

Parasitoid competitive displacement and coexistence in citrus agroecosystems: linking species distribution with climate

JUAN SORRIBAS,¹ RAQUEL RODRÍGUEZ, AND FERRAN GARCIA-MARI

Instituto Agroforestal Mediterráneo, Universidad Politécnica de Valencia, Camino de Vera s/n 46022 Valencia, Spain

Abstract. The introduced parasitoid wasp *Aphytis melinus*, the most widespread natural enemy of the California red scale (*Aonidiella aurantii*) and the superior competitor, has displaced the native *Aphytis chrysomphali* from most citrus areas of the Mediterranean basin and other citrus areas all over the world. However, our extensive survey data on the scale parasitoid populations collected in 2004–2008 show that in large citrus areas of eastern Spain both parasitoids coexist. Using field data from 179 orchards spatially divided in five citrus-producing agroecosystems, we examined the mechanisms that could explain displacement or coexistence between both *Aphytis* species in relation to weather conditions. The distribution and abundance of the parasitoid species are related to the mean summer and winter temperatures and relative humidity of each ecosystem. The relative proportion of *A. melinus* is higher during the warm months, and the abundance of *A. chrysomphali* increases from south to north, being higher in the cooler northern areas. *Aphytis melinus* has displaced *A. chrysomphali* from hot and dry areas, whereas regions with mild summer temperatures and moderate relative humidity present the optimal conditions for the coexistence of the two parasitoids. The more negative effects of winter temperatures on *A. melinus* allow the earlier use of the available host resource in late winter and spring by *A. chrysomphali* and the coexistence of both parasitoids in the same orchard via temporal niche partitioning. We combine previous literature on the behavior of *Aphytis* species in the laboratory under different temperature and humidity conditions with our field results to confirm the role of spatiotemporal weather conditions and seasonal changes in host stages on the variation of *Aphytis* relative abundance and parasitoid coexistence.

Key words: *Aonidiella aurantii*; *Aphytis chrysomphali*; *Aphytis melinus*; California red scale; climate effects; interspecific competition; parasitoid wasp; temporal niche partitioning; Valencia Region, Spain.

INTRODUCTION

The hypothesis of competitive displacement in ecological homologues is still highly controversial; sometimes species that have become extinct in one habitat after the introduction of a superior competitor coexist in another habitat with the same competitor. As Hardin (1960) assessed, “ecological differentiation is the necessary condition for coexistence.” Intrinsic superior parasitoids can eliminate inferior species by outcompeting them for host resources and altering host–parasitoid population dynamics (Hassell 1986), but species may avoid exclusion by employing isolation mechanisms to reduce overlap and partition common resources (Schoener 1974, Diamond 1978). Resource partitioning results in the maximization of habitat availability, the formation of competitive refuges, and the facilitation of coexistence (Durant 1998). When there is asymmetric competition for a limiting resource, coexistence typically occurs via a trade-off between competitive ability and some other trait (Tilman and Pacala 1993). The

mechanisms that explain coexistence or displacement between parasitoids can be very helpful for applying biological control programs.

Most displacements between arthropods that have been observed were triggered by the introduction or invasion of an exotic species, although environmental factors may predispose a species to being displaced (Reitz and Trumble 2002). The regulation of pests by natural enemies in poikilotherm organisms is greatly influenced by weather. Climate has a major influence not only on the parasite–host association, but also on interspecific competition between scale parasitoids (Benassy 1961). Direct or indirect climatic influences on the host scale insects or the parasites are important factors in the natural enemy’s effectiveness because the dynamics of the same species may vary considerably under different weather regimes (Huffaker et al. 1971, Huffaker and Gutierrez 1990, Rochat and Gutierrez 2001). The influence of weather on control by natural enemies has been described for the olive scale (*Parlatoria oleae* (Colvée)) (Rochat and Gutierrez 2001), the oleander scale *Aspidiotus nerii* (Bouche) (Gutierrez and Pizzamiglio 2007), and other scale parasite associations.

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¹ E-mail: juasorme@etsia.upv.es

THE STUDY SYSTEM

The California red scale (CRS) *Aonidiella aurantii* (Maskell) is a hemipteran armored scale that infests citrus all over the world. Thus, the natural enemy complex of CRS has been widely studied and especially the most effective natural enemies controlling CRS, the aphelinid ectoparasitoids of the *Aphytis* Howard genus (Rosen and DeBach 1979). *Aphytis melinus* DeBach is considered the most successful and widespread biological control agent of this micro-wasp genus (Murdoch et al. 1989, DeBach and Rosen 1991, Forster et al. 1995). Other *Aphytis* species, which can be found in many countries on CRS as native or introduced parasitoids, are *Aphytis chrysomphali* (Mercet) and *Aphytis lingnanensis* Compere (Luck and Podoler 1985, Dahms and Smith 1994, De Santis and Crouzel 1994, Asplanato and Garcia-Marí 2002).

The Valencia Region (eastern Spain) is the most extended citrus area in Europe, and citrus is the most important production in Spanish Mediterranean agriculture. *Aonidiella aurantii* was first found as a pest in the locality of Alzira (Valencia) in 1986 (Garcia-Marí et al. 1988, Alfaro et al. 1991) and since then, it has slowly expanded to almost all the citrus orchards. The parasitoid *A. chrysomphali* is considered a native species initially parasitizing *Chrysomphalus dictyospermi* (Morgan) (Mercet 1912). It has also been described parasitizing *Chrysomphalus aonidum* (Linnaeus), *Aonidiella aurantii*, and *Aonidiella citrina* (Coquillett) (DeBach and Rosen 1991). As *A. citrina* is not present in Spain and *C. dictyospermi* and *C. aonidum* are nowadays almost absent (Franco et al. 2006), no other hosts are present apart from CRS. *Aphytis melinus* has been reared and released in the field since 1976 (Melia and Blasco 1980) to prevent a predictable expansion of the pest. Since 1995, *A. lingnanensis* has also been released in different areas (Verdú and Pina 2007). Previous studies in Valencia on *A. aurantii* parasitoids present in the field have been performed in a reduced number of orchards; observations between 1988 and 1994 yielded almost 100% of *A. chrysomphali* (Troncho et al. 1992, Rodrigo et al. 1996), whereas in 1999–2000 Pina et al. (2003) obtained 78% of *A. chrysomphali* and 22% of *A. melinus*.

