



Negative effect of global warming on biological control is mitigated by direct competition between sympatric parasitoids



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ABSTRACT

Parasitoids are among the most important and successful groups of natural enemies used in the biological control of insect pests. In most systems, several parasitoid species can parasitize the same pest. The coexistence of parasitoids in agroecosystems and their efficacy as biological control agents may be disrupted by global warming. An increase of approximately 3 °C is predicted by the end of the twenty-first century in the Mediterranean basin (IPCC, 2014). In this context, we compared the present and future performance of two sympatric parasitoids of the genus *Aphytis* (Hymenoptera: Aphelinidae), which control the armoured scale *Aonidiella aurantii* (Hemiptera: Diaspididae) in Mediterranean citrus, either alone or in combination. The net reproductive rate (R0) of the introduced *Aphytis melinus* DeBach was higher than that of its competitor, the native *Aphytis chrysomphali* (Mercet), under current conditions. The two parasitoids responded differently to higher temperature and competition. The R0 of *A. chrysomphali* decreased by 50% when both parasitoids competed in the same patch, but was not affected by the temperature increase. The R0 of *A. melinus* decreased approximately 46% with the increase in temperature because the proportion of females was reduced. However, the presence of *A. chrysomphali* competing in the same patch mitigated the negative effect of the increase in temperature on *A. melinus* (R0 decreased by only 16%). Overall, our results suggest that global warming will have a negative effect on the biological control of *A. aurantii* and that this effect will be higher in areas, such as southern Spain, where *A. melinus* has displaced *A. chrysomphali*.

1. Introduction

Due to global warming, average temperatures have risen by approximately 0.8 °C since the early twentieth century, and a further increase of 3 °C is predicted by the end of the twenty-first century for summer temperatures in the Mediterranean basin (IPCC, 2014). Because insects are ectotherms, their physiology, behaviour and fitness are directly affected by ambient temperature variation (Hance et al., 2007). The impact of global warming is likely to be less predictable in higher trophic levels than in lower trophic levels because the former also depend on the capacity of the lower trophic level to adapt to these changes (Hance et al., 2007; van Baaren et al., 2010). That impact is observed for parasitoids in which immature individuals feed and develop in (endoparasitoids) or on (ectoparasitoids) hosts. Parasitoids are the most important and successful group of natural enemies used in the biological control of insect pests (Godfray, 1994; Jervis, 2005), and their efficacy could be disrupted by changes in environmental

conditions (van Baaren et al., 2010).

An increase in temperature can affect host-parasitoid relationships, mostly because they may have different thermal preferences (developmental or phenological), which can affect the temporal or geographical synchronization of the suitable instar/stage of the host with the adult parasitoids (Hance et al., 2007). For parasitoids, an increase in temperature can affect their morphology (body size, wing size, wing loading), fecundity, longevity, dispersal capacity, metabolism rate, trade-offs between life-history traits, capacity to locate and evaluate host quality and the capacity of the larvae to evade or overcome the host immune response (Hance et al., 2007; Moiroux et al., 2010; Vayssade et al., 2012; Vuarin et al., 2012; van Baaren et al., 2010). Indeed, an increase in temperature may induce a number of physiological changes, the cost of which may be expressed by a reduction in reproductive output, decrease in growth of immature stages and in lifespan and/or changes in mating behaviour (Angilletta, 2009; Hance et al., 2007; Omer et al., 1996; Režucha et al., 2010). Understanding

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these characteristics is crucial for using parasitoids as biological control agents.

Because of interspecific differences in thermal responses among parasitoid species (Berg et al., 2010), global warming can also have a major influence on interspecific competition between species (Northfield and Ives, 2013). As such, global warming will have consequences for parasitoid species distributions, community compositions, and ecosystem services, i.e., biological control (Bale et al., 2002; Hance et al., 2007; Northfield and Ives, 2013; Tougeron et al., 2017).

In this context, we investigated the influence of the expected temperature increase on the efficacy and competition of parasitoids of the genus *Aphytis* (Hymenoptera: Aphelinidae), which are the most successful and widespread biological control agents of *Aonidiella aurantii* (Hemiptera: Diaspididae) in citrus (DeBach and Rosen, 1991; Forster and Luck, 1996; Murdoch et al., 2005; Pekas et al., 2016). These specialist parasitoids can reduce their shared host to levels nearly 200 times below the average density observed in their absence (DeBach et al., 1971), suggesting strong resource competition between parasitoid species because they parasitized the same host stages and niches (Borer et al., 2004; Pekas et al., 2016). Species of the genus *Aphytis* represent one of the best-known cases of competitive displacement in insects (Luck et al., 1982; Luck and Nunney, 1999; Luck and Podoler, 1985; Pekas et al., 2016; Sorribas et al., 2010). In the Mediterranean basin, *A. aurantii* became a key citrus pest at the end of the last century, and it was rapidly parasitized by the native parasitoid *Aphytis chrysomphali* (Mercet). Later, its coevolved parasitoid *Aphytis melinus* DeBach was introduced into a classical biological control programme, and it has displaced *A. chrysomphali* in some areas, whereas both species coexist in others (Boyero et al., 2014; Sorribas et al., 2010). Both parasitoids are present in the field from February to November showing higher parasitism levels between August and November (highest in September) and lower in February and March (Pekas et al., 2010). Although *A. chrysomphali* reproduces parthenogenetically and produces only females (Pina, 2007; Cebolla et al., 2017a,b), *A. melinus* is considered to be a superior competitor in the field because it has a higher capacity for dispersion (McLaren, 1976) and is better adapted to dry and hot climates where citrus is cultivated (Abdelrahman, 1974a; Rosen and DeBach, 1979). Consequently, 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. This alteration 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 (Sorribas et al., 2010). Therefore, we hypothesize that the superiority of *A. melinus* will be accentuated when the temperature increases due to global warming, possibly leading to the extinction of the weaker competitor. To test this hypothesis, we performed laboratory experiments to evaluate how the increase in temperature in summer, when *A. chrysomphali* is a weaker competitor, will affect i) the fecundity and parasitism rate of both parasitoids when they exploit hosts alone or in competition and ii) the influence of temperature and competition on their efficacy as the biological control of *A. aurantii* by comparing their net reproductive rates (R0) and host-induced mortality.

