants, thereby considering the benign case in which food was present. The second experiment measured survival in the harsh case when aphids were not on plants. In addition to considering survival on and off host plants, we also varied the host plant, using both alfalfa and peas. Different pea aphid races are known to show differential survival and fecundity on different host plants (Bommarco and Ekbom 1996). Using both alfalfa and peas allowed us to investigate differences in survival caused by variation in food quality. Although it would have been preferable to use alfalfa plants that vary in quality, rather than introduce a new host plant, there is no consistent way to manipulate alfalfa quality for pea aphids.

Survival on plants.—Two experiments were conducted to determine the survival of parasitized vs. unparasitized aphids on plants. In the first experiment, two sets of 10 second- and third-instar aphids were placed in plastic dishes with a cut stem of alfalfa. Six to eight mated *A. ervi* females were added to one dish for 20 h; the second dish was treated like the first, except no parasitoids were added. The aphids in the dish with parasitoids were then removed and their left antenna clipped in the middle of the second segment from the tip; aphids in the other dish had their right antenna clipped. This method of marking aphids remains during molting and appears to have no effect on aphid survival (Mackauer 1972). The 20 marked aphids were placed on alfalfa plants with 0, 5, 10, or 15 additional aphids. The additional aphids were used to manipulate the stress on the alfalfa plant and therefore the overall survival of the marked aphids. A plastic dish coated with fluon (a slippery compound) was placed around the base of each plant to stop aphids from escaping, and a plastic Mylar tube was placed over the plant.

The aphids were observed daily until the first mummy formed, at which point all living and dead aphids were removed. Marked aphids were counted, and living aphids with the left antenna clipped were dissected to determine whether they were parasitized. Not all of the left-clipped aphids were parasitized; of the total of 19 trials, 37 (19.5%) of the total of 190 left-clipped aphids were unparasitized. We analyzed the results by including all left-clipped aphids in the ''parasitized'' group. This approach is conservative, because using the approach will make it more difficult to detect an effect of parasitism on survival. The alternative approach of excluding the unparasitized left-clipped aphids from the analysis has two disadvantages. First, we could not determine whether dead left-clipped aphids were parasitized, so excluding the living unparasitized left-clipped aphids introduces unknown biases. Second, pseudoparasitism (insertion of the ovipositor without oviposition) could affect survival, and unparasitized left-clipped aphids could have been pseudoparasitized and therefore should be included in the parasitized group.

The second experiment was conducted like the first, except aphids were kept on either alfalfa or pea plants. A total of 21 trials were performed with both alfalfa and pea plants. As before, not all left-clipped aphids were parasitized; 64 (15.2%) of the total of 420 left-clipped aphids were unparasitized. As before, we lumped these in the ''parasitized'' group for analysis.

Survival off plants.—This experiment was designed to determine if there is differential survival of parasitized and unparasitized aphids when removed from

their host plants. Unlike the preceding experiment, removing aphids from plants presumably increases stress and may decrease survival of parasitized vs. unparasitized aphids. Following harvesting, alfalfa may not produce new growth for several days, and because the remaining stubble dries, aphids will likely go without feeding for this period.

We performed this experiment on aphids fed either alfalfa or pea plants in order to vary their nutritional status. From a colony maintained on fava (broad) beans, we placed 20 second- and third-instar aphids on each of two alfalfa and two pea plants. A dish was placed around the base of each plant, and the plant was covered with a mesh lid. Six to eight mated female *A. ervi* were added to one each of the alfalfa and pea plants. After 20 h the parasitoids were removed. After another 48 h all aphids were counted and removed from the plant and dish. Live aphids were transferred to plastic dishes (11-cm diameter, 8-cm tall), and the lids of the dishes were lightly misted with water. The dishes were then placed into a plant growth chamber on a 24-h daylight cycle at 25°C. The dishes were initially inspected for dead aphids after 12 and 22 h, and then consecutively every 2 h. Any dead aphids that had been exposed to parasitoids were dissected to determine parasitism.

Field experiments

Two field experiments were designed to determine the importance of survival of aphids and parasitoids for the recovery of their populations following harvesting. Field cages were used to prevent immigration in both experiments, and aphid abundances were experimentally manipulated in the second experiment to investigate whether initial aphid abundance affects the recovery of aphid and parasitoid populations.

Field experiment 1.—Five 2 × 2 × 2 m cages were set up in each of fields A and C three days after mowing (2 July and 9 July for fields A and C, respectively). The cut alfalfa in field A had not been collected, so it was removed by hand before cages were set up. The cut alfalfa was collected and bailed from field C on the day after mowing (7 July). No adult parasitoids or predators (coccinellids, nabids, syrphids, and neuropterans) were observed in the cages immediately after the cages were set up, and the cages were checked twice per week until the end of the experiment to remove any predators other than parasitoids. This procedure did not remove carabid predators, which can feed on aphids and mummies when alfalfa is low following harvesting (Snyder and Ives 2001). In addition to the five cages in each field, five 2 × 2 m plots were established as ''sham'' cages. At weekly intervals for 4 wk starting on 6 July (Field A) and 9 July (Field C), aphid and mummy abundances in cages and sham cages were counted on 100 alfalfa stems. After the last sample, we collected 50 aphids from each cage and dissected them to determine parasitism.

