Experimental evidence for competitive exclusion of *Myzus persicae nicotianae* by *Myzus persicae* s.s. (Hemiptera: Aphididae) on sweet pepper, *Capsicum annuum* (Solanaceae)

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Abstract. The importance of interspecific competition as a force promoting specialization in phytophagous insects has been long debated. *Myzus persicae* sensu stricto (Hemiptera: Aphididae) is one of the most polyphagous aphids. Its subspecies, *M. persicae nicotianae*, is found mainly on tobacco, although it can survive and reproduce on a relatively wide range of plant species in the laboratory. Since life history traits of these taxa make competitive interactions likely, we hypothesize that asymmetrical competition occurs between *M. p. nicotianae* and *M. persicae* s.s., and accounts for the exclusion of the former when they share a common resource. This hypothesis was tested in laboratory experiments, which examined the population growth of colonies of both taxa coexisting on sweet pepper. A replacement series experiment was set up with both aphid taxa on sweet pepper plants, and the rates of population growth (RPG) evaluated at 5 day intervals for 25 days. *M. p. nicotianae* showed a significantly lower RPG when interacting with *M. persicae* s.s. than when in monotypic colonies, while *M. persicae* s.s. RPG was unaffected by competition. The relative population growth from the second census onwards of *M. persicae* s.s. was consistently higher than that of *M. p. nicotianae*. Finally, the RPG of *M. p. nicotianae* was significantly reduced when the plant was infested with *M. persicae* s.s. The results suggest that the absence of *M. p. nicotianae* from sweet pepper in the field in Chile can be partly explained by competitive exclusion by *M. persicae* s.s.

INTRODUCTION

Competition is defined as a reciprocal negative interaction between individuals in response to interference by one of the competitors, or to the exploitation of limiting shared resources leading to reduction in survival, growth or reproduction of at least some of the competing individuals (Calow, 1999; Chase et al., 2002; Begon et al., 2006). Even though initially the evidence suggested that competition did not occur among phytophagous insects (e.g. Wise, 1981; Strong, 1982), and hence had no significance for insect communities (Lawton & Strong, 1981), extensive reviews by Damman (1993) and Denno et al. (1995), and more recently by Kaplan & Denno (2007), established competition as an important force, as influential as other ecological forces such as predation, in shaping the communities of phytophagous insects. In particular, Denno et al. (1995) concluded that competition is most likely to occur among closely related, introduced, sessile, and aggregative species inhabiting managed environments; moreover, Kaplan & Denno (2007) recently demonstrated that phylogenetic relatedness can influence competition among sap-feeding insects.

Several cases of interspecific competition are reported for phloem feeding insects, particularly aphids (i.e. Inbar et al., 1995; Gianoli, 2000; Petersen & Hunter, 2001; Gonzáles et al., 2002). Among them, bottom-up phenomena in response to previous infestation, i.e. changes in the plant affecting the interacting insects, are reported as a force mediating competition (Petersen & Hunter, 2001; Gonzáles et al., 2002; Kaplan & Denno, 2007).

Myzus persicae sensu stricto (Hemiptera: Aphididae) is described as one of the most polyphagous aphids (Dixon, 1998; Blackman & Eastop, 2000), with *Prunus* spp. (Rosaceae) as its primary host and over 400 species of plants from more than 40 plant families as secondary hosts (Blackman & Eastop, 2000). The tobacco adapted morph of *M. persicae* s.s., currently considered by Eastop & Blackman (2005) as a subspecies, *M. persicae nicotianae*, is found in the field in Chile only on tobacco, *Nicotiana tabacum* L. (Solanaceae). However, laboratory experiments have demonstrated that *M. p. nicotianae* is able to survive and reproduce on species from at least five plant families, with a performance on sweet pepper, *Capsicum annuum* L. (Solanaceae), as good as on tobacco (Semtner et al., 1998; Basoalto et al., unpubl. data), and has been found on non-tobacco host plants in other countries (Clements et al., 2000). Additionally, all putative hosts of *M. p. nicotianae* (Semtner et al., 1998) can be colonized by *M. persicae* s.s., with the exception of *N. tabacum*, on which the latter cannot survive. It is interesting to note that although the tobacco aphid is able to feed on a wide variety of plants, in Chile it infests only tobacco, which cannot be colonized by the generalist *M.*