2. Materials and methods

2.1. Abiotic conditions and treatments

The climate data used for rearing hosts and parasitoids and for experiments was $26/20 \pm 1^\circ\text{C}$ (day/night) to mimic average summer temperatures in the last fifteen years in the Valencia Region (Moncada meteorological station: <http://riegos.ivia.es/>) and $29/23 \pm 1^\circ\text{C}$ (day/night) to mimic warmer average summer temperatures predicted by the end of the twenty-first century (IPCC, 2014) at $70 \pm 5\%$ RH and. Similarly, the photoperiod was selected to mimic the average number of light-darkness hours in summer months in the Valencia Region

(Moncada meteorological station: <http://riegos.ivia.es/>), this is L:D 12:12.

The experiment consisted of four treatments in the two different abiotic conditions explained above for a total of eight combinations: 1) exploitation of 40 third-instar *A. aurantii* per patch by a single female of *A. melinus* ($n = 42$); 2) exploitation of 40 third-instar *A. aurantii* per patch by a single female of *A. chrysomphali* ($n = 46$); 3) exploitation of 40 third-instar *A. aurantii* per patch by *A. melinus* and *A. chrysomphali* simultaneously ($n = 44$); and 4) 40 third-instar *A. aurantii* (number of replicates = 37).

2.2. Insects

The phytophagous host, *Aonidiella aurantii*, was reared on lemons from a laboratory colony at the Instituto Valenciano de Investigaciones Agrarias, IVIA (Moncada, Valencia, Spain). This colony was initiated in 1999 from scales collected in citrus fields in Alzira (Valencia, Spain) and renewed every 2–3 years with field-collected scales. Approximately 2/3 of the surface of each lemon was covered with red paraffin around the mid-section to retard its desiccation. The red paraffin was prepared with a mixture of 1 kg of paraffin pearls (Parafina USP Perlas; Guinama S.L., Alboraya, Spain) and 1 g of red pigment (Sudan III; Panreac Química S.A., Castellar del Vallés, Spain). The remaining surface (aprox. 24-cm² area) of the lemons was infested by exposing them to gravid female scales of the *A. aurantii* colony for 48 h at $27 \pm 1^\circ\text{C}$ at $70 \pm 5\%$ RH and LD 14:10. Once infested, lemons were kept in climate chambers (SANYO MLR-350; Sanyo, Japan) at the two temperature conditions described above until female scales reached the third nymphal instar (19–25 days), which was later used for rearing the parasitoids and for the experiments (Treatments 2,3 and 4) or until females become gravid (43–50 days) for the fecundity investigation (Treatment 1).

Aphytis melinus and *A. chrysomphali* are facultative gregarious ectoparasitoids (Rosen and DeBach, 1979). Females of both species mature eggs throughout their adult life (synovigenic) and lay between 2 and 6 eggs per day (Heimpel et al., 1997; Casas et al., 2000; Tena et al., 2015). These species are also idiobionts (i.e., the host is paralyzed and arrests development once parasitized) and feed on the haemolymph of hosts which they do not use to lay eggs. Individuals of both species were obtained by exposing third-instar *A. aurantii* on lemons to parasitism by insectary-reared adult wasps. The colonies of *A. melinus* and *A. chrysomphali* were initiated in 2008 and 2013, respectively, from *A. aurantii* scales collected in citrus fields located in the Valencia region (Valencia, Spain). Both colonies are renewed yearly with field-collected parasitoids.

For this experiment, five adults of each species were transferred to rearing cages containing third-instar *A. aurantii* on lemons reared in the two abiotic conditions (described above) and were maintained in climatic chambers at these two abiotic conditions to obtain parasitoids. Between 10 and 12 days later, scales were observed under binoculars and late-stage pupae of both parasitoids were removed from parasitized scales. Pupae were held in crystal vials 8 mm in diameter and 35 mm long tapped with a cotton plug and with a drop of honey on the wall. At emergence, parasitoids were held in these vials for one day to obtain mated females of *A. melinus* [*A. chrysomphali* reproduces parthenogenetically (Gottlieb et al. 1998)]. Next, parasitoids were sexed, and females were isolated in vials (same as above). One *A. aurantii* female was introduced daily to let them feed on the host until they were used 2–3 days later (Heimpel et al. 1997). Vials were stored in a climatic chamber at the two different abiotic conditions until they were used in the experiment (Treatments 2, 3 and 4).

2.3. Experimental microcosm and measures

For all treatments, the experimental microcosm was composed of a polystyrene plastic box (10 × 14 × 14 cm) with a lateral hole

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