Field experiment 2.—Experiment 2 was conducted like experiment 1, except only one field (field A) was used, and two aphid-abundance treatments were employed, ambient and supplemented. On the same day as field A was mowed (30 July), 10 cages were set up. All adult parasitoids and predators were removed from the cages. Before the field was mowed, aphids for the supplement treatment were collected from the area surrounding the cages using sweep nets; the aphids were kept in vials and cooled in an ice chest. Immediately after the cages were set up, five cages were stocked with the supplemental aphids by gently broadcasting aphids over the area of the cage. The supplemental aphids were collected by sweep-netting an area equal to that of a cage (2 × 2 m), and the numbers added to each cage (137, 195, 166, 119, and 168 aphids) therefore represent roughly a doubling of the ambient aphid density. The mowed alfalfa was left in the cages for 4 d to mimic the surrounding field, and it was then removed by hand. The cages were sampled for 4 wk in the same manner as experiment 1. After the fourth sample, aphids were collected from cages with a sweep net and returned to the laboratory for dissection. At the last sample, five sham cages were sampled in the same way. We did not sample sham cages at earlier samples, because field A was simultaneously being intensively sampled as part of the field observations.

Flight of parasitized aphids

If parasitized alate aphids can fly, then parasitoids may have a mode of recovery within fields not shared with generalist natural enemies—they can hitchhike within immigrating hosts. To determine whether parasitized alate aphids are capable of flight, we conducted a laboratory experiment in which parasitized and unparasitized alates were placed in a chamber and allowed to initiate flight. We established aphid populations on fava bean plants and allowed populations to reach high densities; high densities promote the production of alates. Once alate production started, we removed 30–70 second and third instars, and placed them into a small dish with mated female *A. ervi*. After 9 h the parasitoids were removed, and aphids were placed into a two-chambered flight box. The lower chamber contained a single fava bean plant within a plastic Mylar 20-cm-diameter tube. The upper chamber consisted of a 20-cm-diameter tube with the top covered with fine-mesh screening. The two chambers were divided so that only flying aphids could migrate from the lower to the upper chamber. Specifically, the bottom of the upper chamber consisted of an inverted funnel. Immediately below the inverted funnel was another, non-inverted funnel with a large (9-cm diameter) hole coated with fluon on the under side. The purpose of the lower funnel was to guarantee that aphids could not walk from the lower to the upper chamber. The upper funnel prohibited aphids that flew to the upper chamber from returning to the lower chamber. We checked the

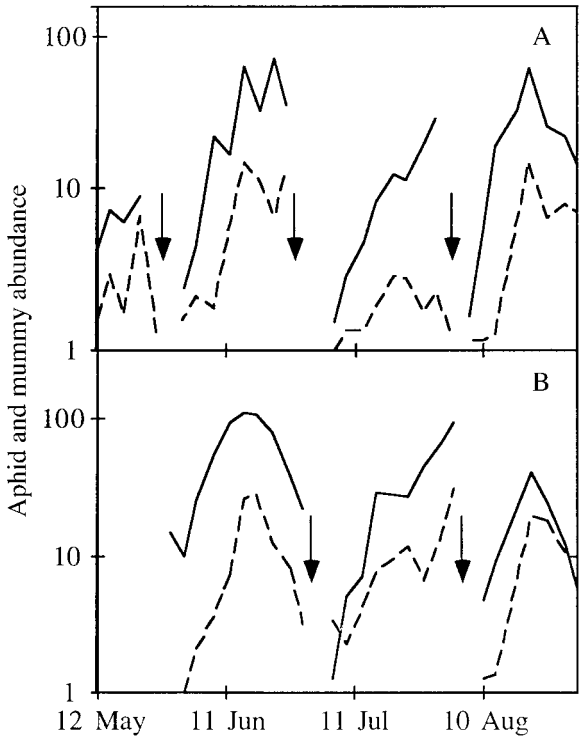

FIG. 1. Aphid (solid line) and parasitoid (dashed line) abundances in fields A and B during summer 1998. Aphid abundance was measured as the number of aphids collected per set of 10 sweeps with sweep nets; *Aphidius ervi* abundance is the number of mummies found per 3-min scan sample. Arrows mark harvest dates. Note the log scale on the *y*-axis.

top chamber every day for flying alates, and any fliers were dissected to determine parasitism and the stage of the parasitoid larva. Twenty-four hours after the first mummy was observed on the fava bean plant in the lower chamber, all alate adults were counted and dissected to determine parasitism. The experiment was repeated for 17 trials.