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persicae s.s. Even though *M. p. nicotianae* prefers tobacco when given a choice of hosts (Margaritopoulos et al., 2005; Vargas et al., 2005), the host preference of the Chilean clone can be affected by previous experience (Troncoso et al., 2005). As these taxa share the features proposed by Denno et al. (1995) as indicative for the possible occurrence of competition among phytophagous insects, i.e., they are closely related taxa (subspecies of the same species), are introduced (both introduced into Chile), aggregate (both form colonies), and inhabit managed systems (both are crop pests), we hypothesize that the generalist *M. persicae* s.s. will outcompete the specialist *M. p. nicotianae* when they are present on a common resource. As in Chile *M. p. nicotianae* is not found on favourable hosts, such as sweet pepper, we hypothesize that the competition is asymmetrical and results in the exclusion of the *M. p. nicotianae*. Replacement series experiments were used to determine the rates of population growth and the competitive ability of colonies of both taxa coexisting on sweet pepper plants. In addition, the rates of population growth of each aphid taxon on sweet pepper plants pre-infested by the other taxon were determined, in order to detect possible indirect competition (bottom-up phenomena) resulting from plant changes due to the previous infestation, which affect the fitness of the taxon that colonizes the host later in the season.

MATERIAL AND METHODS

Aphids, plants and experiments

Aphids of both taxa were collected from parthenogenetic populations in agricultural fields in the neighbourhood of Talca, Chile (*M. persicae* s.s. from sugarbeet, *Beta vulgaris* L. (Chenopodiaceae) and *M. persicae nicotianae* from tobacco, *N. tabacum* cv. BY 64). Clonal characterization of the colonies was done using microsatellite markers (Fuentes-Contreras et al., 2004). In our cultures, morphs of *M. persicae s.s.* are yellow to green and morphs of *M. p. nicotianae* are red, and genotypification indicates that these taxa do not share genotypes (Cabrera-Brandt et al., 2007). This allowed us to visually distinguish the taxa. In order to duplicate the conditions of Chilean populations in the field, a colony of the only clone of *M. persicae nicotianae* present in Chile (Fuentes-Contreras et al., 2004), and a polyclonal colony of *M. persicae s.s.* were reared in the laboratory for several generations on sweet pepper plants in isolated chambers in rooms in which the temperature and photoperiod was controlled (21 ± 1°C; 14L : 10D).

All the experiments were carried out under the same environmental conditions as those used for rearing. Each potted plant, representing one replicate, was isolated individually inside plastic transparent cylinders covered by muslin, and placed randomly inside a room. For all experiments, two month-old sweet pepper plants and adult aphids whose age did not vary by more than 24 h were used. Apterous aphids were used in all direct competition experiments since they are directly responsible for population growth. Alate aphids were only used in the indirect competition experiments, which duplicate the process of colonization of a new plant.

Direct competition

A replacement series design was used to evaluate direct competition between *M. persicae* s.s. and *M. p. nicotianae* (see Harper, 1977; Jolliffe, 2000; Williams & McCarthy, 2001).
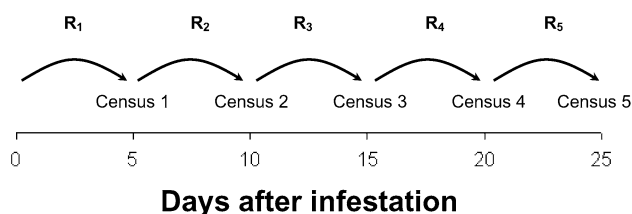

Fig. 1. Experimental design, where R_n represents the successive values of the rates of population growth determined using equation $N_t = N_0 \times R^t$.

