Host plant and natural enemy impact on cereal aphid competition in a seasonal environment

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Competition between phytophagous insects could be mediated by differential impact of natural enemies or by induced changes in host plant quality. The interaction between the aphids *Sipha flava* and *Rhopalosiphum maidis* on the shared host plant, *Sorghum halepense*, was evaluated during the fall and spring seasons in the presence or absence of natural enemies in a garden experiment. During the fall, *S. flava* was negatively affected by *R. maidis* in all treatments. However, during the spring season, *S. flava* was not affected by *R. maidis* when natural enemies were excluded, and positively affected by *R. maidis* with natural enemies present. *Rhopalosiphum maidis* was negatively affected by *S. flava* during the fall and spring seasons under all treatments. Laboratory experiments demonstrated that changes in host plant quality induced by *S. flava* attack and the presence of the parasitoid *Lysiphlebus testaceipes* negatively affected *R. maidis*, but not *S. flava*. Under abiotic conditions simulating fall and spring (lower temperature and daylength in the fall than in the spring), *S. flava* showed lower performance than *R. maidis* under "fall" conditions, and both aphid species showed similar life history traits under "spring" conditions. For *S. flava*, the time to the first reproduction and longevity were longer, and the nymphal production was lower, under "fall" conditions than under "spring" conditions. Our results showed that *S. flava* is benefited when *R. maidis* and the parasitoid *L. testaceipes* are present but the abiotic conditions are not adverse.

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Competitive interactions between herbivores may be mediated by the shared host plant (Fritz et al. 1986, Mopper et al. 1990, Moran and Whitham 1990, Fritz 1992, Denno et al. 1995, Inbar et al. 1995), or by natural enemies (Settle and Wilson 1990, Karban et al. 1994, Bonsall and Hassell 1997, Pallini et al. 1997, Hudson and Greenman 1998). Insect attack may produce changes in host plant quality (e.g., induced defenses, decrease in nutrient concentrations), which often have a negative effect on the inducing insect or on later-colonizing insects (Hanhimäki 1989, Karban 1993, Karban and Baldwin 1997, Denno et al. 2000). Differential susceptibility/resistance of herbivorous insects to natural enemies (Blumberg 1997, Asgari et al. 1998) or preferences of natural enemies for particular insect species (Bonsall and Hassell 1997), may give rise to differential impacts on interacting herbivorous insect populations.

The relative importance of these bottom-up (host plant) and top-down (natural enemy) forces on the interaction between herbivores may change depending on variations in the abiotic setting (Hunter and Price 1992). Thus, abiotic conditions could differentially affect herbivore populations (Waloff 1968, McClure and Price 1975, Valle et al. 1989), thereby changing the relative importance of host plant quality or natural enemies on the final outcome of the interspecific interactions between herbivores.

In this report, we investigated the effect of the shared host plant and the presence of natural enemies on the interspecific interaction between two cereal aphids. *Sipha flava* (Forbes) (Hemiptera: Aphididae) has recently been reported as an introduced aphid in Chile (Gonzáles et al. 1998), colonizing Johnson grass, *Sorghum halepense* (L.) Pers. (Poaceae), a common perennial weed around cultivated areas (McWhorter 1989, Matthei 1995). *Sorghum halepense* is a host plant for other cereal aphids, including *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae) (Brown and Blackman 1988, McWhorter 1989, Nieto-Nafría et al. 1994). Colonies of *S. flava* are located on the bottom part of the plant (Long and Hansley 1972, Holman 1974), where they often induce local production of a reddish pigment, chlorosis, and eventually death of the older leaves (Hayward 1944, Long and Hansley 1972, Breen and Teetes 1986a, b, 1990). In contrast, colonies of *R. maidis* are located on the upper part of the plant, on the younger leaves (Foott 1977, Young and Teetes 1977, Ortega et al. 1980), where they produce no evident plant damage (Young and Teetes 1977). In the area of study (near Santiago, Chile), *Lysiphlebus testaceipes* (Cresson) (Hymenoptera: Braconidae), is the principal parasitoid associated with this aphid–host plant system (Gonzáles et al. 2001).

Although these aphid species show different patterns of within-plant distribution, the possibility of competition cannot be excluded because the two aphids feed from the phloem sap of the host plant (Moran and Whitham 1990, Denno et al. 1995, Inbar et al. 1995, Dixon 1998, Gianoli 2000). We addressed whether: (1) *S. flava* and *R. maidis* show evidence of interspecific competition on the shared host plant, *S. halepense*. In order to find the mechanistic explanation of this interaction, we evaluated: (2) the role of changes in host plant quality produced by the aphid attack, and (3) the effect of a major natural enemy, *L. testaceipes*, on the interaction between these two aphid species. Finally, because the highest population densities of these aphids occur in the fall and spring seasons, we studied: (4) the *S. flava–R. maidis* relationship in an experimental garden during each season, and the effect of abiotic changes (temperature/photoperiod) associated with fall and spring seasons, on some life history traits of these two aphid species.

Materials and methods

Natural history

Sipha flava (yellow sugar cane aphid) is an aphid species that probably originated in the American tropical area (Medina-Gaud et al. 1965, Smith and Cermeli 1979), but its geographical distribution range reaches some temperate areas (Blackman and Eastop 2000). *Rhopalosiphum maidis* (corn leaf aphid) is an aphid with putative Asian origin, with a wide geographical distribution that includes temperate and warm areas (Blackman and Eastop 2000). Both aphid species have parthenogenetic reproduction and show similar host-plant ranges, mainly wild and cultivated Poaceae of the genera *Digitaria*, *Hordeum*, *Paspalum*, *Saccharum*, *Sorghum*, *Triticum*, and *Zea* (Blackman and Eastop 2000).