RESULTS

Field observations

Fig. 1 shows the aphid and parasitoid abundances in fields A and B during the summer of 1998. Harvesting is followed by a large drop in both aphid and mummy abundance. Both aphid and parasitoid populations then build rapidly, in some cases reaching a plateau or even decreasing before the next harvest.

A more detailed look at the drop in aphid and mummy abundance following harvesting shows that the loss is not immediate but instead occurs over several days (Fig. 2). The mummies found following harvesting generally occurred on dead alfalfa leaves or unattached on the ground, and were presumably knocked off plants during the removal of cut vegetation. Additionally, a few mummies were found attached to plants; these had formed recently (after mowing), as indicated by the incomplete sclerotization of the mummy. The loss of aphids and mummies after harvesting could be due to predation. Snyder and Ives (2001) showed that carabid beetle predation on both aphids and mummies can be strong immediately following harvesting when aphids and mummies are close to the ground and accessible to the primarily ground-dwelling carabids. Additional loss of mummies could be due to the emergence of adult parasitoids.

Combining data from all four fields and all three samples following harvesting, dissections revealed 51.8% ($N = 114$ aphids) parasitism. The intensive sampling of field D made it possible to estimate percentage parasitism separately in each daily sample. For the consecutive days following mowing, parasitism was 38% ($N = 13$ aphids), 67% ($N = 36$ aphids), and 57% ($N = 44$ aphids). This incidence of parasitism in surviving aphids suggests the importance of survival in aphids for the recovery of parasitoid populations in fields following harvesting.

Finally, despite extensive sampling, we found no *Aphidius ervi* adults.

Survival experiments

Survival on plants.—Two experiments were conducted to determine whether the survival of parasitized

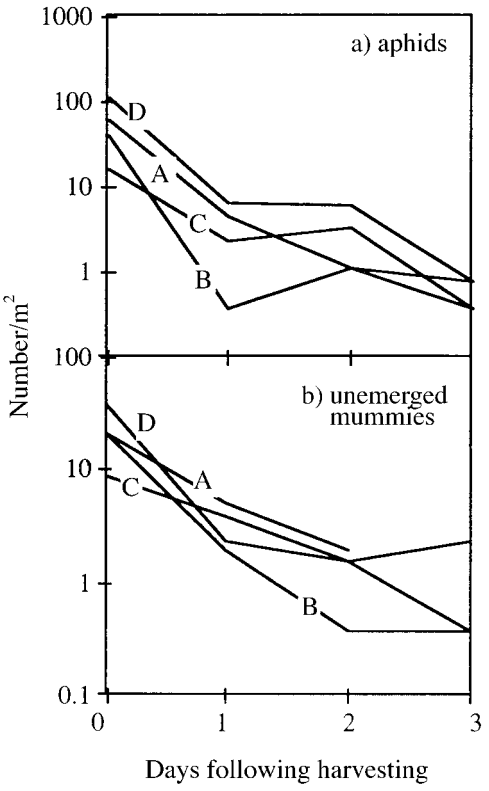

FIG. 2. Numbers of (a) aphids and (b) unemerged mummies in four alfalfa fields immediately before harvesting (day 0) and three consecutive days following harvesting. Fields A, B, C, and D are marked. Note the log scale on the *y*-axis.