Sweet pepper plants were colonised with ten apterous adults randomly placed on the plants, in five treatments, in which the number of individuals of *M. persicae* s.s. and *M. p. nicotianae* were 10/0, 7/3, 5/5, 3/7 and 0/10, respectively. In the controls for each taxon the initial numbers were three, five and seven aphids (N = 12). For treatments that involved both taxa, colonization was simultaneous. Rates of population growth (RPG) were assessed for five inter-census periods (as depicted in Fig. 1) and calculated using the equation, $N_t = N_0 \times RPG^t$, which has been used in other studies on aphid competition (Gianoli, 2000; Petersen & Hunter, 2001). The treatments allowed the construction of performance curves for monotypic colonies and coexistence conditions. In order to compare the performance of monotypic colonies and coexistence levels, a relative performance index was defined for each taxon, using the equation $RPG^{rel}_A = RPG^B_A/RPG_A$, where RPG^B_A is the rate of population growth of taxon A when coexisting with taxon B, and RPG_A is the rate of population growth of monotypic colonies of taxon A (Harper, 1977). Values lower than one indicate that intertaxon competition is greater than intrataxon competition and hence, a reduced competitive ability of taxon A in relation to taxon B. For RPG values, comparisons of data at the intrataxon level were performed using a one-way repeated measures ANCOVA, where the factor was the competition state with two levels, monotypic colonies or coexistence. On the other hand, RPG^{rel} values were compared at the intertaxon level using a one-way repeated measures ANCOVA, where the factor was the taxon with two levels, *M. persicae* s.s. and *M. p. nicotianae*. For both parameters, the initial population sizes, with three levels (three, five and seven individuals per taxon), was the covariate and time (intercensus period) was the repeated measure. Post-hoc comparisons of the relative performances (RPG^{rel}) when the initial population sizes differed were performed using a one-way repeated measures ANOVA followed by Tukey HSD tests. As the RPG^{rel} values for treatments 10/0 and 0/10 were trivial, they were not included in the comparison; RPG values for these two treatments were compared using a one-way repeated measures ANOVA.

Indirect competition

To evaluate the effect of previous infestation of sweet pepper plants on aphid performance, 90 day-old plants were infested with six apterous adults of either *M. persicae* s.s. or *M. p. nicotianae*. Thirty days later, two treatments were set up with aphids left on the plant, or removed from it. Each plant was then infested with three similarly aged (to within 24 h) alate adults of the other taxon; alate aphids were used in the second infestation as this morph is responsible for host plant selection, and may respond directly to the effects of previous infestation of the plant. Plants not previously infested were also colonized with both taxa as a control treatment. The aphids were haphazardously placed on the plants in all treatments. Fifteen days later, the number of individuals resulting from the second infestation present on the plant were counted. The rates of population
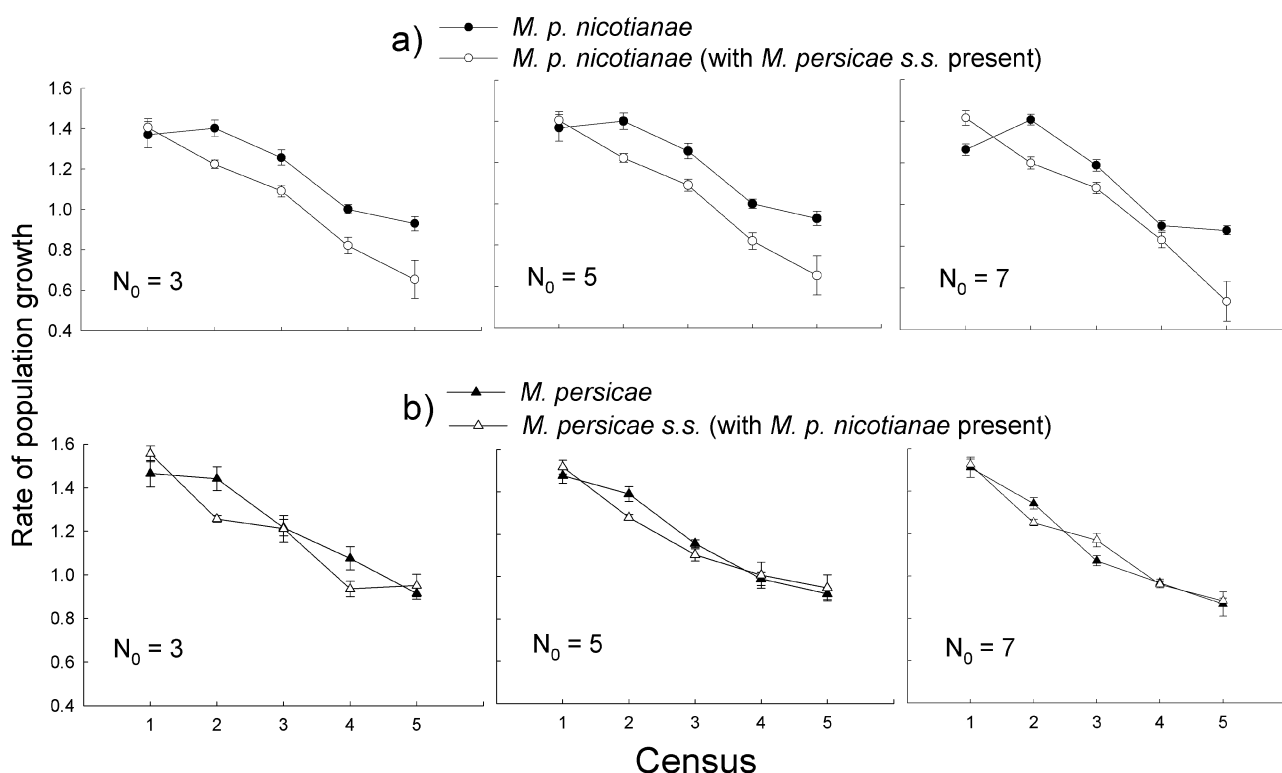
Fig. 2. Rate of population growth during the periods depicted in figure 1 of a) *Myzus persicae nicotianae*, and b) *Myzus persicae* s.s., for the following initial numbers of each respective taxon: $N_0 = 3$, $N_0 = 5$ and $N_0 = 7$. Plots with black dots represent rates of population growth in monotypic colonies and white dots rates of population growth when the other taxon is present.

