Parasitism of leafrollers in Washington fruit orchards is enhanced by perimeter plantings of rose and strawberry

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HIGHLIGHTS

▶ *Rosa woodsii* gardens supported overwinting of mature *Ancylis comptana* larvae.
▶ The parasitoid *Colpoclypeus florus* used *A. comptana* larvae as overwintering host.
▶ Positioning rose plantings next to orchards increased parasitism by *C. florus.*
▶ Movement of *C. florus* from roses into an orchard was tracked by protein marking.

GRAPHICAL ABSTRACT
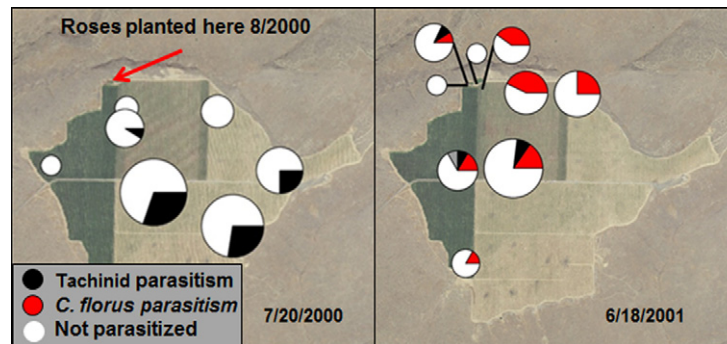
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ABSTRACT

Pandemis pyrusana and *Choristoneura rosaceana* (Lepidoptera: Tortricidae) are dominant leafroller pests in fruit orchards in Washington State. Parasitism rates of orchard leafrollers are low in spring and moderate in summer. In a previous study, parasitism rates of leafrollers were high in two orchards adjacent to thickets of *Rosa woodsii*. Here we show that plantings of *R. woodsii* and strawberry can significantly increase parasitism rates of leafrollers in adjacent orchards. In late summer of 2000, *R. woodsii* and strawberries were planted near four apple orchards and plantings were infested with the strawberry leafroller, *Ancylis comptana*, which overwinters as mature larvae on rose. In fall, these larvae were parasitized by *Colpoclypeus florus* (Hymenoptera: Eulophidae), a leafroller parasitoid of European origin that was recently discovered in central Washington. In the following spring of 2001, moderate rates of parasitism by *C. florus* were observed on *P. pyrusana* larvae placed along transects in apple orchards up to 200 m from three experimental plantings. Parasitism by *C. florus* increased in summer and was observed up to 500 m from the plantings. This pattern of parasitism by *C. florus* was observed through 2005 at one site. In contrast, little or no parasitism by *C. florus* was observed at these sites in 1999 and 2000 before planting of the rose habitats. Using a protein marking technique, self-marked *C. florus* originating from a marked rose planting were captured up to 100 m away in an adjacent orchard. We conclude that rose and strawberry plantings showed potential value as a sustainable landscape modification to improve biological control of leafrollers in Washington fruit orchards.

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1. Introduction

Natural habitats surrounding agricultural landscapes may enhance natural enemy diversity and result in increased biological control in the cropping system (Starý, 1970; Thies and Tscharntke,

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1999; Tscharntke et al., 2005; Bianchi et al., 2006; Isaacs et al., 2009). Several recent studies show that natural enemies are often more abundant and diverse in crop edges near non-crop habitats (Williams and Martinson, 2000; Bianchi and Van Der Werf, 2003; Miliczky and Horton, 2005; 2007; Isaacs et al., 2009; Thomson and Hoffmann, 2009; 2010; Thomson et al., 2010; Pfannenstiel and Unruh, 2003). In attempts to bolster biological control, various types of plant habitats that provide resources useful for natural enemies have been experimentally created in or near crops (Thies et al., 1997; Bugg et al., 1998; Pickett and Bugg, 1998; Rieux et al., 1999; Debras et al., 2006). These include habitats designed to provide floral subsidies for both predators and parasitoids (Tylianakis et al., 2004; Lavandero et al., 2006; Jonsson et al., 2008; Isaacs et al., 2009). Plant species that harbor alternate hosts for parasitoids have been created in or adjacent to crops, which have produced significant increases in attack rates on the target pest (Allen, 1932; Van den Bosch and Telford, 1964; Nguyen et al., 1984; Thomas et al., 1991; Murphy et al., 1998; Letourneau and Altieri, 1999). The studies presented here describe the potential of a habitat harboring an alternate host for a leafroller parasitoid in order to enhance biological control of leafroller pests in fruit orchards.

The *Pandemis* leafroller (PLR), *Pandemis pyrusana* Kearfoot, and the obliquebanded leafroller (OBLR), *Choristoneura rosaceana* (Harris) (Lepidoptera: Tortricidae), are the major leafroller pests in apple, pear, cherry, and peach orchards of central Washington and British Columbia (Brunner and Beers, 1996; Cossentine et al., 2004). Both species are bivoltine, with adult flights in late spring and late summer. The summer generation of larvae is found from July to mid-August. The subsequent larval generation overwinters as second or third instar larvae and begins to feed again at bud burst (Chapman, 1973; Beers et al., 1993; Brunner and Beers, 1996; Jones et al., 2005). Insecticides are often applied prophylactically in spring to control the overwintering larval generation, and again in July to control the summer generation if needed (Brunner and Beers, 1996).

A diverse complex of parasitoids attack OBLR and PLR in orchards but parasitism rates are typically low in spring and only modest in summer, seldom exceeding 10% and 50%, respectively (Brunner, 1996; Brunner and Beers, 1996; Vakenti et al., 2001; Cossentine et al., 2004, 2007). In 1999–2000 in south-central Washington, similarly low spring and summer parasitism of leafrollers was seen across 659 ha of apple, pear and cherry orchards in southern Yakima County, Washington, the same setting of the studies reported here (Pfannenstiel et al., 2012). In that study, *Nilea erecta* (Coquillett) (Diptera: Tachinidae), produced the highest parasitism rates followed in decreasing order by *Apanteles polychrosidis* Viereck, *Oncophanes americanus* (Weed) (Hymenoptera: Braconidae), and *Colpoclypeus florus* (Walker) (Hymenoptera: Eulophidae). In contrast, higher rates of parasitism, largely due to *C. florus*, were observed in two orchards adjacent to rose habitats harboring the strawberry leafroller (SLR), *Ancylis comptana* (Frolich) (Lepidoptera: Tortricidae) (Pfannenstiel et al., 2012). The SLR is a minor pest in some strawberry production areas of North America (Obrycki et al., 1993) but in central Washington it is found only in home strawberry gardens and on *Rosa woodsii* Lindl. or the Nootka rose, *Rosa nutkana* C. Presl. (Pfannenstiel et al., 2010).