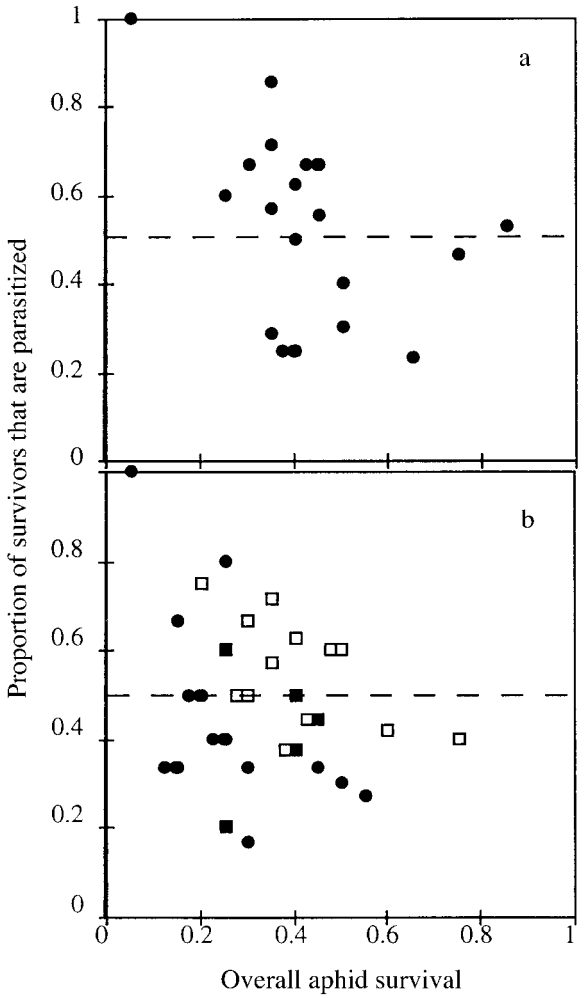

FIG. 3. Proportion of surviving aphids on plants that are parasitized vs. survival of all aphids (parasitized and unparasitized) for the period between parasitism and formation of the first mummy. Survival of parasitized aphids is greater than survival of unparasitized aphids for all trials above the dashed line. (a) First experiment conducted on alfalfa. (b) Second experiment conducted on both alfalfa (solid circles) and pea plants (open squares); solid squares are overlapping solid circles and open squares.

aphids was less than the survival of unparasitized aphids when aphids were on host plants. In the first experiment using alfalfa plants, the survival of parasitized aphids was the same as unparasitized aphids over the period between parasitism and mummy formation (Fig. 3a, Table 1). The results of the second experiment involving both alfalfa and pea plants are more complicated (Fig. 3b, Table 1). There was a strong plant-type (alfalfa vs. pea) effect on survival, with higher survival on pea plants. The effects of parasitism and the interaction of plant type × parasitism on aphid survival were both marginally statistically significant ($P < 0.049$); this was caused by survival of parasitized aphids on pea plants being *higher* than survival of unparasitized aphids on pea plants (Fig. 3b). These results

TABLE 1. Results of logistic regression for aphid mortality as a function of whether or not the aphid is parasitized.

Source of variation	df	χ^2	P
Alfalfa (N = 360 aphids)			
Parasitism	1	0.11	0.74
Trial	17	28.1	0.044
Alfalfa and peas (N = 840 aphids)			
Parasitism	1	3.9	0.049
Plant species	1	14.5	0.001
Trial	20	46.9	0.0006
Parasitism × Plant species	1	3.9	0.049

show that parasitism does not reduce aphid survival until the parasitoid kills its host.

Survival off plants.—Parasitized aphids died sooner than unparasitized aphids when they did not have access to a host plant, although the difference was not great (Fig. 4, Table 2). Survival time was significantly longer for aphids fed on alfalfa than for those fed on pea plants. This presumably reflects differences in nutritional status of the aphids, with alfalfa providing a better food source. Parasitism reduced mean survival time from 34.5 h to 29.1 h (15.9%) for aphids fed on alfalfa and from 25.5 h to 22.0 h (13.6%) for aphids fed on pea plants. Although these differences were highly statistically significant (Table 2), the magnitudes of the differences in survival times between parasitized and unparasitized aphids were nonetheless small

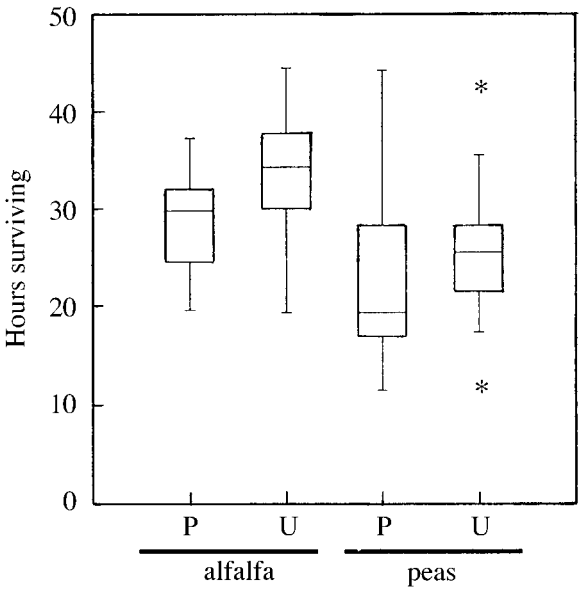

FIG. 4. In the absence of a food plants, the survival times of parasitized (P) and unparasitized (U) aphids that were previously fed on alfalfa and pea plants. Plots give the median and 50% inclusion areas as the central box, with the vertical lines encompassing all values except those shown by asterisks; for the points shown by asterisks, their distance from the 50% inclusion box exceeds 1.5 times the height of the box (Wilkinson 1988).

TABLE 2. ANOVA results for the log survival time of aphids without access to host plants.

Source of variation	df	*F*	*P*
Trial	19	2.94	0.001
Plant†	1	25.2	0.0001
Parasitism†	1	9.37	0.004

Notes: $N = 79$ aphids. On one plant in each of three trials, no aphid survived for a minimum of 12 h; these plants are excluded.