growth of each taxon in the control and treatments were compared using a Kruskal-Wallis one-way ANOVA on ranks, followed by a Dunn's test for multiple comparisons (N = 15 per treatment).

RESULTS

Direct competition

For *M. p. nicotianae*, there were significant differences in RPG in monotypic and mixed colonies ($F_{1,57} = 42.26$, $P < 0.001$), with time ($F_{4,228} = 13.24$, $P < 0.001$) and for the treatment × time interaction ($F_{4,228} = 12.26$, $P < 0.001$), and only a marginally significant effect of the initial number of aphids on RPG ($F_{1,57} = 3.85$, $P = 0.055$) (Fig 2a). For *M. persicae s.s.*, RPG changed significantly with time ($F_{4,228} = 14.88$, $P < 0.001$), and there was a significant treatment x time interaction ($F_{4,228} = 3.97$, $P < 0.004$), but no significant differences were found between monotypic and mixed colonies. In addition, a significant effect of the initial number of aphids on RPG was found ($F_{1,57} = 10.21$, df = 1, $P = 0.002$) (Fig. 2b).

The relative RPGs of the two taxa differed significantly ($F_{1,57} = 126.64$, $P < 0.001$) and with time ($F_{4,228} = 19.74$, $P < 0.001$). There was a marginally significant effect of the initial number of aphids on the relative RPGs ($F_{4,228} = 2.37$, $P = 0.054$) (Fig. 3). Furthermore, the relative RPG of *M. persicae* s.s. was higher than that of *M. p. nicotianae* from the second census onwards ($P < 0.05$) (Fig. 3).

Values of RPG for *M. p. nicotianae* were significantly lower than those of *M. persicae* s.s. in monotypic colonies ($F = 20.56$, df = 1, $P < 0.001$), with a significant decrease with time in both taxa ($F = 141.08$, df = 4, $P < 0.001$) (Fig. 4).

Indirect competition

Previous infestation by *M. persicae* s.s. significantly reduced the RPG of *M. p. nicotianae* ($H = 29.076$, df = 2, $P < 0.001$), both when the former was left and removed from the plant; no differences were found between the two pre-infestation treatments (Fig. 5a). Previous infestation by *M. p. nicotianae* significantly reduced the RPG of *M. persicae* s.s. ($H = 26.012$, df = 2, $P < 0.001$), only when the former was left on the plant (Fig. 5b).