Colpoclypeus florus is perhaps the most important parasitoid of leafrollers in much of Europe (Gruys and Vaal, 1984; Dijkstra, 1986). It was discovered in Washington in 1992, 24 years after its introduction in southern Ontario, Canada (Hikichi, 1971; Brunner, 1996). This external parasitoid attacks relatively large leafroller larvae on which it lays up to 50 eggs (Dijkstra, 1986). The parasitoid overwinters as an aggregation of mature larvae in a leafroller retreat and requires a large leafroller larva on which

to overwinter. In central Washington the SLR is the most common host used by *C. florus* (Pfannenstiel et al., 2010); in contrast OBLR and PLR overwinter as young larvae that are too small to be used as an overwintering host. *C. florus* requires only 233 day-degrees C from egg to adult (Milonas and Savopoulou-Soultani, 2000), suggesting it can have 6 or more generations in central Washington and at least 2 generations on the spring and late summer larval generation of OBL and PLR. Here we test the hypothesis that providing habitats of *R. woodsii* and strawberry infested with the SLR near to fruit orchards will increase parasitism of pest leafrollers in orchards by supporting and exporting *C. florus*.

2. Materials and methods

2.1. Planting and infesting experimental habitats

Experimental habitats were planted in August 2000, 15–50 m from the perimeter of four orchards at sites where *C. florus* was not found in spring and summer of 1999 and 2000 (Pfannenstiel et al., 2012). Habitats P1 (46° 31′ 14″N, 120°25′56″ W) and P2 (46° 30′ 29″ N, 120°25′59″ W) were on the edge of ∼234 ha mosaic of apple, pear, and cherry orchards that abutted shrub-steppe habitat in the Parker area of south central Yakima County. Experimental habitats W1 (46° 30′ 21.4″N, 120°20′09″ W) and W2 (46° 28′ 40″N, 120°22′42″ W) were in the Wapato area, a 425 ha landscape of mixed fruit orchards 4 km to the south of Parker.

Habitats were composed of *Rosa woodsii* that were collected locally from a rose thicket known to harbor the SLR and purchased (Lawyer Nursery Inc., Plains, MT) as bare rooted plants in late winter. Strawberry (*Fragaria x ananassa*, cv. Quinault) was purchased from a nursery (Koppes, Watsonville CA) as dormant plants. Roses were planted into 20 cm diameter pots and strawberries into 10 cm pots and were grown for 3–5 months in a greenhouse. After plants had established and produced mature leaves in the greenhouse, they were conditioned out-of-doors in July and August before being planted in the experimental habitats. Roses were planted on two sides of each habitat and comprised ∼75% of the habitat area and strawberries were planted in the middle 25%. Habitats varied from 75 to 250 m^2 in size and contained ∼50 roses and strawberry plants each. Plantings were irrigated by plastic piping connected to the orchard irrigation system and received extra watering by hand during the 3 months after planting. In late summer of 2002, three additional rose and strawberry habitats were planted by a cooperating grower on the western, southern and northern perimeter of the 40 ha orchard where site P1 was planted in 2000. Habitats created in 2000 and 2002 were infested at planting with rose terminals infested with SLR larvae collected from an infested rose thicket adjacent to the Washington State University, Columbia View Research Orchard (120°14′37.29″W, 47°33′55.25″N) (described in Pfannenstiel et al., 2012).

2.2. Sentinel larvae and parasitism estimation

In 2001, we measured parasitism of leafrollers in orchards by placing PLR (and OBLR, see below) sentinel larvae into the orchards because we could not control the presence or spatial position of naturally occurring leafrollers. PLR larvae were derived from a colony maintained at the Washington State University Tree Fruit Research and Extension Center and provided to us as egg masses laid on sheets of waxed paper. PLR for deployment were reared on a bean-based diet (Multiple Species diet; Southland Products Inc., Lake Village, AK) prepared as directed by producer. Ten mls of diet was poured into 29 ml portion cups with snap on lids (Solo, Highland Park, IL) and a single egg mass was attached to the lid to allow neonates to fall to the diet below. Larvae were

raised to third instar at 15–27 °C and used directly from diet cups in the field. We placed 30 sentinel larvae on each of five potted apple trees (cv. Red Delicious) to create a site. Many such sites were created throughout the orchard landscapes of the Parker and Wapato areas with a bias toward orchards near the planted habitats. Sarvary et al. (2007) showed sentinels larvae placed in orchards on potted apple trees provided a similar measure of parasitism to leafrollers placed directly on orchard trees. Potted trees were watered one–two times each week, depending on weather. Sentinel larvae were exposed to predators and parasitoids for 14–21 days for deployments in June to early September and up to 30 days for the deployment in April or May. These durations of exposure were used to allow larvae to mature with a small percentage forming pupae, thereby providing hosts for parasitoids that attack medium and large sized leafrollers. We found no evidence for parasitoids emerging before collection.

After 2001, we made two changes in our methods for estimating parasitism in orchards. First, we used OBLR larvae for sentinels because the PLR colony of had become infected with a granulovirus (Pfannenstiel et al., 2004) and uninfected larvae were not available in the abundance required. We conducted side-by side exposures of PLR and OBLR sentinel larvae in 2003 in order to detect bias and preference for particularly host by the parasitoids to understand how best to compare results across years.

Second, the sentinel larvae were placed directly onto branches of orchard trees instead of potted trees. In all such deployments, 150 larvae were deployed in each position with 30 larvae/branch and 5 branches on 3–5 adjacent trees, depending on tree architecture. To confine sentinel larvae to a specific branch, a 4 cm wide band consisting of #00 steel wool was wrapped twice around the branch just below leaves where we placed the larvae. This deterred most movement off the branch but brief searches for escaped larvae and rolled leaves on other branches of the infested trees were made when larvae were retrieved. Potted trees were still used for sentinel larvae outside the orchards and next to in the rose-strawberry habitats.

In 2001, some of the sentinel deployment sites were organized along transects away from the four habitats into the nearby orchards. Sentinels deployed during 2003–2005 were placed 2–4 tree rows (10–15 m) into the orchard near the rose planting and then at varying distances into the orchard (see results for spacing of deployments positions).

After field exposure, sentinel leafrollers in their retreats were collected, brought to the lab, placed individually into 9×50 mm plastic Petri dishes (Falcon # 6006) and covered with a tight fitting lid. They were reared at 22 ± 2 °C and 16:8 (L:D) photoperiod until adult parasitoids or moths emerged. Larvae were checked two or three times per week and were provided an unsprayed apple leaf as needed. Parasitism rates were assessed after feeding had stopped in a given collection (within 30–60 d). Parasitism rates were estimated as the ratio of the number of PLR or OBLR larvae that produced a given parasitoid species (not the number of parasitoids that emerged) divided by the sum of the larvae that that produced parasitoids or leafroller adults. The majority of parasitism was by C. florus and the tachinid flies of which Nilea erecta comprised more than 95%, a few Nemorilla pyste (Walker), and unmerged puparia (all report as tachinids). Two other parasitoid species, A. polychrosidis, O. americanus, were not abundant and are reported by name or grouped as "other". Parasitoids were identified using comparisons to those in a voucher collection described in previous study (Pfannenstiel et al., 2012). Levels of parasitism of the sentinels are displayed graphically as pie-charts with the center of the pie charts corresponding to the position where sentinels were deployed. Some pie charts were displaced in the fig. and a leader line directs the reader to the spatial position where the larvae were deployed.