† Plant and parasitism scored as binary variables (alfalfa vs. peas, parasitized vs. unparasitized).

enough to suggest that harboring a parasitoid larva does not have a large effect on survival when aphids cannot feed.

Field experiments

Field experiment 1.—In the first field experiment, five cages and five sham cages were set up in each of two fields following mowing to determine whether immigration was required for the recovery of aphid and parasitoid populations. Aphids occurred in all of the cages despite lack of immigration, and the populations within cages sizably exceeded those in the sham cages by the third sample (Fig. 5a). At the last sample, there were statistically significantly more aphids in the cages than in the sham cages (Table 3), although there was also much variability among cages (Fig. 6a).

Before harvesting (22 June), the percentage parasitism measured by dissection of adult aphids was 40% ($N = 100$ aphids) in field A and 45% ($N = 199$ aphids) in field C. Following harvesting, percentage parasitism was low in the cages. Parasitism was determined both by counting mummies on 200 stems and dissecting 50 aphids at the last sample. Only three of five cages in each field had either mummies or parasitized aphids, and dissections at the last sample revealed 4.3% parasitism averaged among cages with at least one parasitized aphid. Aphid densities in the sham cages were too low to provide 50 aphids for dissections. For aphids collected in the surrounding alfalfa, percentage parasitism was 16% ($N = 100$ aphids) and 10% ($N = 50$ aphids) in fields A and C, respectively.

Although parasitoids occurred in some cages, thereby demonstrating that immigration was not necessary for recovery of populations, percentage parasitism was lower in cages than in the surrounding field, and 4 of 10 cages contained no parasitoid individuals. One possible explanation for this result is that the population size of parasitoids surviving within cages was too low to sustain itself. For observations in the field (Fig. 2), aphid densities may drop to <1 aphid/m^2. Since cages are 4 m^2, only a handful of aphids may survive in cages, with even fewer of these parasitized. There is a high probability that no parasitized aphid survived within cages, or that any surviving female parasitoids did not have mates. Thus, the loss of parasitoids from some of the cages could represent a ''cage effect''—cages were too small to have enough surviving parasitoids for the effective recovery of a parasitoid population. An alternative (and not mutually exclusive) explanation is that parasitoid searching efficiency is very low at very low aphid densities. Therefore, the first generation of parasitoids could not successfully establish a second generation in the cages.

Field experiment 2.—In the second field experiment we included a treatment to double the aphid abundance within cages (supplement treatment). In the cages with ambient aphid abundances, the initially small aphid populations increased rapidly (Fig. 5b), with the mean number of aphids per cage in the ambient treatment surpassing the mean of the supplement treatment in the last sample, despite higher initial densities in the sup-

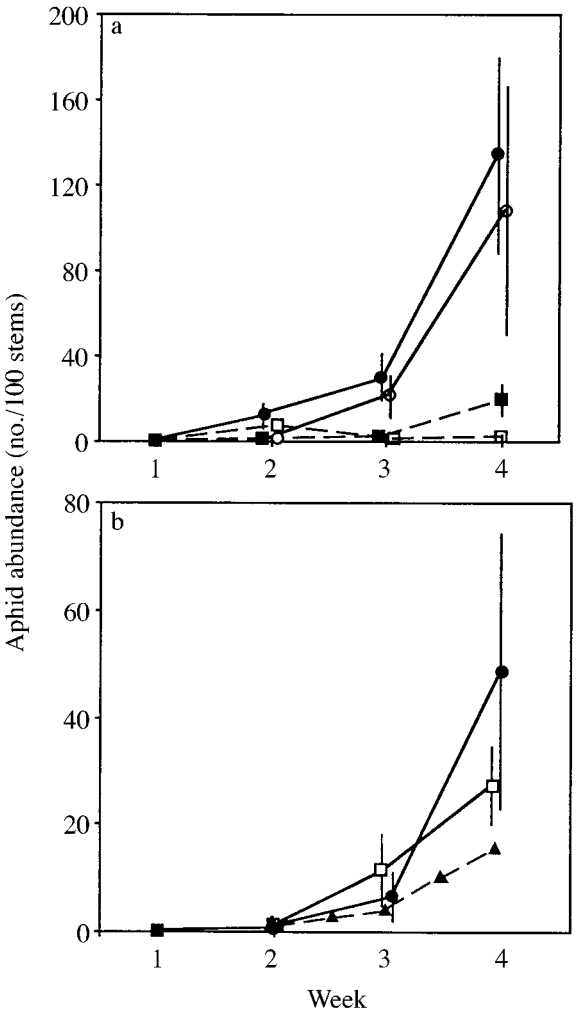

FIG. 5. Aphid abundances in (a) field experiment 1 and (b) field experiment 2. Data are means ± 1 SE. In (a), circles denote cages, and squares denote sham cages, with solid and open symbols corresponding to fields A and C, respectively. In (b), solid circles and open squares represent ambient and supplement cage treatments, respectively, and solid triangles represent data collected during field samples (Fig. 1, field A).