DISCUSSION

Asymmetric competition between *M. persicae* s.s. and *M. p. nicotianae*, favouring the former, was revealed by the laboratory experiments. The RPG of *M. p. nicotianae* was reduced in the presence of *M. persicae* s.s., and the relative RPG of *M. persicae* s.s. was consistently higher than that of *M. p. nicotianae* from the second census onwards. At the first census, the RPG was higher when both taxa were present than when either taxon was present alone, which resulted in a significant time x treatment interaction in RPG for both taxa.

Population density affects the occurrence of direct competition between aphid taxa on a plant (Bergeson & Messina, 1997). In a one-year field study the populations of *M. persicae* s.s. on sweet pepper were estimated by counting aphids manually dislodged from plants (Quiroz et al., 2005). Although the estimated numbers appear lower than those giving rise to competition in our labora-
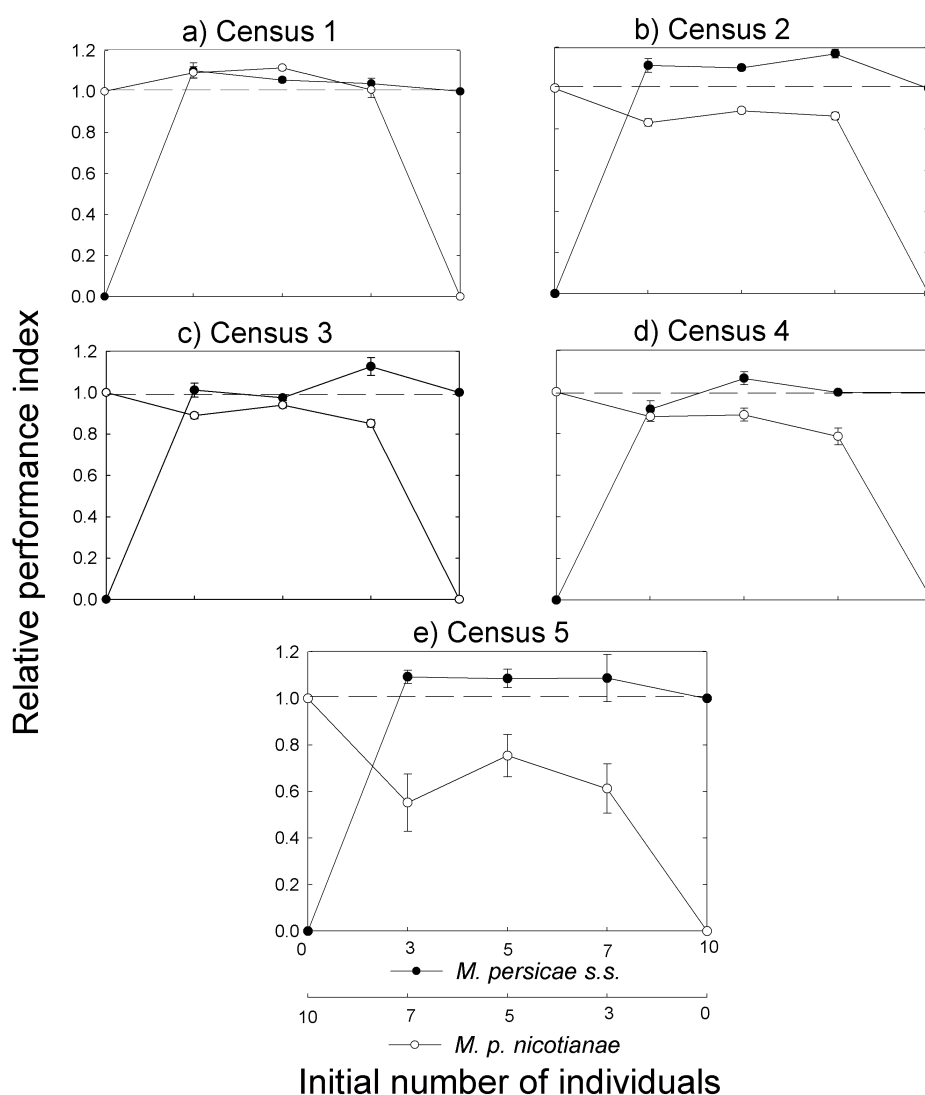
Fig. 3. De Wit curves for relative performance indices of *Myzus persicae* s.s. (black dots) and *Myzus persicae nicotianae* (white dots), in replacement series experiments, at census: a) 1, b) 2, c) 3, d) 4, and e) 5 (see Fig. 1).