### 2.3. Overwintering densities of C. florus in experimental habitats

SLR and C. florus densities were estimated in mid-winter of 2002–2003, 2003–2004 and 2004–2005 in three of the habitats planted in 2000 (P1, P2, W2) by collecting and examining all strawberry leaves or fallen rose leaves encompassed by a hoop $1/3$ m² area. The hoop was placed arbitrarily at four positions where rose leaves were evident and at four positions on strawberry plants. The leaves were collected into paper bags and returned to the laboratory where we counted healthy diapausing SLR larvae and SLR larvae parasitized by C. florus. The P2 habitat was mowed down by the grower in the autumn of 2004 and was not sampled.

2.4. Movement of C. florus from habitats

2.4.1. Protein marking

We used an in situ mark and capture technique to determine if C. florus was issuing from a rose/strawberry habitat and dispersing into the adjacent orchard and to determine when it was foraging in the orchard. Marking was a variation on the soy flour self-marking method developed by Jones et al. (2006) and Hagler and Jones (2010). Inexpensive, tulle netting (5 mm mesh opening) was placed over ~10% of the rose plants at the study site (Wenatchee Valley Community College Study Orchard – East Wenatchee; (46° 23' 32″N, 120°12'06″ W). Soy flour was applied to the netting using a hand-held rotary spreader. C. florus acquired the mark by walking on the dust on the netting or on the foliage below. To capture C. florus, a trap was fashioned from a white pheromone sticky trap liner (plastic Delta Trap sticky insert, AST 0014; Alpha Scents, Portland, OR). A 1 cm diam. hole was cut through the sticky liner and a floral water pick containing an apple shoot with 5–10 leaves was placed into the hole with water. Each shoot was infested with a single fourth instar OBLR larva, which was allowed to form a leaf roll in the laboratory for 24 h before field deployment. The traps were affixed to branches of trees in the orchard using wire floral ties. In 2005, traps were deployed at 34 positions ranging from 5 to 52 m or 1–13 tree rows distant from the rose habitat. The experiment ran from late July to the first week of September. In 2006, 65 traps were deployed from early May to mid-September with the positions of traps ranging from 5 to 93 m, 22 tree rows, from the habitat. Soy flour was applied on the day before trap deployment at the beginning of each season and re-applied as needed throughout the trapping period. Soy flour was not handled before handling the traps. Traps were checked at 3–4 day intervals and replaced weekly. In the laboratory, C. florus caught on the sticky surface of the liner were individually transferred to micro-centrifuge tubes; any wasps found in the leaf shelters were also removed and transferred to micro-centrifuge tubes to determine if they were marked.

Presence of the soy mark was determined by indirect enzyme-linked immunosorbent assay (ELISA) modified from Jones et al. (2006). Each captured wasp was soaked for 3 min in 200 µl of 1× TBS–EDTA solution (TBS, pH 8.0, [T-664, Sigma–Aldrich] with 0.3 g/L EDTA [S657, Sigma–Aldrich]). An 80 µl aliquot of rinse solution was transferred into individual wells of a 96-well microplate (Nunc Polysorp; Nalge-Nunc, Naperville, IL), as were control wasps reared from parasitized hosts collected in Yakima, WA more than 100 km distant. After the samples incubated for 2 h, each plate was emptied and washed three times with 300 µl phosphate buffered saline (PBS; P3813; Sigma–Aldrich) containing 2.3 g/liter sodium dodecyl sulfate (SDS; L-4509; Sigma–Aldrich) (PBS–SDS), followed by two washes with 1× PBS. Wells were blocked for 1 h with StartingBlock (37538; Pierce Biotechnology which was also used as diluent for primary and secondary antibodies) and subsequently washed once with 1× PBS–Triton-X100 (0.09%) (PBS–T). Then 80 µl of primary antibody was added
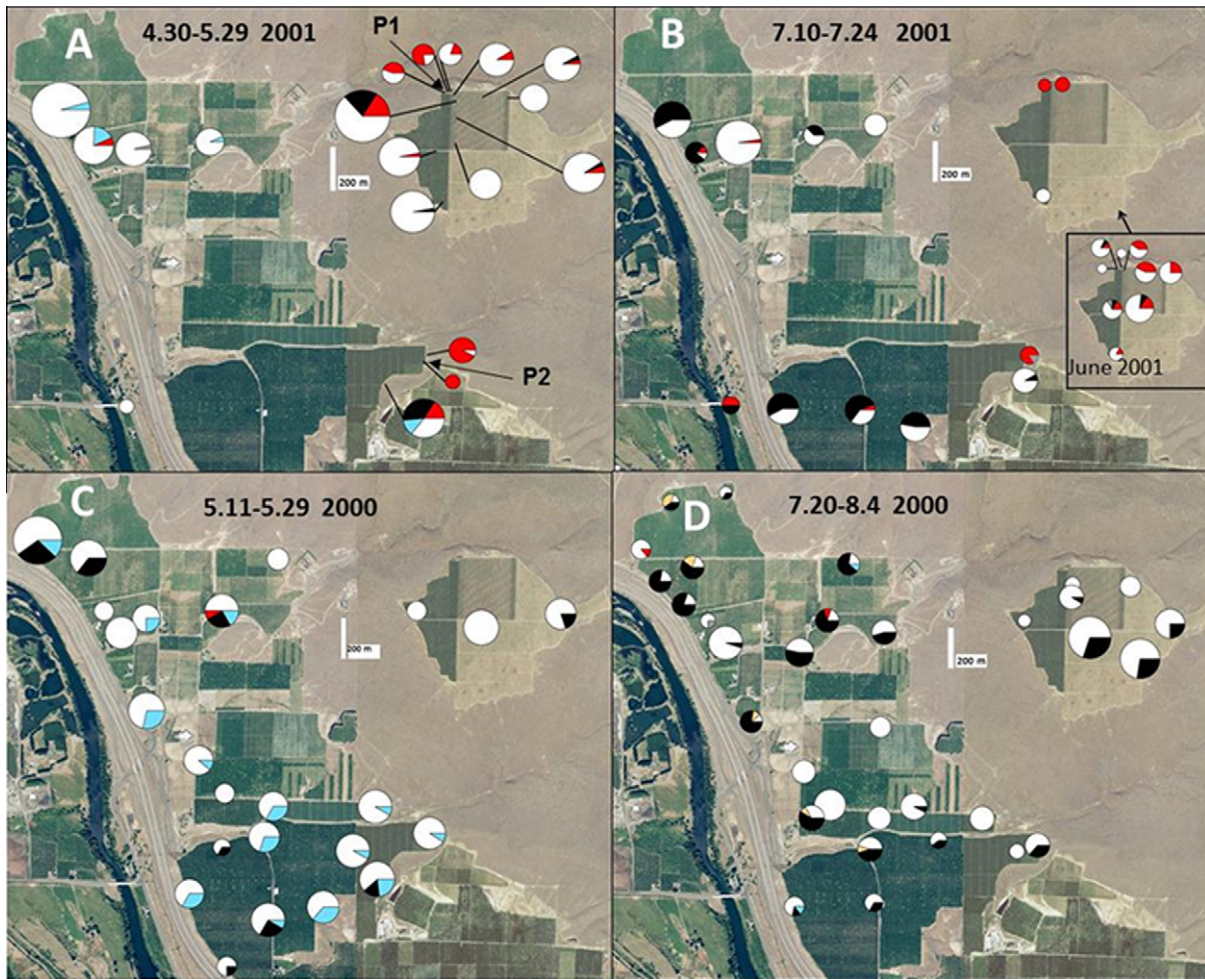
Fig. 1. Landscape overview of parasitism of sentinel *Pandemis pyrusana* at exposure sites in the Parker area in May (panel A) and July (Panel B) of 2001, the year following planting of rose/strawberry habitats at P1 and P2 (arrows in panel A); a 200 m scale bar is shown. An inset in panel B shows higher parasitism rates by *C. florus* during June of 2001. For comparison, parasitism at the same site observed in May (panel C) and July (panel D) of 2000 prior to creation of rose/strawberry habitats is depicted (from Pfannenstiel et al., 2012). *C. florus* is shown in red, tachinids in black, *Apantales* in blue, *Oncophanes* in yellow, unparasitized in white pie slices).