Here we examine the seasonal abundance and variation of the two more extended California red scale parasitoids throughout the year and their geographical distribution in relation to the weather conditions. We use field data and literature on the behavior of *Aphytis* species under different temperature and humidity conditions to identify the mechanisms of coexistence between *A. chrysomphali* and *A. melinus*. The coexistence or displacement between *Aphytis* species in the field in five spatially divided agroecosystems is examined and related to the climatic characteristics. Mechanisms to explain the coexistence of *A. chrysomphali* with the superior competitor *A. melinus* and the niche partitioning between both parasitoids species are analyzed.

BACKGROUND DATA

Parasitoid competition

Since DeBach and Sundby (1963) first described competitive exclusion of *A. chrysomphali* by *A. lingnanensis*, followed by the displacement of the latter by *A. melinus* in the inland drier citrus areas of California, several papers have dealt with the factors and mechanisms of competitive displacement of these ecological homologues parasitoids after their serial introduction in the United States (Podoler 1981, Luck et al. 1982, Kfir and Luck 1984, Luck and Podoler 1985). DeBach and Sundby's theories were based on the supposition that the three *Aphytis* species have identical ecological niches, and thus they are ecological homologues. Previous studies on the competition mechanisms between *Aphytis* species concluded that the superior competitor *A. melinus* (see Plate 1) displaced the ecological homologue *A. chrysomphali* because it possesses superior or intrinsic biological and physiological capabilities, exhibits a higher capacity of dispersion, and moves twice as fast when temperatures are higher than 16°C (McLaren 1976). Further examples of competitive displacement between *Aphytis* species have been described in other citrus-producing countries like Australia (Smith et al. 1997) and South Africa (Bedford and Cilliers 1994).

Aphytis melinus is considered a superior competitor in the field because it is better adapted to dry and hot climates (Rosen and DeBach 1979). The displacement of *Aphytis* species by *A. melinus* has been related to climate adaptability and to other biological differences between species (Kfir and Luck 1979, Huffaker 1990). The effects of temperatures on the different natural enemies of CRS have been widely studied (Abdelrahman 1974a, b, Atkinson 1983, Kfir and Podoler 1983, Kfir and Luck 1984, Hoffmann and Kennett 1985). DeBach and Rosen (1991) experimentally demonstrated that some *Aphytis* parasitoids can be precluded from exerting adequate control by adverse climatic factors. Bennet (1993) observed that when two *Aphytis* species were cultured together in the laboratory, one species was eventually eliminated: which species survived was influenced by the temperature and humidity regimes of the experiment.

*Aphytis chrysomphali displacement
in the Mediterranean area*

In the Mediterranean basin, CRS has been a serious pest for many years in eastern countries. The first recorded infestation was in 1926 in Palestine, and later on it was also found in Greece, Cyprus, Turkey, Syria, and Egypt (Bodenheimer 1951). It slowly expanded to the west during the second half of the 20th century (Delucchi 1965, Liotta 1970). *Aphytis chrysomphali* is considered native to the Mediterranean, where it previously parasitized other armored scale species, mainly *C. dictyospermi* (Mercet 1930, Viggiani 1988). It was first described by Mercet in 1911 in the Valencia

TABLE 1. Climatic data of the five Valencia Region citrus areas for the period 2002–2007 (annual mean of 5–8 weather stations) and invasion period of *Aonidiella aurantii* (California Red Scale [CRS]) for each area. Correlation (r) with the percentage of *Aphytis melinus* is reported in the last row.

Area number and name	Mean temperature (°C)					No. days <10°C	Mean relative humidity (%)	Mean rainfall (mm)	CRS invasion period (yr)
	Overall	Minimum	Maximum	Winter	Summer				
1) La Plana	16.6	11.6	21.9	9.8	24.6	58.4	61.8	584	2001–2007
2) Valencia city area	16.9	11.7	22.6	10.3	24.9	54.7	62.4	498	1995–2000
3) La Ribera, La Safor	17.2	11.5	23.2	10.1	25.5	57.0	63.7	690	1986–1991
4) La Marina	17.7	12.8	23.3	11.3	25.6	36.8	63.6	692	1988–1995
5) Bajo Segura	17.9	12.8	23.5	11.2	25.8	34.7	60.1	302	1997–2006
r	0.97**	0.92*	0.89*	0.88*	0.91*	0.91*	0.42	0.53	

Notes: Climatic data are from the Agriculture Department of the Valencia Region Government climatic database (<http://estaciones.ivia.es>). For details on the five citrus areas, see *Materials and methods: Study area*. CRS invasion period was obtained from previous works (Garcia-Mari et al. 1988, Rodrigo et al. 1996, Alfaro et al. 1999, Moner 2000, Verdú and Pina 2002, Garcia-Mari 2003) and our field data. Pearson correlation coefficients (r) show the relationship between each climatic parameter and the percentage of *A. melinus*.

* $P < 0.05$; ** $P < 0.01$.

Region (Spain) and then in Algeria and Tunisia (Mercet 1912). In 1913 *A. chrysomphali* was reported in Corfu and the Aegean islands (Malenotti 1918). It was later found in France, Italy, Greece, Algeria, and Lebanon (Ferrière 1965). *Aphytis melinus*, which originated in India, was successfully introduced after *A. aurantii* progressively reached pest status in most Mediterranean citrus-producing countries. Following this introduction, displacement of *A. chrysomphali* by *A. melinus* was reported in most cases. Pelekassis (1974) indicated the successful establishment in Greece in 1962 of the released *A. melinus* and nine years later, Argyriou (1974) confirmed the total displacement of the native *A. chrysomphali* in Greece. Guirrou et al. (2003) pointed out *A. melinus* as the main parasitoid of CRS in Morocco, where *A. chrysomphali* had previously been present (Delucchi 1965). Similar situations were described in Cyprus, Israel, Sicily (Italy), Turkey, Portugal, and Egypt (Hafez 1988, Viggiani 1994, Siscaro et al. 1999, Erler and Tunç 2001, Gonçalves et al. 2002, Kamel et al. 2003). In the citrus-producing area of Andalucía (southern Spain), with a warmer and drier climate than the Valencia Region and where previously *A. chrysomphali* had been widespread (Mercet 1930), *A. melinus* is nowadays the only parasitoid present (Vela et al. 2007).