tory experiments, differences can partly be explained by the different methods used for estimating aphid abundance. More evidence is required to establish meaningful comparisons between field and experimental densities of *M. persicae* s.s. and *M. p. nicotianae* on sweet pepper.

Several factors can explain the competitive superiority of *M. persicae* s.s. The greater relative performance of *M. persicae* s.s. (Fig. 3) enables it to outcompete by interference competition, resulting in faster physical occupation of the resource, "extraction" of the nutritional components, or utilisation of microhabitats on the host. This is the case in the interaction between *M. persicae* and *Aphis fabae* on sugar beet (Williams et al., 1999), which results in an asymmetric competition favouring *A. fabae*, which has a higher performance than *M. persicae* on sugarbeet.

Competitive superiority can also be achieved by the earlier colonization by one aphid species. This may produce physiological changes in the plant that reduce its quality as a resource. For example, phloem composition may be negatively affected (Olmstead et al., 1997; Petersen & Sandström, 2001), defences selectively delete-

rious for one of the competitors triggered (Moran & Whitham, 1990; Inbar et al., 1999; Messina et al., 2002), phloem flow among plant tissues modified (Inbar et al., 1995), or plant volatile composition changed (Bernasconi et al., 1998). In our system, some changes associated with aphid infestation are conspicuous (for instance, the presence of leaves with chlorotic spots, honeydew, and moulds), but the specific plant changes responsible for the competition observed are unknown. The lower RPG of aphids on previously infested plants may be related to internal modifications of the plant in terms of nutrients or defences or reduced availability of suitable space. In the case of *M. p. nicotianae* colonizing plants already infested with *M. persicae* s.s., the massive presence of individuals of this species and internal modifications of the plant might be acting simultaneously. The numerical effect seems to be the only factor affecting the success of *M. persicae* s.s., which was able to survive and grow similarly on previously infested plants from which the individuals of *M. p. nicotianae* were removed and control plants. Although the identity of the species that first
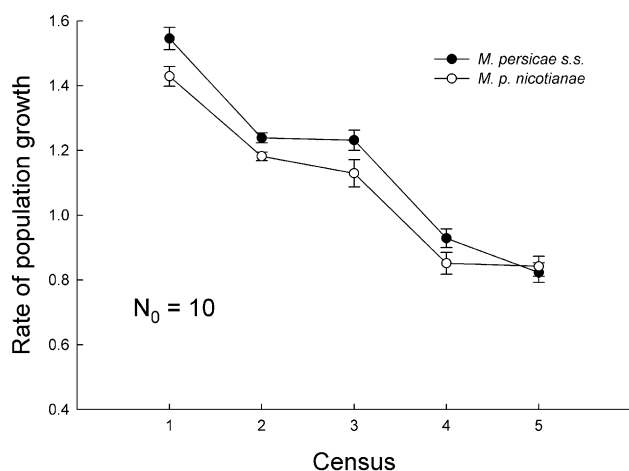
Fig. 4. Rates of population growth during the periods depicted in figure 1, for *Myzus persicae* s.s. (black dots) and *Myzus persicae nicotianae* (white dots), in monotypic colonies, with initial number of aphids $N_0 = 10$.

infests a host plant is important in determining the outcome of a competitive interaction (Dugravot et al., 2007), and an asymmetry in indirect competitive interactions in phytophagous insects is to be expected (Kaplan & Denno, 2007), further experiments are necessary to determine the process underlying the asymmetry of the interaction between *M. persicae* s.s. and *M. p. nicotianae* and the factors that affect it.