and incubated for 30 min. The primary antibody was discarded and wells were washed five times with 1× PBS–Triton. Next, 80 µl of secondary (conjugated) antibody was added to each well and incubated for 2 h. The secondary antibody was discarded and the plate was washed three times with PBS–SDS followed by two washes with PBS. Afterward, 80 µl of TMB (ImmunoPure Ultra TMB substrate kit 34028; Pierce Biotechnology) was added and the plate was placed on a rotary shaker and incubated in the dark at room temperature for 20 min. After incubation, the reaction was stopped by addition of 80 µl of 2 N H_2SO_4 to each well and the optical density (OD) was read at 450 nm using 490 nm as the reference standard (EMax Endpoint ELISA Microplate Reader, Molecular Devices LLC, Sunny Vale, CA). All readings were corrected against wells with TBS–EDTA. Specimens were categorized as positive for the soy marker if the OD exceeded the mean plus 3 standard deviations of the absorbance of the eight control wasps in each plate.

2.4.2. Spatial analyses of movement from habitats

The spatial positions where sentinel PLR or OBLR larvae were deployed in orchards were mapped using ArcMap (ArcGIS 9.2; ESRI, Redlands CA) as described previously (Pfannenstiel et al., 2012). Briefly, the spatial positions of sentinel deployment site

were based on hand-drawn, annotated field maps and subsequently marked on 2002 ortho-rectified photos of Yakima County WA (33 cm resolution). The distance tool in Arc Map was used to estimate distances to each sentinel deployment site to each habitat. These distances and the parasitism rates by *C. florus* and by tachinids at the sentinel sites were regressed using various transformations of the distance, including the inverse of distance, the inverse of distance squared, the inverse of the square root of distance, inverse of the log of distance (exponential decay). The best fitting transformations based on adjusted R^2 of the regressions are reported. Regressions were conducted in Microsoft Excel with the Poptools 3.2.1 add-in for calculating model significance (Hood, 2010).

In the marking study, straight-line distances were calculated from the GPS coordinate of the trap site where a *C. florus* was trapped to the nearest perimeter coordinate of the marked rose habitat. Spatial coordinates of the habitat perimeter and the traps were taken using a Garmin 400C GPS receiver (Garmin International, Olathe KS). The resulting positions are presented on an ortho-photo of the orchard and habitat site. Finally, the timing of the captures of marked *C. florus* in 2006 was compared to the expected life stages of PLR (Jones et al., 2005, 2010) in the adjacent orchard through the trapping period.

3. Results

3.1. Parasitism of sentinels larvae in orchards

3.1.1. Parasitism in 2001

Parasitism of sentinel leafrollers in orchards near the four rose plantings was assessed from May through Mid-August of 2001. Relatively high rates of parasitism by *C. florus* were observed in the orchards near to three of the four habitats planted in 2000. At the P1 site in the Parker area, parasitism by *C. florus* was observed up to 275 m from the rose/strawberry planting (Fig. 1, panel A; P1 identified with black arrow). A significant association of par-

asitism rate by *C. florus* at sentinel sites to the distance from habitat P1 was observed and was well described by the inverse square of the distance (para = $3.52d^{-2}$ + 0.04; R^2_{adj} = 0.97; n = 11, P < 0.001). There was no association of parasitism with distance for the tachinid flies at P1 in May (P > 0.2). Sentinel larvae were only recovered from three sentinel sites deployed near habitat P2 (Fig. 1, panel A; P2 identified with black arrow); other sentinel sites were not used due to pesticide applications for codling moth control. Parasitism rates by *C. florus* approached 100% in the P2 habitat and also evident at one orchard sentinel site 250 m away.