However, in some areas around the world, the native or previously existing CRS parasitoids (*A. chrysomphali* or *A. lingnanensis*) persisted in small favorable habitats after the introduction of *A. melinus*, as in coastal areas of Israel and Cyprus, small areas of South Africa and Australia, and some humid areas of Uruguay (Avidov et al. 1970, Bedford and Grobler 1981, Orphanides 1984, Bedford and Cilliers 1994, Dahms and Smith 1994, Asplanato and Garcia-Mari 2002).

MATERIALS AND METHODS

Study area

We collected samples from 179 citrus orchards in eastern Spain. Orchards were distributed all over the

citrus-growing areas of the Valencia Region covering 182 000 ha along the Mediterranean coast in an almost continuous citrus belt of 400 km long from north to south and 50 km wide. The citrus acreage was spatially divided into five surface agroecosystems (labeled Area 1 to Area 5) according to their geographical location from north to south. These ecosystems are independent natural regions that had homogeneous climatic conditions.

A minimum of 15 orchards were monitored in each of the five citrus ecosystems. The orchards were representative of the cultural practices usually applied by local growers, including organic orchards, orchards managed by IPM practices, and orchards under traditional chemical management. The proportion of each agricultural practice was the same in the five agroecosystems studied. All the citrus species or varieties usually cultivated in eastern Spain were included: oranges (*Citrus sinensis* [L.] Osbeck), lemons (*Citrus limon* [L.] Burm.), clementine mandarins (*Citrus reticulata* Blanco), hybrids, and satsuma mandarins (*Citrus unshiu* Markovitch). However, most of the orchards selected for sampling were oranges (>90%), and the percentage of this species was similar in the five agroecosystems considered. Two different systems of sampling CRS parasitoids in the field were used: pheromone sticky traps and chromatic sticky traps placed on citrus trees and field-collected samples of branchlets and/or fruits containing *A. aurantii*.

The citrus area of Valencia presents a typical Mediterranean coastal climate with temperatures very seldom below 0°C during winter due to the sea influence, high average relative humidity (>60%) but dry summer, especially in the southern areas. The climatic data for each agroecosystem (area) are provided in Table 1, together with the approximate period in which *A. aurantii* started and completed the invasion of the area (Garcia-Mari et al. 1988, Rodrigo et al. 1996, Alfaro et al. 1999, Moner 2000, Verdú and Pina 2002, Garcia-Mari 2003). These data were obtained from the

Agriculture Department of the Valencia Region Government climatic database (*available online*).²

Pheromone and chromatic field traps

Between June 2005 and May 2006, traps coated with adhesive (Frutect, RonPal, Bnei Zion, Israel) collected from 100 commercial citrus orchards in full production were observed. The orchards were included in a survey net established by the Agriculture Department of the Valencia Region Government (Citrus Phytosanitary Survey Project [Plan de Vigilancia Fitosanitaria de Cítricos]) to monitor citrus pest populations all along the Valencia citrus area (*available online*).³ CRS pheromone traps, as well as several color traps, are known to be effective in the capture of *Aphytis* parasitoids (Sternlicht 1973, Moreno et al. 1984).

Two of the trap types used in the survey were selected for this study as they showed captures of CRS parasitoids: *A. aurantii* pheromone sticky traps and yellow sticky traps. Pheromone traps consist of a 19 × 19 cm tent-type white cardboard with a synthetic *A. aurantii* female pheromone lure (AgriSense BSC, Pontypridd, UK) attached to the center underside ceiling. Yellow sticky traps are non-pheromone rectangular plastic traps of 15 × 20 cm. The two traps were randomly placed in different trees in each orchard. Every week 50 of the traps were collected and replaced, so that each trap spent 14 days in the field. The pheromone lure was changed every six weeks. In the laboratory the parasitoids captured were located in the traps under the binocular stereoscope, extracted, mounted, and identified under the microscope.

The CRS males were also captured on the *A. aurantii* pheromone sticky traps and counted. Orchards with low capture levels of males or parasitoids were excluded from the study, so that finally a total of 60 orchards remained. The CRS infestation level on fruits and branchlets was evaluated in the orchards by direct observation in the field of 80 fruits and 40 branchlets per orchard. These observations were made every two weeks throughout the year for branchlets and when fruits were present.

Laboratory experiments

During the period November 2004 to March 2008, samples of branchlets (twigs with leaves) and/or fruits infested with *A. aurantii* were randomly collected from 134 citrus orchards located throughout the citrus-producing areas of the Valencia Region. During this period each orchard was sampled once per season (spring, summer, fall, and winter) except on those orchards in which CRS was eliminated by chemical treatments or where captures of *Aphytis* were lower than 10 specimens. In this case the orchard was replaced for another orchard in the same area. Thus, at the end of the

whole sampling period, four samples from each orchard were obtained. A similar number of orchards were sampled for each agroecosystem considered, and samples were regularly distributed along the sampling period. Branchlet samples consisted of 35–45 young branches (0.5–1.5 years old) ~30 cm long with leaves taken from different trees. Samples of 20–35 fruits were collected when >3 cm in diameter and were kept in the rearing cages to capture emerging adult parasitoids. Rearing cages consisted of 40 × 30 × 22 cm transparent plastic boxes covered with a gauze and maintained inside climatic chambers (26–28°C, 60% relative humidity, 16:8 h photoperiod) for 20 days to allow all parasitoids to develop to adults (*A. melinus* needs ~18 days from egg to adult at 26°C). Adult parasitoids were captured on yellow 12 × 12 cm sticky traps placed inside the cages or collected dead from the bottom of the cage. The total number of parasitoids was counted, and a maximum of 100 parasitoids per sample was identified.

In order to speed up the identification procedure we looked for an alternative to the traditional method described by Rosen and DeBach (1979) for the digestion of *Aphytis*. Several methods and products were tested to eliminate the glue and digest the insects (xylene from 1 h to 48 h, lactic acid, potassium hydroxide solution, and Nesbitt liquid). The option chosen was 20 h xylene + 30 min Nesbitt digestion + 1 min heating under flame, which provides fast location and observation of insects because they are not completely digested and their red heads are easily identified (the body of *Aphytis* is digested faster than the head).

Data analysis

For the estimation of *A. melinus* sex ratio we only considered the insects captured on rearing cages because field sticky traps always capture many more males than aspirator-vacuum techniques or direct counting of parasitoids on plant material and thus are not representative of the male proportion in the field (Reeve and Murdoch 1986; R. F. Luck, *personal communication*).