TABLE 3. ANOVA results for aphid number and percentage parasitism in field experiments.

Source of variation	df	SS	*P*
Experiment 1			
Log aphid number ($N = 20$ cages)			
Field	1	10.9	0.136
Treatment	1	36.2	0.0001
Experiment 2			
Log aphid number ($N = 15$ cages)			
Treatment	2	7.1	0.032
Sham cages excluded ($N = 10$ cages)			
Treatment	1	0.28	0.87
Arcsin square-root % parasitism ($N = 15$ cages)			
Treatment	2	0.57	0.0085
Sham cages excluded ($N = 10$ cages)			
Treatment	1	0.39	0.013

plement treatment cages. Due to variability among cages, however, the difference between aphid numbers in the ambient and supplement treatments in the final sample was not statistically significant (Table 3, Fig. 6b). The sham cages at the end of the experiment had fewer aphids (4.0 ± 1.4; mean ± SE) per 100 alfalfa stems than either the ambient (49 ± 25.9 aphids) or supplement (27.2 ± 7.2 aphids) treatments (Table 3, Fig. 6b).

Before harvesting (27 July), the percentage parasitism determined by dissections of adult aphids was 16% ($N = 100$ aphids). At the final sample, the mean percentage parasitism in the supplement treatment was 35%, very similar to the mean of 36% parasitism in the sham cages, and greater than the 5.9% parasitism in the ambient treatment (Table 3). The increased parasitism in the supplement treatment has two explanations. First, the greater number of aphids could have allowed a large-enough initial cohort of parasitoids to reproduce successfully, thereby overcoming the ''cage effect.'' Second, the first generation of parasitoids could have had a higher searching efficiency at the higher supplemented aphid densities, thereby increasing the parasitoid population in subsequent generations.

In addition to showing that immigration is unnecessary for the recovery of aphid and parasitoid populations following harvesting, this experiment also demonstrates the effect of parasitoids on aphid populations. To measure the effect of parasitoids on aphid populations, we calculated the per capita aphid population growth rate as the difference in log abundance between the last and next-to-last samples for each cage. Combining ambient and supplement treatments, the per capita aphid population growth rate declined significantly with percentage parasitism in the cages (Fig. 7). Thus, the greater the success of the parasitoid to recover following harvesting, the greater the biological control of the aphid population.

Although parasitoids alone (i.e., in cages) caused a decrease in aphid population growth, other natural enemies are also likely to be important in open-field conditions. The supplement and sham treatments had similar percentage parasitism (Fig. 6b), yet the mean abundance in supplemented cages, 27.2 aphids, was higher than in the sham cages, 6.2 aphids. Some of this difference is due to a doubling of the aphid abundance in the supplement treatment, and there was no statistically significant difference between the aphid abundance in the sham cages and one half the abundance of aphids in the supplemented cages (*t* test on log-transformed abundance, $P > 0.065$). Also, the abundance of aphids in the simultaneous and more extensive (1600 alfalfa stems) survey in field A (Fig. 1A) was 15.8 aphids per 100 stems, more than half the number of aphids found in the supplement treatment. Therefore, although other natural enemies undoubtedly depress aphid densities in the field, our experiments do not show a strong effect.

Flight of parasitized aphids

Although some parasitized alate aphids did fly, the proportion of parasitized alates that flew was less than the proportion of unparasitized aphids that flew. Among the 17 trials, the number of alates ranged from 7 to 59 (average 25.8 alate aphids), and the total percentage of alates that flew ranged from 5% to 60% (average 30.8%). Averaged among trials, of the alates that flew only 3.9% were parasitized, while of the alates that did not fly, 28.4% were parasitized. There was a highly statistically significant effect of parasitism on whether or not an alate flew (Table 4). Furthermore, of the four parasitized alates that flew, all contained first instar *A. ervi* larvae, and three of the four flew on the first day that alates were observed flying; the fourth flew 2 d following the first observed flight of unparasitized alates. These results suggest that parasitized alates only fly if they contain small parasitoid larvae that have not fed extensively on host haemolymph or tissues (Sequeira and Mackauer 1992).