Parasitism by *C. florus* at Parker in July was evident on sentinels placed in habitat sites P1 and P2 but not in the adjacent orchards
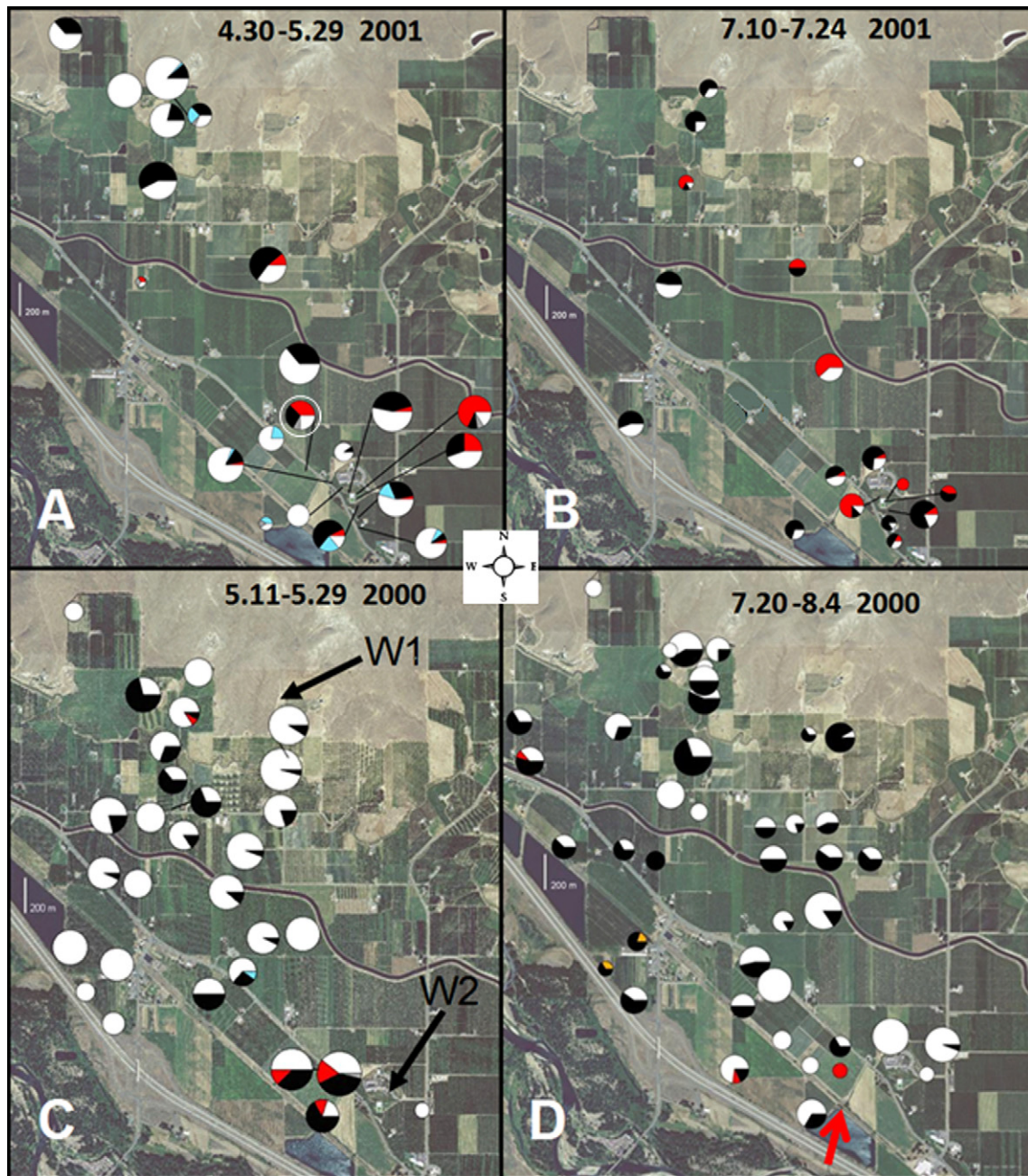
Fig. 2. Landscape overview of parasitism of sentinel *Pandemis pyrusana* at exposure sites in the Wapato area in May and July of 2001 (panels A and B), the year following planting of rose/strawberry habitats at W1 and w2 (arrows identifying gardens in panel C); a 200 m scale bar is shown. For comparison, parasitism at the same sites observed in May (panel C) and July (panel D) of 2000 prior to creation of rose/strawberry habitats is depicted (from Pfannenstiel et al., 2012). *C. florus* is shown in red, tachinids in black, *Apantales* in blue, *Oncophanes* in yellow, unparasitized in white pie slices). Red arrow impanel D indicates a naturally occurring rose thicket discovered in spring of 2000.

(Fig. 1, panel B); pesticide use and poor recovery of sentinel larvae precluded demonstration of significant movement away from the gardens. However, parasitism by *C. florus* was seen at five sites between 50 m and 610 m distant from P1 in June (Fig. 1, panel B, inset). Parasitism by *C. florus* near the habitats in 2001 contrast with our studies in 2000 where no parasitism by *C. florus* was observed near the future P1 and P2 (Fig. 1, panels C and D); similarly, parasitism by *C. florus* was not observed near P1 or P2 in 1999 (see Pfannenstiel et al., 2012).

In spring 2001 at the Wapato area, habitat W1 failed to thrive and no rose or strawberry plants survived to support SLR (see Fig. 2, panel C for positions of habitats). Hence, we expected and saw no *C. florus* activity at this site. At W2, parasitism of sentinel larvae by *C. florus* was evident up to 250 m from the habitat (Fig. 2, panel A) and again showed a decline with increasing distance from the rose/strawberry habitat proportional to the inverse square root of the distance (para = $0.74d^{-0.5} - 0.024$; $R^2_{adj} = 0.94$, $n = 11$, $p < 0.001$). One sentinel exposure site $\sim$300 m from habitat
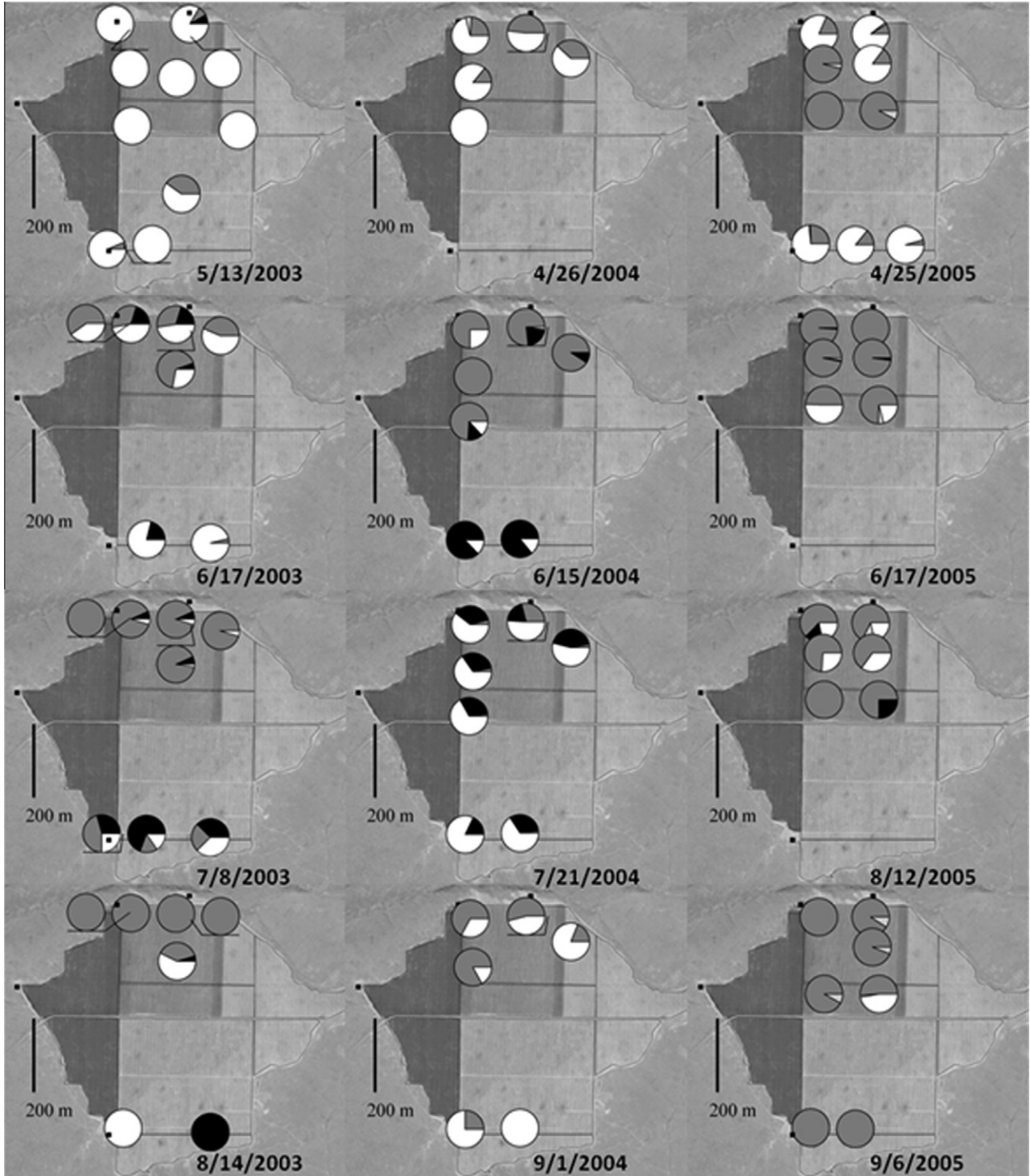
Fig. 3. Seasonal pattern of parasitism in 2003–2005 in the 40 ha orchard portion of the Parker area below planting P1 and three other rose plantings added in summer of 2002. Plantings are seen as perimeter black squares; P1 is topmost on left. Pie slices correspond to parasitism by *C. florus* (dark gray), by tachinid flies (black), other (light gray) or not parasitized larvae (white).