The correlation between the mean percentage of *A. melinus* of each agroecosystem with the more significant weather parameters was performed using the Pearson product-moment correlation coefficient. Within each matrix the pairwise correlations between variables were calculated. The statistical significance of these correlations was assessed using standardized tables.

Differences in the percentage of *A. melinus* between the orchards of the five agroecosystems were analyzed using one-way analysis of variance (ANOVA); differences between the three years were analyzed using two-way ANOVA, with year and agroecosystem as main factors. Comparison between captures of CRS males and the percentage of *A. melinus*, comparison of different types of traps, and the influence of the season of the year on *A. melinus* sex ratio were analyzed using one-way ANOVA. Means were compared using Fisher's LSD test. Data on the percentages were arcsine square-

² (<http://estaciones.ivia.es/>)

³ (<http://www.agricultura.gva.es/rvfc/index.htm>)



PLATE 1. Adult of *Aphytis melinus* palpating with its antenna (drumming phase) on a young female stage of California red scale attached to a twig of a citrus tree. This is a recognition process of the scale prior to oviposition. Photo credit: J. J. Sorribas.

root-transformed before ANOVA to stabilize the variance. Statistical analyses were performed using the Statgraphics 5.1 program (Statgraphics 2000).

RESULTS

The two ectoparasitoid species are present together in most of the citrus orchards with California red scale. *Aphytis melinus* was present in most samples, showing the successful establishment and widespread dispersion of this species in the Valencia Region 30 years after its introduction. A total of 21 276 parasitoids were identified from trap captures and emerging from plant material, 51% belonged to *Aphytis melinus* and 47% to *Aphytis chrysomphali*. The presence and establishment of the endoparasitoid *Encarsia perniciosi* (Tower) was observed in a small humid valley of La Marina County (Area 4). The 503 specimens of *E. perniciosi* captured represent only 2% of the total number of parasitoids but 13% of the parasitoids captured in this area, where it was present in most of the samples. *Aphytis lingnanensis*, not previously documented in Spain as naturally occurring on *A. aurantii*, was also found (107 insects) in two neighboring orchards of Area 4. These orchards were very close to the point where a release of *A. lingnanensis* was carried out in 1995 (Verdú and Pina 2007). No other *A. lingnanensis* specimens were captured out of these orchards.

Spatial distribution

There are slight climatic differences in the five areas sampled. Average air temperatures increase from north to south. Areas 4 and 5 have higher minimum temperatures and Area 5 is the most arid. Rainfall is

higher in Areas 3 and 4. Average winter temperatures stay around 10°C in Areas 1–3 but reach higher than 11°C in Areas 4 and 5. In Areas 1–3 the number of days per year with average temperatures <10°C is also higher (54.7–58.4, respectively) than in Areas 4 and 5 (36.8 and 34.7).

The mean relative percentage of *A. melinus* for each area (Areas 1–5) was 24%, 39%, 48%, 67% (in relation to *A. chrysomphali*), and 95%, respectively (Fig. 2). Area 4, in which *A. lingnanensis* and *E. perniciosi* appear, exhibits semitropical conditions with much lower number of days with temperatures <10°C. The correlation between the mean percentages of *A. melinus* of each agroecosystem with the weather parameters is shown in Table 1 together with the more significant weather parameters.

Aphytis melinus has almost completely displaced the native *A. chrysomphali* from the south of the Valencia Region (Area 5), but both *Aphytis* species coexist in different proportions in all other citrus ecosystems. The relative proportion of *A. melinus* increases progressively from Area 1 (northernmost of the five agroecosystems) to Area 5 showing a statistical correlation between the percentage of *A. melinus* in the orchards belonging to each area and the mean temperature of the area ($F_{4,168} = 30.90$, $P < 0.0001$). The mean overall temperature of each agroecosystem presented the better Pearson correlation coefficient of the weather parameters analyzed ($r = 0.97$). In some orchards in Areas 1 and 2 the percentage of *A. chrysomphali* reaches >90% (Fig. 1A). No significant changes on *Aphytis* proportions for each area between the years were observed when we compared the three years (2005, 2006, and 2007) in