DISCUSSION

In combination, our experiments demonstrate that the recovery of pea aphid populations in alfalfa fields following harvesting can occur in the absence of immigration; due to their high potential population growth

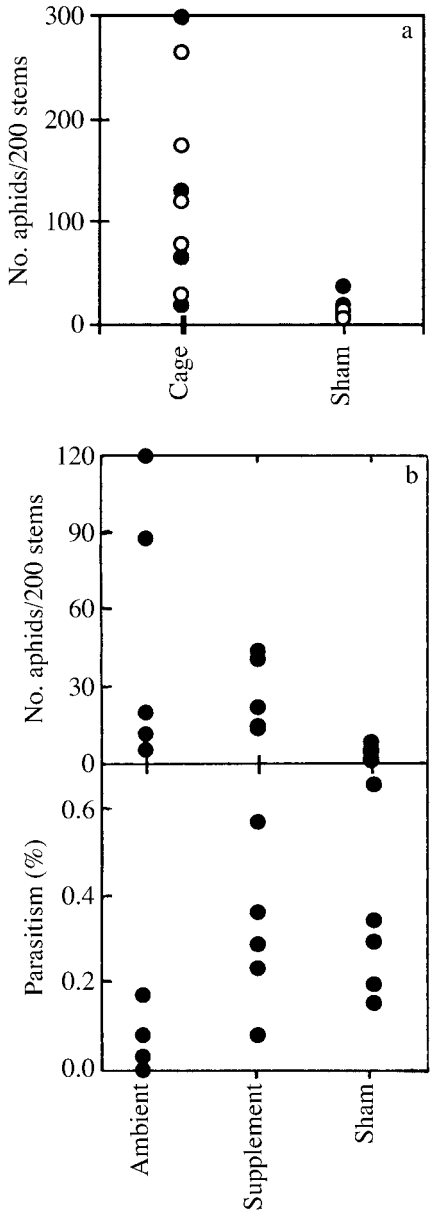

FIG. 6. Number of aphids and percentage parasitism in the last sample during the (a) first and (b) second field experiments. In (a), solid circles indicate field A, and open circles indicate field C. In (b), treatments are ''ambient'' for cages that were not supplemented with aphids, ''supplement'' for cages that were, and ''sham'' for 2 × 2 m areas without cages. Percentage parasitism was determined from dissections of 50 aphids per cage.

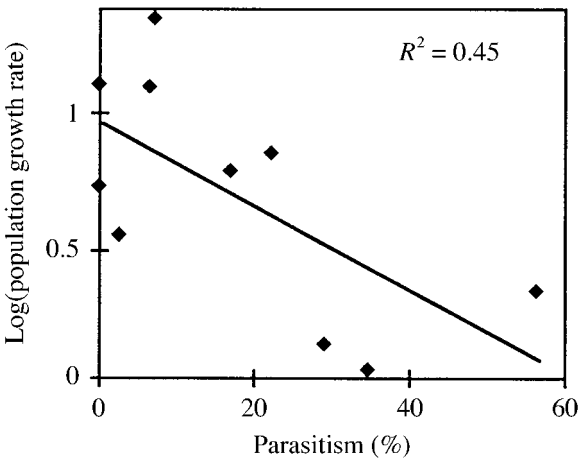

FIG. 7. Per capita population growth of aphids between the samples at weeks 3 and 4 of the experiment vs. percentage parasitism determined from dissections at the last sample. Data are from the ambient and supplement treatments of field experiment 2. The slope of the regression line is statistically significant ($t = -2.55$, df = 8, $P < 0.02$).

rate, the aphids that survive harvesting cause a rapid recovery of the pea aphid population. Furthermore, because some of the surviving aphids are parasitized, the *Aphidius ervi* population can recover through the parasitoid larvae in surviving aphids, or through the mummies that are not removed during harvesting. Finally, the success of parasitoid recovery directly impacts the aphid population, with higher success leading to greater suppression of aphid population growth several weeks following harvesting. Therefore, the ability of *A. ervi* to suppress pea aphid populations may critically depend on the parasitic phase of the life history of parasitoids.

The ability of *A. ervi* populations to recover in alfalfa fields following harvesting depends at least in part on the survival of parasitized aphids. Laboratory experiments showed that the survival of parasitized aphids was not lower than unparasitized aphids when both had access to plants (Fig. 3). When aphids could not feed, as is likely the case until alfalfa resprouts following harvesting, parasitized aphids die sooner than unparasitized aphids, although the difference (roughly 15%) is not great (Fig. 4). Thus, the laboratory experiments demonstrate the potential for parasitoids to survive disturbances in the field by being in parasitized aphids. Detailed observations immediately following harvesting show that the percentage parasitism of the surviving aphids can remain high. Furthermore, the field cages demonstrate the ability of parasitoid populations to recover in the absence of immigration. We did not exclude mummies that remained on vegetation left in the cages, and therefore some of the parasitoid recovery could be due to pupal parasitoids within mummies rather than larval parasitoids within aphids. Nonetheless,

TABLE 4. Logistic regression for alate flight as a function of parasitism status.

Source of variation	df	χ^2	P
Parasitism†	1	21.42	<0.0001
Trial	16	48.6	<0.0001

Note: $N = 439$ aphids.
† Parasitism scored as a binary variable.

this does not detract from our general argument that recovery of the parasitoid population within fields following disturbances can result from life stages remaining within the field rather than immigrating adults.