W2 (circled in Fig. 2, panel A) showed higher than expected parasitism by *C. florus* and was excluded from the above distance calculation; with the outlier included the effect is still significant ($P < 0.01$, $R^2_{adj} = 0.72$). In May of the previous year (2000) Fig. 2, panel C), we observed unusually high spring parasitism of PLR by *C. florus* near the future habitat at W2 and in late summer of 2000 discovered a naturally occurring rose thicket on the edge of the irrigation pond that was infested by the SLR (indicated by a red arrow in Fig. 2, panel D). In mid to late July 2001, parasitism by *C. florus* again showed a significant association with distance from habitat W2 (Fig. 2, panel B). Parasitism rate was predicted from the log of the distance from the habitat (para = -0.383 $\log(d) + 1.02$; $R^2_{adj} = 0.74$, $P < 0.002$; $n = 9$). However, it is evident from Fig. 2 that *C. florus* was widely distributed in the landscape in the Wapato area by this time. Parasitism by tachinids was high but not related to distance from W2.

Sentinel deployments in orchards in both the Parker and Wapato landscapes were compromised by pesticide applications during July and August, 2001. In exposures from mid-September to early October (not shown), parasitism was very high, 57% by *C. florus* and 33% by tachinids across 12 sentinel sites ($n = 510$). Exceptionally high parasitism is commonly observed in fall (Pfannenstiel et al., 2010, 2012). Parasitism by *C. florus* in autumn is indicative of parasitism that may occur on an overwintering host if available in the landscape. Such hosts are not normally available in apple orchards and are seldom near to orchards embedded in the shrub-steppe of central Washington (but see Nobbs, 1997). We conclude that much of the parasitism by *C. florus* of sentinel larvae in orchards in spring and summer of 2001 was due to wasps that were exported from planted habitats and one naturally occurring habitat.

3.1.2. Parasitism in 2003–2006

A disease in the PLR colony reduced the availability of PLR for use in sentinel studies beginning in 2001 when we used OBLR for sentinels in one study (Pfannenstiel et al., 2012) and switched to using OBLR in 2003 for these studies. In 2003, we compared the use of OBLR and PLR larvae to understand the implications of using OBLR in future studies. The *C. florus* parasitism rates on OBLR were numerically lower than those for PLR across all dates (67% parasitism of OBLR vs. 77% of PLR) where side-by-side exposures were made; these differences were not significant ($P = 0.30$; paired *t*-test, $n = 12$; total larvae = 693). A numerical bias favoring OBLR was observed for tachinid parasitism (12% of OBLR vs. 4% of PLR) but was also not significant ($P = 0.34$, paired *t*-test, $n = 12$). However, the successful recovery and emergence of PLR moths or parasitoids from PLR deployments (6.9 emerging/exposure site) was significantly lower than that for OBLR (22.1 emerging/site; $P = 0.015$, *t*-test, $n = 12$). A correspondingly higher death rate of PLR sentinels was observed during rearing in the laboratory after exposure (41% for OBLR and 59% for PLR; $P = 0.013$). While PLR deaths did not manifest themselves as larvae infected with the granulovirus (Pfannenstiel et al., 2004) it cannot be completely eliminated. The above forms of bias are modest suggesting both species are suitable for estimating parasitism rates across years but that higher recovery using OBLR supported our use of OBLR over PLR in 2003–2005.

In 2003–2005, parasitism was monitored with sentinel OBLR in the 40 ha where habitat P1 was created in late summer of 2000 (Fig. 1) and where three additional habitats were planted in late summer of 2002. The locations of all four habitats are found in Fig. 3. Parasitism monitored through the season in each year increased from spring to autumn. High parasitism rates by *C. florus* on sentinel OBLR were observed in most deployment intervals each season after spring (Fig. 3). Average parasitism rates by *C. florus* exceeded 65% in 2003 and 2004 during the summer leafroller generation (late-July to mid-August; Fig. 3). The spatial patterns of parasitism rates for *C. florus* in springtime of 2004 and 2005 showed a decline of parasitism with increasing distances from the habitats, but these patterns disappear later in the season. We hypothesize that high parasitism rates by *C. florus* on sentinel larvae in June or later stem from the activity of subsequent generations of wasps developing on feral leafroller in the orchard and
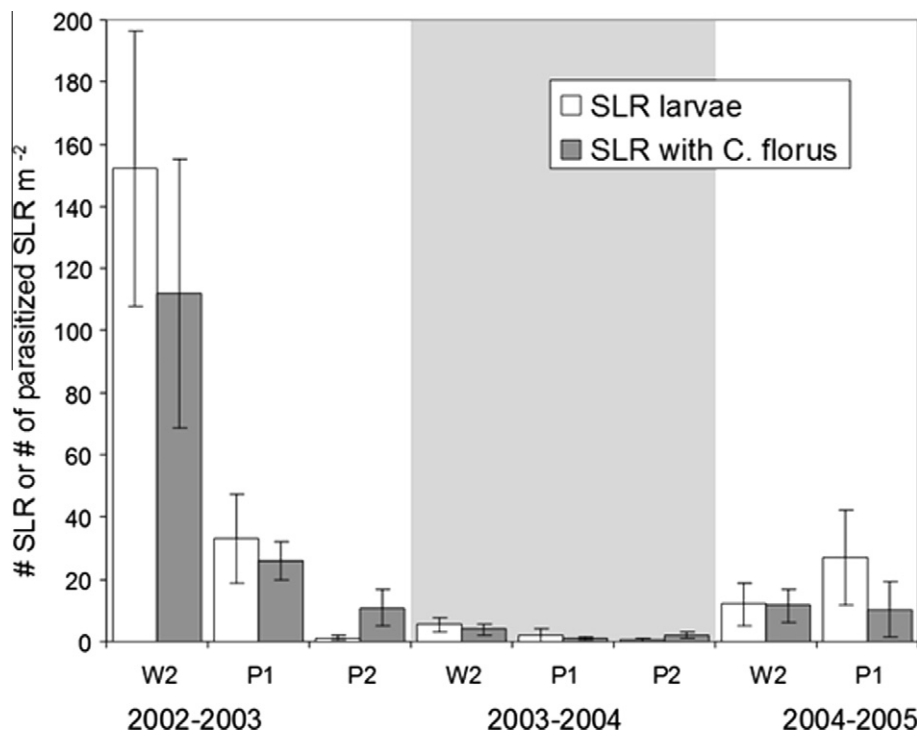

Fig. 4. Mean number m^{-2} (±SE) of diapausing larvae of *Ancylis comptana* (SLR) and of SLR larvae parasitized by *Colpoclypeus florus* estimated from mid-winter samples of fallen rose leaves and dormant strawberry plants.