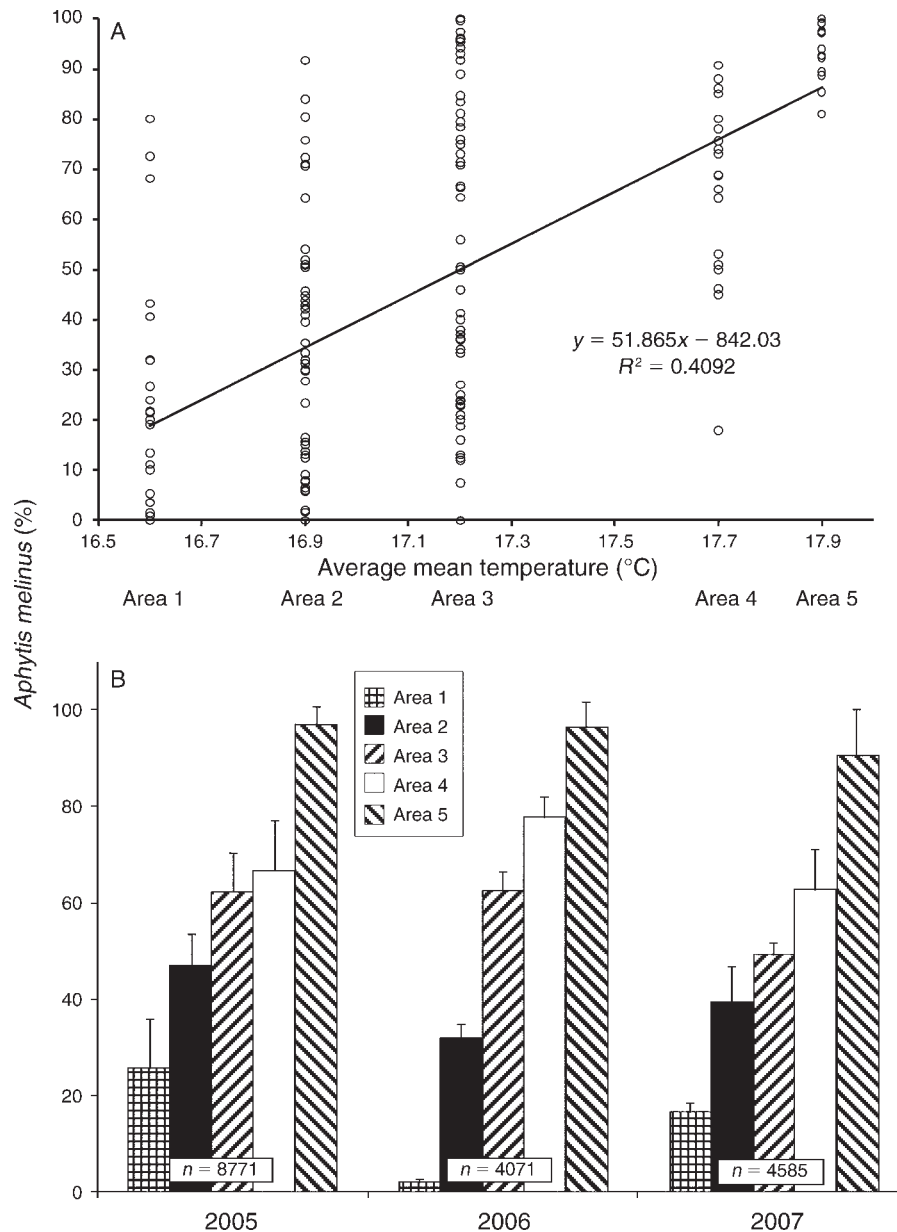


FIG. 1. Distribution of the percentage of *A. melinus* for the five areas into which Valencia citrus surface is divided (see *Materials and methods: Study area*) (A) in each orchard (the average mean temperature of each area is also indicated) and (B) for each year (average and SE; only full-sampled years are represented). Sampling methods were field traps and rearing cages with plant material. The differences are significant between areas ($P < 0.0001$) and not significant between years. We considered only the 173 orchards in which >10 *Aphytis* were captured.

which samples were collected. Thus the differences in the percentage of *A. melinus* between the areas remained constant for the three years (two-way ANOVA; $F_{2,14} = 1.00$, $P = 0.409$ for years; $F_{4,14} = 47.82$, $P < 0.0001$ for agroecosystem; Fig. 1B).

Seasonal abundance

The field traps show almost no captures of parasitoids during January and February and steadily increasing *Aphytis* captures from March, reaching maximum levels

in August for *A. melinus* and in October for *A. chrysomphali*. Captures of *A. aurantii* adult males show two main peaks, in June–July and September (Fig. 3A). For the rearing cages the analysis of seasonal changes in *Aphytis* abundance and species composition throughout the year was carried out in branchlet samples, as this is a substrate where citrus red scale populations are present all the year round. In this case, captures are observed throughout the year, reaching a peak in August for *A. melinus* and in November for *A. chrysomphali* (Fig. 3B).

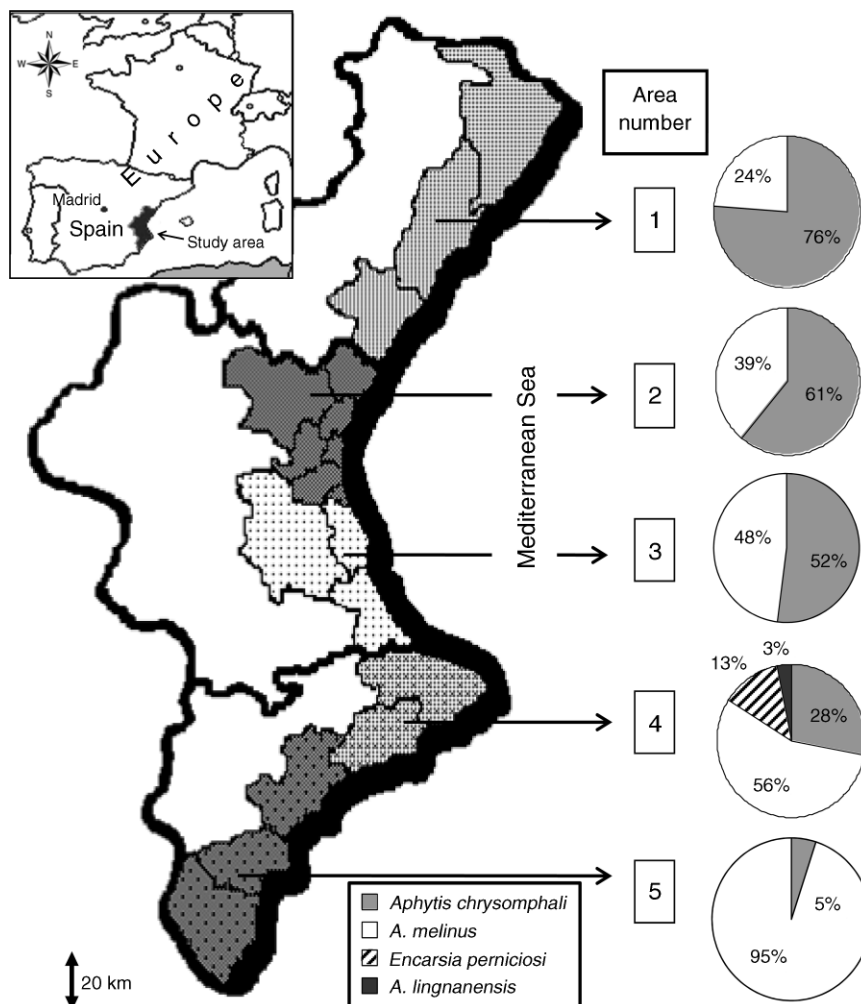


FIG. 2. Relative percentage of *Aonidiella aurantii* parasitoids in five areas (see *Materials and methods: Study area*), which includes all citrus acreage of Valencia Region, eastern Spain. The sampling period was 2004–2008. Lines inside shaded areas delimit counties.

Overall, the total data from field traps and rearing cages show that the relative proportion of *Aphytis* species varied throughout year, *Aphytis chrysomphali* being more abundant during the cooler periods of the year (late autumn and winter) and *A. melinus* predominant during the summer (Fig. 4).

Both *Aphytis* species were present in most of the groves sampled and those that contained only one species of parasitoid were rare. When the two species of *Aphytis* are present in the same orchard, our observations show that their monthly relative abundance can fluctuate widely throughout the year.