Optimal hosts for Chilean clones of *M. p. nicotianae* and *M. persicae* s.s. are tobacco and sweet pepper, respectively (Olivares-Donoso et al., 2007). Thus, these taxa colonize sweet pepper after overwintering in hosts where their reproduction potential is not fully achieved. Differences in the performance of these taxa when transferred from a suboptimal to an optimal host have been reported (Olivares-Donoso et al., 2007). *M. persicae* s.s. reared on a suboptimal host and then transferred to an optimal host (sweet pepper) significantly increased its performance over several generations, while *M. p. nicoti-*

anae did not show a change in performance following a similar host transfer. Hence, when *M. persicae* s.s. migrating from the winter host colonizes sweet pepper in the field, progressively improved performance is to be expected. On the other hand, when *M. p. nicotianae* colonizes sweet pepper, no improvement in performance is expected, and thus, these differences in performance may also increase the competitive advantage of *M. persicae* s.s. over *M. p. nicotianae*.

In general, it is unlikely that a single factor explains patterns of distribution and specialization in phytophagous insects, as has already been pointed out by Bernays and Chapman (1994). It should also be stressed that the competitive phenomenon described may apply only to Chile, where there is a monoclonal asexual line of *M. p. nicotianae*, which is reproductively isolated from *M. persicae* s.s. (Fuentes-Contreras et al., 2004; Cabrera-Brandt et al., 2007). Different outcomes may be expected in other places where crossing between *M. persicae* s.s. and *M. p. nicotianae* may expand the diet breadth of *M. p. nicotianae* and modify some of its life history traits (Margaritopoulos et al., 2002; Nikolakakis et al., 2003).

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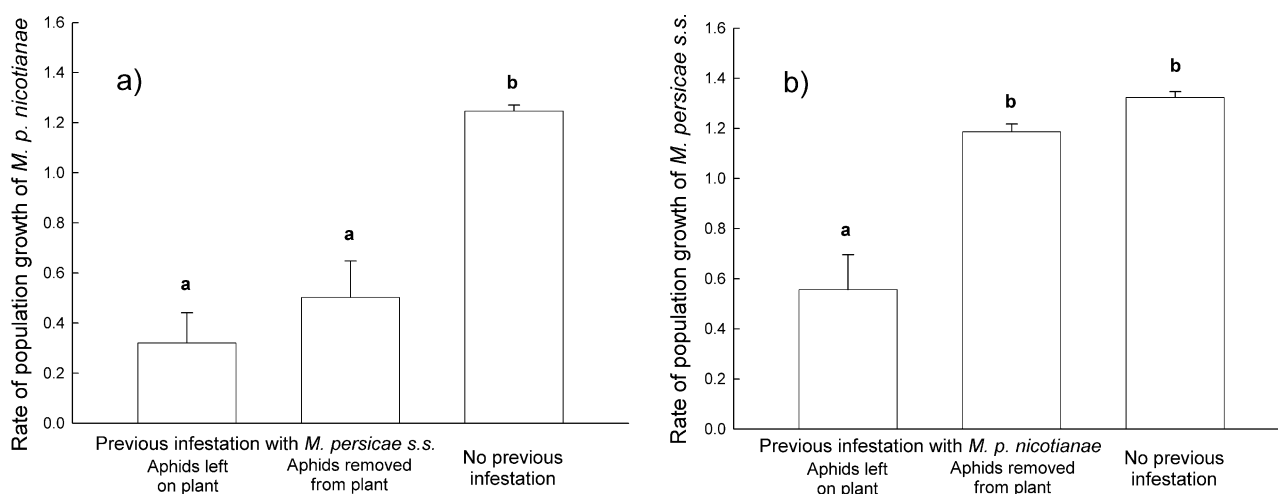

Fig. 5. Rates of population growth of a) *Myzus persicae nicotianae* and b) *M. persicae* s.s. after 15 days growing on plants that were previously exposed to different infestation treatments. Statistical comparisons were performed using a Kruskal-Wallis one-way ANOVA on ranks, followed by a Dunn's test for multiple comparisons. Different letters indicate significant differences.

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