Fig. 5. Pattern of trap deployment at the WVC orchard for 2005 (inset) and 2006; the trap positions where marked *C. florus* were caught are dark gray circles. A white polygon identifies the position of the rose garden and a black rectangle identifies which portion of the garden that was marked in each year. The most distant captures of marked *C. florus* from the marked portions of the garden were 52 m in 2005 and 96 m in 2006.
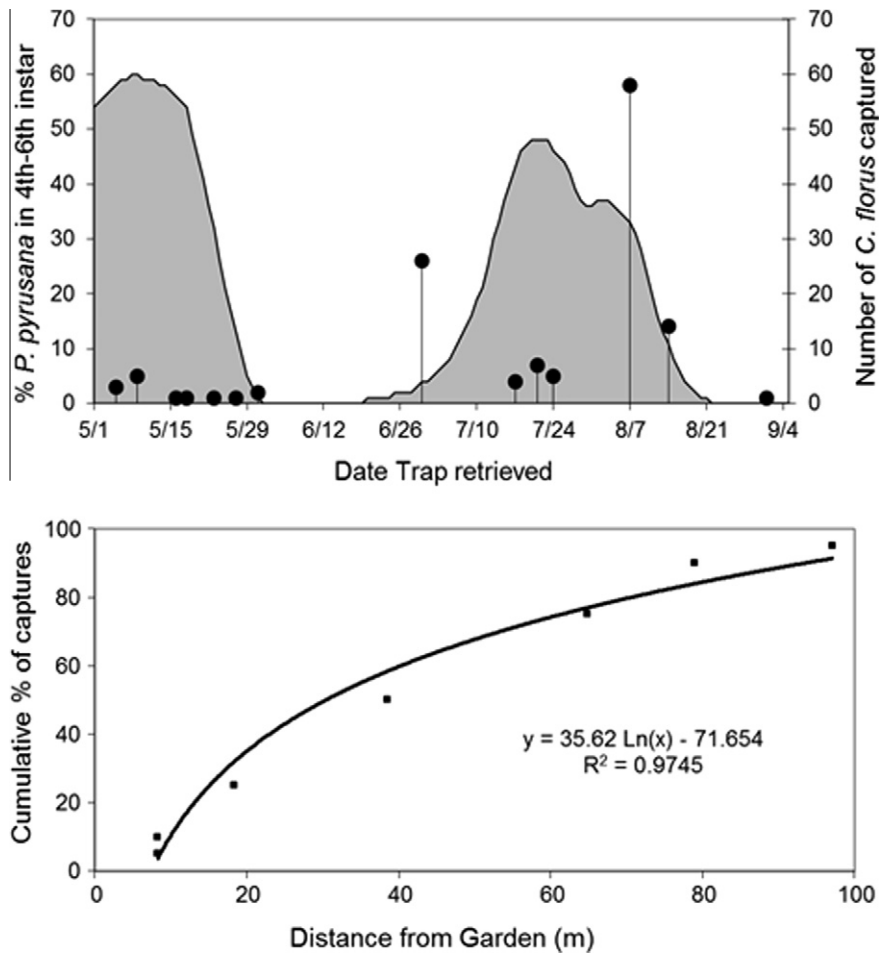
Fig. 6. Panel A: Capture of *C. florus* at the WVCC orchard is shown as circles with drop-lines overlaid on the predicted occurrence of 4th–6th instar *Pandemis pyrusana* based on day-degree accumulation in 2006 following model described by Jones et al. (2005) and implemented in Jones et al. (2010). Panel B: The cumulative trap catch of marked *C. florus* (*y* = capture, *x* = distance in m).

ongoing movement from habitats and within the orchard. Clearly, *C. florus* became the dominant parasitoid at this 40 ha area after habitats were established.

3.2. Overwintering densities of SLR and C. florus

The abundance of SLR larvae per m^2 in diapause both healthy and parasitized by *C. florus* in the leaf litter in three experimental habitats are summarized in Fig. 4 for the winters of 2002–2003, 2003–2004, and 2004–2005. There was a statistically significant decline in densities at all three habitats between 2002–2003 and 2003–2004 ($P < 0.05$) but densities appeared to rebound slightly in the following year. Only 2% of the SLR that were found came from samples of rose leaves, the remainder was from leaves attached to dormant strawberry plants. In contrast, 65% of the *C. florus* parasitized larvae were found in the fallen rose leaves. It is difficult to compare the rose and strawberry samples to one another or across years (rose leaves are susceptible to being wind-blown away from the site). Nonetheless, the accumulated data provide clear evidence of overwintering by *C. florus* in all years. The dynamics underpinning the different parasitism rates of SLR on rose and strawberry will be addressed in a subsequent paper.

3.3. Self-marking and dispersal of C. florus

In the marking-dispersal study of 2005, 182 *C. florus* were captured at 14 of the 32 trap positions; 24 (13%) of the wasps carried the soy flour marker (Fig. 5, inset). The percentage of *C. florus* captured that carried the mark roughly corresponded to the percentage of the habitat that was treated with the soy flour.

In 2006, 131 *C. florus* were captured, of which 38 (29%) were marked (Fig. 5), corresponding to a larger percentage of the habitat that was marked. Fully 75% of all *C. florus* were captured on three dates in 2006 (6/30, 8/7, 8/14) and these accounted for 100% of the marked wasps and bracketed the second generation of large larvae (Fig. 6, panel A). When the phenology of *C. florus* capture was compared to the availability of 4th–6th instar larvae of PLR as predicted by a phenology model (Jones et al., 2005, 2010), there was only a modest congruence. No *C. florus* were captured during the period in June when PLR larvae were not in the appropriate stage, but peak captures fell at the beginning and end of the second larval cohort.

Cumulative captures increased in a logarithmic fashion with the distance from the habitat to the trap sites where marked wasps were captured (Fig. 6, panel B) (the data is equally well fit by a linear relationship, $R^2 = 0.972$), suggesting that wasps likely dispersed significantly beyond where our most distant traps were deployed (96 m). Because trapping intensity should increase with distance from the source to maintain an equal trapping intensity on a per area basis, we may be further underestimating movement over longer distances, both here, and in the deployment of sentinel larvae in the landscape studies above. These results show, however, that *C. florus* is leaving (or visiting) the marked portion of the garden during both the spring and summer generation periods.