Relationship of CRS–*Aphytis* species

There was a significant relationship ($F_{1,53} = 8.77$, $P = 0.0051$) between the percentage of *A. melinus* in a particular orchard and the level of captures of adult male CRS (an index of the abundance of parasitoid hosts). We found that when the number of males is low

(which means low to moderate infestation levels for *A. aurantii*), most of the parasitoids are *A. melinus*, but when the captures of CRS males are high, both *Aphytis* species are usually present. In the first case the number of captures was <2000 insects per trap and year for most of the samples but in the second case the number of males captured was usually much higher (Fig. 5).

Trap captures and sex ratio

There were differences between types of traps in relation to the number of parasitoids captured ($F_{1,179} = 45.13$, $P < 0.001$). The number of *Aphytis* captured per trap and year on pheromone traps was 32.2 ± 3.9 *Aphytis*/trap (mean \pm SE), much higher than on yellow traps (4.5 ± 0.6 *Aphytis*/trap).

All the *E. perniciosi* specimens captured were females. Most *A. chrysomphali* observed were females; only 48 males (0.5%) were found among 8862 adults identified. The sex ratio (M:F) of *A. melinus* was male-biased in

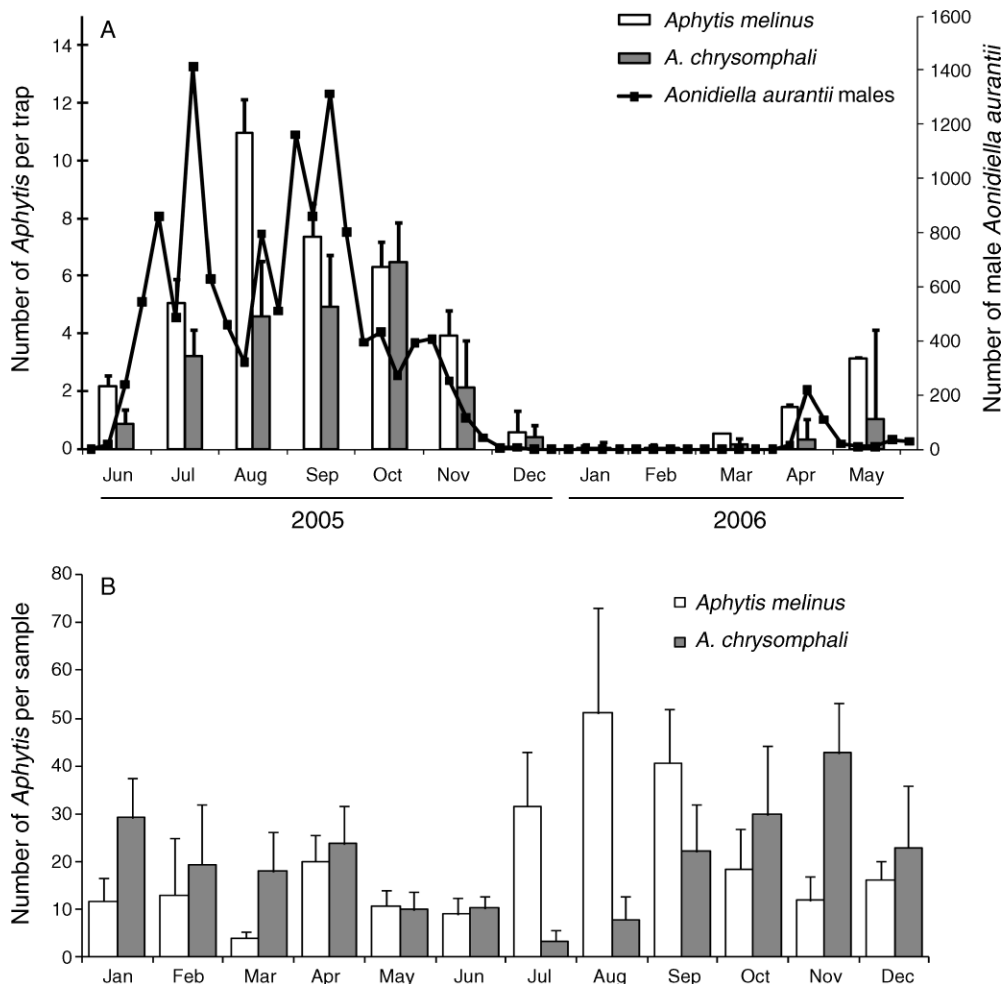


FIG. 3. Monthly average (and SE) captures of *Aphytis melinus* and *A. chrysomphali* along five areas of Valencia Region (see *Materials and methods: Study area*) (A) in traps placed in 60 citrus orchards between June 2005 and May 2006 (weekly captures of males of *Aonidiella aurantii* are represented by the line) and (B) in rearing cages from samples of branchlets during the period 2004–2007.

most of the samples. The percentage of *A. melinus* males in the field traps was 79%, but data from the rearing cages indicate the percentage of males at 56%. A seasonal analysis of the sex ratio of *A. melinus* in rearing cages showed that it was lower in spring and summer, with values approaching 53% and increased significantly to 64% in the winter months ($F_{3,78} = 1.8, P = 0.16$), while autumn gave intermediate values (Table 2).

DISCUSSION

Early research on CRS parasitoids in the Mediterranean area showed that the native *A. chrysomphali*, which was the most widespread and important species during the first half of the 20th century, had been displaced from most citrus-producing areas after the introduction of *A. melinus* in the early 1960s, which increasingly spread from the east of the Mediterranean basin to the west. This confirms *A. melinus* as the better competitor and corroborates previous displacement of

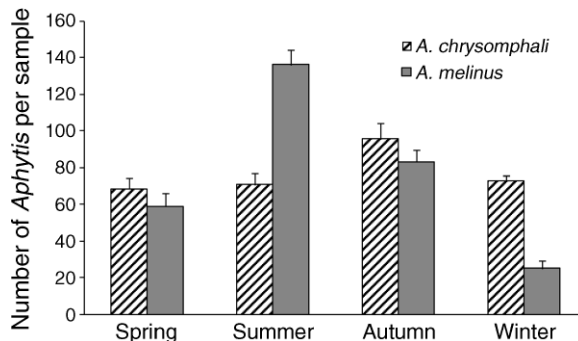


FIG. 4. Influence of season of the year on abundance of *Aphytis* species. Data are from field traps and rearing cages (fruits and branchlets) in 173 orchards sampled throughout Valencia Region (Spain) between 2004 and 2008. Values are averages and SE.