Although we have focused on parasitoid population recovery via non-adult stages that survive within fields during harvesting, adult immigrants likely also play a role. For biological control, however, parasitoid population recovery via immigration imposes a time lag with respect to the recovery of the aphid population. The surviving population of parasitoids within fields potentially occur at all non-adult stages. Eggs and larvae will be present in living aphids, and mummies may occur on cut alfalfa before it is bailed or on the debris left after bailing. The distribution of parasitoids among egg, larval, and pupal stages retains much of the stage structure of the parasitoid population before harvesting. Furthermore, based on our laboratory studies of survival, and field studies of aphid survival and percentage parasitism immediately following mowing, percentage parasitism will likely be the same shortly after harvesting as it was before. If recovery only occurred via immigration, the stage distribution of the parasitoid population would be disrupted, and there would be a time lag before parasitism began to reduce the aphid population growth rate. In addition, immigration of adult parasitoids into recently harvested fields is unlikely to be high, given the very low densities of hosts present.

The flight experiments in the laboratory show that parasitized alate aphids may fly, although only if parasitoid larvae are small. Therefore, the immigration of *A. ervi* into fields as larvae within alates is unlikely to be important for the recovery of parasitoid populations. Immigration of *A. ervi* within alate aphids may be unimportant for another reason. The field cage experiments demonstrate that aphid populations can recover rapidly in the absence of immigration. Therefore, immigration of alate aphids may not be very important, and hence immigration of *A. ervi* within alate aphids would be rare.

In the second field experiment, supplementing (i.e., doubling) the number of aphids within cages increased percentage parasitism, even though increasing the number of aphids had no effect on the initial percentage parasitism because the aphids were collected from the field. This is probably a cage effect caused by the very low initial number of parasitoids in cages. Supplementing aphids ensured that the initial parasitoid population within cages exceeded the minimum size needed to establish a population. In support of this explanation is the high variability in percentage parasitism found among cages (Fig. 6b), which is expected due to demographic stochasticity of the initially small populations. Nonetheless, we cannot exclude the alternative explanation that supplementing aphids increased parasitism at the end of the experiment by providing more hosts to the generation of parasitoids that emerged from the initially parasitized aphids. Regardless of the explanation, however, an important result is that percentage parasitism within the supplemented cages was the same as in the sham cages. Therefore, even though there was no parasitoid immigration into cages, percentage parasitism was the same as in the surrounding field.

We demonstrated the impact of successful parasitoid population recovery by showing that aphid population growth rates within cages were inversely related to percentage parasitism (Fig. 7). For cages with low percentage parasitism, the difference in log densities between the last and second-to-last samples was roughly 1, which corresponds to a population doubling time of roughly 5 d. With high percentage parasitism, population growth dropped to near zero. This magnitude of the effect of percentage parasitism on pea aphid population growth was also demonstrated by Snyder and Ives (2001). Even though percentage parasitism decreases the aphid population growth rate, other predators are also probably important. This is seen in the comparison between the supplemented cages and the shams (Fig. 6b). However, after accounting for the doubling of aphid abundance in the supplemented cages, evidence for the impact of other predators is weak (see *Results. Field experiment 2*, above). We are currently conducting experiments explicitly designed to quantify the impact of other natural enemies in addition to *A. ervi*.

Many agricultural systems experience episodic disturbances due to harvesting or insecticide application. The ability of biological control agents to establish populations rapidly following disturbance is a key to successful pest suppression (Doutt and DeBach 1964, Force 1972, Wallner 1987). The fact that parasitoids survive within living hosts could facilitate their rapid recovery. However, this depends on the mode of pest population recovery following disturbances. If pest recovery occurs via immigration, and if immigrants have low probability of being parasitized, then the parasitic life stages will not facilitate recovery of parasitoid populations. On the other hand, if the pest population recovers by in situ survivors, then the parasitoid population may recover simultaneously. This occurs for pea aphids and *A. ervi* in alfalfa. One could argue that this will only be important for perennial systems like alfalfa that are periodically harvested, in contrast to annual crops that are planted and harvested only once or perennial crops like orchards that do not experience large harvesting disturbances. Nonetheless, our general conclusions could be relevant to annual or perennial crops that are sprayed with insecticides. If the insecticide knockdown rate is not 100%, resurgence of the pest population could occur largely from survivors, some of which will carry parasitoid larvae. Recovery of the parasitoid population could be further enhanced if mummies were resistant to insecticides, as has been found for another *Aphidius* species, *A. rhopalosiphi*

(Borgemeister et al. 1993). Thus, one of the advantages of generalist predators as biological control agents—that they are capable of establishing populations within agricultural fields early (Doutt and DeBach 1964, Miller 1977, Ehler and Miller 1978, Miller and Ehler 1978, Riechert and Lockley 1984, Riechert and Bishop 1990, Settle et al. 1996)—may be shared by specialist parasitoids.

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