4. Discussion

The patterns of parasitism presented here demonstrate the potential for success of created habitats of rose or rose and strawberry to enhance parasitism of leafrollers in Washington orchards. More than 35 rose or rose and strawberry habitats have been planted by growers in central Washington in addition to those discussed. The efficacy of those plantings has not been adequately evaluated but some show high parasitism by *C. florus* in spring and summer, but not all of these have been successful in

harboring SLR and hence, *C. florus* (Unruh and Peters, pers. obs.). We do not have a recipe to make such habitats productive exporters of *C. florus*, but maintenance of a large population of SLR is necessary and quite possibly sufficient. The potential for extirpation of SLR population in autumn by *C. florus* returning from orchards seems plausible and supports the use of companion strawberry habitats to enhance SLR populations. The contribution of rose (few SLR but high numbers of *C. florus*) and that of strawberry (high numbers of SLR but lower parasitism by *C. florus*) suggests we should have habitats of each plant species in future. The apparent refuge from parasitism provided by strawberries and their much greater productivity of SLR argues for habitats of strawberry to be added to areas where roses alone are not proving adequate.

This value of plant diversity in this system parallels the observations on the value of a diversity of alternate hosts on assorted trees and shrubs for *Anagrus spp.* preventing it from greatly reducing the alternate hosts after its return from vineyards to blackberry and woodlot habitats in fall (Williams and Martinson, 2000; Doutt and Nakata, 1973). For these reasons, we recommend that growers also plant and carefully husband strawberries, without using insecticides near to the habitat that would destroy SLR or *C. florus* (Brunner et al., 2001).

The phenology of *C. florus* entry into orchards may depend greatly on habitat placement, exposure, and the composition of habits (with or without strawberry). It is clear that research is needed on this issue based on the unexplained timing of captures of *C. florus* in the marking study and on our common observation of high parasitism of sentinels in June when suitably sized pest leafroller are unlikely to be found in abundance. The availability of government support for growers to create wildlife habitats (Natural Resources Conservation Service, EQIP Program; Brewer et al., 2009) may lead to a significant increase in habitat plantings to service orchards in central Washington. Additional research can help make those habitats more productive for SLR and provide additional opportunity to understand these and other factors which may inhibit or enhance export of *C. florus* for leafroller biological control.

Conservation biological control and cultural control are important alternatives to insecticides in IPM systems (Stern et al., 1959; Jones et al., 2009). Habitat modification embodies both cultural control and conservation biological control and may act to foster and preserve natural enemies of pest arthropods (Van den Bosch and Telford, 1964; Pickett and Bugg, 1998; Landis et al., 2000; Isaacs et al., 2009). These concepts are described as part of broader terms such as farmscaping (Bugg et al., 1998) and ecosystem services (Isaacs et al., 2009; Daily, 1997). Many western orchards may be deficient in key beneficial insects such as parasitoids of leafrollers, aphid predators and other pests because they are distant from riparian habitats and mesic-adapted plants which appear to harbor a more diverse assemblage of beneficial natural enemies than do the sage-steppe habitats (Pfannenstiel et al., 2012; see Miliczky and Horton, 2005, 2007 for predators).

Several studies have focused on the provision of alternative hosts for key parasitoids of pests (van den Bosch and Telford, 1964). In France, hawthorn hedges supported alternate psylla species, which act as hosts to parasitoids of *Cacopsylla pyri* L. (Heteroptera; Psyllidae) (Nguyen et al., 1984; Delvare, 1984). While many hedge plantings persist in France, their value has been difficult to evaluate (Rieux et al., 1999; Debras et al., 2006). The most comprehensively studied habitat modification was designed to augment populations of *Anagrus epos* (Girault) (Hymenoptera: Mymaridae) attacking the Western grape leafhopper *Erythroneura elegantula* (Osborn) (Heteroptera: Cicadellidae) in vineyards. These studies have spanned more than 40 years. Blackberry bushes (Doutt and Nakata, 1965; 1973) and later French prune trees (Kido et al., 1984, Murphy et al., 1998) were shown to harbor non-pest

leafhoppers that supported *A. epos* or a related species (Triapitsyn, 1998). These parasitoids move from prunes (Corbett and Rosenheim, 1996) or blackberries (Doutt et al., 1966) into adjacent grape vineyards and parasitize the grape leafhopper, a major pest of grapes in the San Joaquin Valley. Unfortunately, various problems have limited the efficacy of these companion plantings. These minute wasps are weak fliers and do not penetrate very far into the vineyards from prunes trees unless winds are in their favor (Corbett and Rosenheim, 1996). *Anagrus* returning to prunes or blackberries after leaving the vineyard in the fall may decimate the alternate host populations (Mills and Daane, 2005). Furthermore, the blackberry leafhopper overwinters as females in reproductive diapause and does not provide adequate numbers of eggs in winter for *A. epos* (Doutt et al., 1966; Flaherty and Wilson, 1999). However, parasitism by *Anagrus* spp. was found to be higher in vineyards embedded in forest and woodlots in New York (Williams and Martinson, 2000) or near blackberry thickets that are protected under oaks in California (Doutt et al., 1966), or near French prunes with other trees and shrubs that support leafhopper eggs (Kido et al., 1984). There is no literature to suggest that these systems have continued to be valuable to growers as sustainable habitat modifications, although growers fortunate enough to be near habitats that export *A. epos* are likely continuing to reap the benefits of that ecosystem service.

Another example finds the SLR to again be a key alternate host. *Ancylis comptana* in strawberry fields in New Jersey provided an alternate host for *Macrocentrus ancylivorus* Rowher (Hymenoptera: Braconidae) whose offspring subsequently dispersed to parasitize Oriental fruit moth (OFM), *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae), in nearby peach orchards (Allen, 1932). This relationship was later duplicated in California when SLR-infested strawberries were inter-planted in peach orchards to provide an off-season host for (Letourneau and Altieri, 1999). We have no information as to whether these efforts using SLR for OFM control have continued but recent studies are exploring if another host, the sunflower moth, can augment *M. ancylivorus* for OFM control (Warner, 2007).

5. Conclusions

Increased parasitism rates of pest leafrollers by *C. florus* occurred in orchards nearby planted rose and strawberry habitats that were infested with the strawberry leafroller, *Ancylis comptana*, the major overwintering host for *C. florus* in Washington. A significant inverse correlation of parasitism rates of *C. florus* in orchards with distance from habitats was observed in nearby orchards providing correlative evidence that the habitats were the source of the parasitoid. We demonstrated overwintering of *C. florus* in three of our planted rose habitats and used a protein marker study at one orchard that showed that *C. florus* captured in a nearby orchard issued from the marked roses to further demonstrate the production of the wasp in these habitats. Studies on habitat design, value of strawberries with rose, topographic placement near orchards and the influence of these factors on the phenology and abundance of *C. florus* and *A. comptana* need to be more fully addressed. Multiple rose planting adjacent to orchards throughout central Washington provide a resource for further investigation of this system.

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