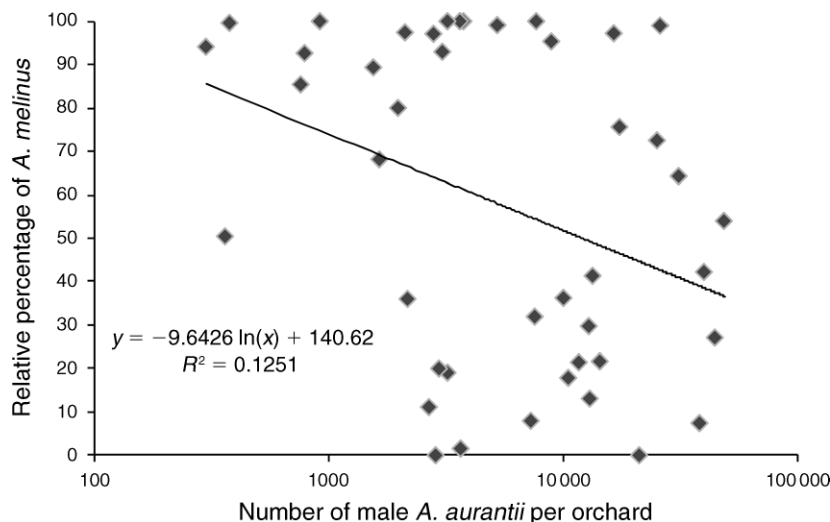


FIG. 5. Relationship between total number of males of *Aonidiella aurantii* per orchard and year and the percentage of *A. melinus*/total *Aphytis* in the orchard. Insects were captured on field traps in 60 citrus orchards distributed throughout Valencia Region during the period June 2005–May 2006 (we considered only orchards in which >300 CRS males or >20 *Aphytis* were captured per year).

other *Aphytis* species found in the United States. This may be the reason why coexistence mechanisms between *A. melinus* and *A. chrysomphali* had not been previously studied. However, our results show that the replacement of *A. chrysomphali* by *A. melinus* has not occurred in eastern Spain. This is possibly the only large citrus area where, a long time after the introduction of *A. melinus*, *A. chrysomphali* remains present in large numbers. If we compare the fast adaptation and establishment of *A. melinus* and the subsequent displacement of *A. chrysomphali* in citrus areas like California, Greece, or Sicily (DeBach and Sundby 1963, Argyriou 1974, Siscaro et al. 1999), with the long period of time since *A. melinus* was released in eastern Spain, there are apparently factors in this area which prevent the displacement of *A. chrysomphali* and allow the coexistence of both parasitoids. The mechanisms that explain this coexistence can be found through the combination of previous literature on biological adaptations to temperature of the two *Aphytis* species and the spatiotemporal variation of *Aphytis* abundance related to weather conditions we have found in the field.

CRS is a relatively recent pest in eastern Spain, and it could be argued that the process of displacement of *A. chrysomphali* by *A. melinus* has not yet concluded. But our observations show a similar percentage of *A. melinus* and *A. chrysomphali* to those reported in previous experimental studies in the same areas (Troncho et al. 1992, Rodrigo et al. 1996, Pina et al. 2003). Also the percentage of *A. melinus* in our results remains constant for the three years sampled. Further proof that *A. melinus* is not expanding with time can be deduced from the fact that the relative abundance of *A. melinus* is no higher in the first area invaded by CRS (late 1980s, Area 3) than in Area 5, where the invasion process has

recently been completed (see Table 1). This suggests that there has not been much change in the relative proportion of both parasitoids in the Valencia area during the last years and the parasitoid population can be considered stabilized.

Valencia citrus acreage shows significant differences in winter and summer temperatures between the cooler north (Areas 1–3) and the warmer south (Areas 4 and 5) areas. The number of days per year with average temperatures <10°C is lower in Areas 4 and 5, where the percentage of *A. melinus* is higher. The temperature of 10°C lies between the thresholds of development for *A. melinus* and *A. chrysomphali*, 8.5°C and 11°C, respectively (Abdelrahman 1974b). The distribution of *Aphytis* species in the Mediterranean coast of Spain apparently follows this climatic pattern, *A. melinus* being the overall predominant species in the hottest and driest Area 5 and *A. chrysomphali* increasing its relative proportion as temperature decreases and/or rainfall increases. There is thus a direct relation between temperature and humidity of one area and the dominant *Aphytis* species. Cooler winter temperatures and not too

TABLE 2. Influence of season of the year on the sex ratio of *Aphytis melinus* in the Valencia Region, eastern Spain.

Season	Number of samples	<i>A. melinus</i> males (%)†
Summer	45	53.6 ^a ± 2.3
Spring	40	52.3 ^a ± 4.2
Autumn	65	57.9 ^{ab} ± 2.1
Winter	47	64.2 ^b ± 4.7

Note: Data are from rearing cages traps (see *Materials and methods: Laboratory experiments*) capturing >20 *A. melinus* during the period 2004–2007.

† Values followed by the same letter do not differ significantly (Fisher LSD test, $P > 0.05$). Error terms are SE.

hot summers are the main differences between Valencia citriculture and other citrus areas where *A. melinus* has totally displaced *A. chrysomphali*. Rochat and Gutierrez (2001) found a similar relation between two parasitoids of the olive scale (*Parlatoria oleae* (Colvée)) that showed how cool regimes were favorable for one species, high temperatures for the other, and both species coexisted at intermediate temperatures.

Kfir and Luck (1984) suggested that susceptibility of *A. chrysomphali* to high temperatures and low relative humidity was probably the main reason why it was replaced by *A. melinus* in California. In the experiments carried out by Kfir and Podoler (1983), total progeny production of *A. melinus* was high at the maximum temperature tested, 32°C, whereas *A. chrysomphali* failed to oviposit at this temperature. In our survey data we found that dry areas with hot summer temperatures are preferred by *A. melinus*, which is able to complete the displacement of *A. chrysomphali*, but areas with mild summer temperatures have a significant abundance of *A. chrysomphali*. In addition, this parasitoid usually appears near coastal or humid zones in Florida, Cyprus, Australia, or Uruguay (Muma 1959, Orphanides 1984, Dahms and Smith 1994, Asplanato and Garcia-Mari 2002) where summer temperatures are milder and humidity higher than in inland areas.

In temperate regions, enforced hibernation during the winter often brings several complications that may prevent the effectiveness of an introduced species (Clausen 1952). Adverse winter temperatures may cause an interrupted period of sufficient length to prevent an otherwise efficient natural enemy from controlling its host as occurred in some areas of California with *A. lingnanensis* (DeBach et al. 1955) due to pupae mortality in winter. Also, it has been experimentally demonstrated that *A. melinus* females held at 15°C for just 24 hours produced only 11 progeny per female as compared with 28 progeny produced at 27°C (DeBach 1969). Cool temperatures during winter in Areas 1–3 are probably responsible for the low *A. melinus* population observed in our data during this season. Our results demonstrate that declining temperatures during autumn and winter have a greater negative effect on *A. melinus* than *A. chrysomphali* because the indigenous *A. chrysomphali* is more cold tolerant and better adapted to these weather conditions. When both parasitoids coexist in the same orchard, *A. melinus* is more abundant during summer and *A. chrysomphali* during winter. This seasonal alternation in parasitoid dominance could be one of the reasons why the more efficient parasitoid *A. melinus* has not completely displaced *A. chrysomphali* in most Valencia citrus orchards.

Another negative effect of cold winter temperatures on *A. melinus* population was the high percentage of males generated (>60%), while lower percentages were observed during spring and summer. Similar results were found in California citrus orchards by Hoffmann and Kennett (1985). As it was assessed by Abdelrahman

(1974a), when cool temperatures prevail, the thelytoky of *A. chrysomphali* might give an advantage over the arrhenotokous *A. melinus* because the former produce female progeny a few hours after emergence, whereas *A. melinus* produces only male progeny until fertilization. Because flying range, males–females encounters, and mating ratio are reduced under these conditions, the progeny will consist of more males than females. *Aphytis melinus* originated in India and is adapted to hot climates, so the cooler winter conditions of Valencia affect negatively its survival, reproduction, and sex ratio.

Excluding Area 5, in most citrus groves both parasitoids coexist most of the year, thus the two parasitoids have a considerable degree of overlap in their niches. However, *A. chrysomphali*, which is smaller in size, utilizes smaller hosts than *A. melinus* to produce progeny because it prefers male scales followed by second instar females, whereas *A. melinus* prefers mainly third instar females (Muma 1959, Forster et al. 1995, Pina et al. 2003, Pekas et al. 2008). When a new generation of CRS starts in spring, the younger host preference and the better cold resistance will give a competitive advantage to *A. chrysomphali* because its feeding resource is available earlier than for *A. melinus*. This lead time allows *A. chrysomphali* to emerge earlier in the year and to build up sufficient densities such that *A. melinus* cannot exclude it. Hence, under some climatic conditions theoretical displacement of *A. chrysomphali* by *A. melinus* is transformed into coexistence due to temporal niche partitioning between both parasitoids. Thus, although a considerable degree of competition between both *Aphytis* species may occur, both species perform in a compensatory manner throughout the year, hot periods being preferred by *A. melinus* and cool periods by *A. chrysomphali*. The combination of both *Aphytis* parasitoids could result in better CRS control because, as suggested by Amarasekare (2000), two natural enemies that coexist via temporal niche partitioning or a dispersal–competition trade-off may provide optimum control of a pest through complementary action. Two of the necessary mechanisms for interspecific competition displacement, higher proportion of female offspring and resource preemption, are not accomplished by *A. melinus* during winter and early spring in temperate regions.

On the other hand, the superior search ability and capacity of dispersion exhibited by *A. melinus* (McLaren 1976, Kfir and Podoler 1983) could explain why we observed a higher relative proportion of *A. melinus* than *A. chrysomphali* in orchards with low scale density but when the scale density was high both *Aphytis* species were present (see Fig. 5).

Humidity is another limiting factor for parasitoid effectiveness; *A. lingnanensis* survives one-third as long at 20% relative humidity as at 80% (Rosen and DeBach 1979). There are big differences in rainfall and humidity between Area 4 and Area 5. This could explain why *E.*

perniciosa is only found in Area 4, which has more rain and where the temperature rarely drops below zero (with an average minimum temperature of 12.8°C it is the only area in Valencia where tropical fruits are grown). This endoparasitoid usually parasitizes CRS in humid or semitropical areas all over the world (DeBach et al. 1971, Furness et al. 1983, Asplanato and Garcia-Marí 2002), but is not common in the Mediterranean. Its spreading to other Mediterranean citrus areas could thus be limited by its climatic requirements and would explain why it has not appeared in other regions of this survey. It is also well known that *A. lingnanensis* needs high relative humidity (Rosen and DeBach 1979, Kfir and Luck 1984), and this could explain why it established around the release point in 1995. However, it is still not clear why it has not expanded to other parts of Area 4.

Aphytis chrysomphali reaches its population peak in October and *A. melinus* in August, before the second male peak of the host *A. aurantii* in September. However, captures of *Aphytis* were very low before the first peak of males of *A. aurantii* in late spring. Consequently, mass releases of *Aphytis* parasitoids in biological control programs should be focused on late spring and early summer, when naturally occurring parasitoids are usually scarce and the scale population is available for parasitism. Releases of new parasitoid species should consider their maximum and minimum temperature threshold and the humidity requirements and be focused on suitable climatic areas.

In conclusion, in contrast with what was widely believed, *A. chrysomphali* is not always displaced after the successful introduction of the better competitor *A. melinus* because they are not strict ecological homologues. Displacement of the former or coexistence of both parasitoids depends on climatic conditions of each agroecosystem: in temperate regions *A. melinus* and *A. chrysomphali* can coexist through temporal niche partitioning that allows the alternation of the predominant species throughout the season and the host sharing between the two *Aphytis* species. Regions with mild summer temperatures and moderate to high relative humidity present the optimal conditions for *A. chrysomphali*; under these circumstances the percentage of *A. chrysomphali* can be similar or higher than the percentage of *A. melinus*. The colonization of new cooler areas in the north by *A. melinus* may be slowed down by its susceptibility to cool temperatures and its low progeny and male-biased sex ratio in winter. We can state that weather changes throughout the season in temperate regions can allow an ecologically inferior parasitoid to coexist in the same habitat with the superior homologue parasitoid due to its different adaptation to cold and hot periods.

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