Lysiphlebus testaceipes is a generalist parasitoid found in different plant–aphid systems, both wild and cultivated (Starý 1993, Starý et al. 1993). It has been extensively used in biological control of pest aphids in agricultural systems (Starý 1987, Starý et al. 1988, Fernandes et al. 1998).

Sorghum halepense is a perennial weed frequently found around several crops (McWhorter 1989). It is a host plant for *S. flava* and *R. maidis* (Nieto-Nafría et al. 1994), as well as for other cereal aphids (e.g. *Schizaphis graminum* (Rondani), *Metopolophium dirhodum* (Walker)).

Insect and plant cultures

Aphids were collected from *S. halepense* growing in fields near Santiago, Chile, and maintained in a greenhouse for several generations on *Hordeum vulgare* L. (Poaceae) seedling ($20 \pm 2°C$, L:D 14:10, 5.7 Klux). *Lysiphlebus testaceipes* was collected from mummies of *S. graminum*, *R. maidis*, and *Aphis* spp. *Sorghum halepense* was grown from field collected seeds.

Experiments

Interspecific competition and exclusion of natural enemies during fall and spring seasons
The reciprocal impact between *S. flava* and *R. maidis* was evaluated considering the influence of natural enemies and season. Isolated six-leaf plants of *S. halepense* (one plant per pot) were infested with adult aphids according to the following treatments: 1) 10 *S. flava*, 2) 10 *R. maidis* and 3) 10 *S. flava* + 10 *R. maidis*, in the presence and absence of natural enemies (six treatments, 11 replicates per treatment). This factorial design was used during two seasons in 1998: fall (April–June) and spring (October–December) in the experimental garden at Universidad de Chile (Santiago, Chile). Aphids were located on the lower part of the stem to allow free plant colonization. Pots (2500 ml) were randomly interspersed at distances less than 50 cm in an experimental garden (48 m²). Porous and transparent plastic cylinders (40 cm × 90 cm, diameter × height, respectively), closed with transparent organdy gauze on the upper part, were used to

isolate each replicate. In the natural enemies treatments, holes were cut in the plastic covers (ca 10×10 cm^2 holes with 40% of plastic cover removed) to allow free access of predators and parasitoids. The activity of natural enemies during the spring season was higher than during the fall season (range: 0–5 and 0–2 parasitoids per experimental aphid colony, respectively, pers. obs. during daytime). Since no phytopathogenic or entomopathogenic fungi were found inside the cages, we presume that no evident microclimatic changes affected the plants or aphids. The number of aphids per plant (measure of population size) was recorded every 4–5 d. At the end of this experiment, the number of aphids walking out of the host plant was lower than 5%, particularly in the exclusion treatments during spring when the population size was higher for each aphid species. Data were ln $(x + 1)$ transformed before the three-factor repeated-measures ANOVA (season: fall/spring, competition: absence/presence of the other aphid species, and natural enemies: absence/presence).

Effect of parasitism by L. testaceipes on the S. flava–R. maidis interaction

To assess the role of the parasitoid *L. testaceipes*, the major natural enemy in this system in our area of study (Gonzáles et al. 2001), on *S. flava–R. maidis* interaction, we repeated the factorial design of the experiment described in the section above, under laboratory conditions (L:D 14:10, $20 \pm 2°C$, 5.7 Klux), this time considering only the parasitoid *L. testaceipes* in the natural enemy treatments (six treatments, six replicates per treatment). In the treatments with parasitoids, one week after the start of the experiment, three mated females of *L. testaceipes* were introduced in each of three consecutive occasions with 3-d intervals, assuring the persistence of parasitoid attack. Aphids were counted 22 d after the start of the experiment, and two-way ANOVA was used to analyse data for each aphid species independently.

Oviposition behaviour of L. testaceipes toward S. flava and/or R. maidis

We evaluated the oviposition behaviour of the parasitoid *L. testaceipes* under laboratory conditions. Groups of 20 aphids of only one species, either *S. flava* or *R. maidis*, feeding on cut leaves of *S. halepense*, were placed in an experimental arena consisting of a Petri plate 6 cm diameter by 2 cm height ($n = 10$ replicates per aphid species). One mated female parasitoid was introduced into the arena and its behaviour was recorded during 16 min. The time to the first stabbing and the number of stabbings were recorded. Similarly, mixed groups of 20 aphids (10 individuals of each species) were exposed to a mated female parasitoid as described above ($n = 12$ replicates). The first aphid species attacked and the number of stabbings to each aphid species were recorded on the mixed groups of aphids, as measures of parasitoid oviposition preference.

Successful development of L. testaceipes in S. flava and R. maidis

To assess the success of parasitism of *L. testaceipes* on each aphid species, fifteen adult aphids (*S. flava* or *R. maidis* separately) were placed on (three- or four-leaf) *S. halepense* seedlings in pots enclosed with a porous plastic bag and exposed to a mated female parasitoid during 24 h (one seedling per pot). After 12 d, the number of mummies was counted as a measure of successful oviposition and subsequent development in a suitable aphid host ($n = 10$ replicates per aphid species).

Effect of previous infestation of S. halepense on S. flava or R. maidis

To examine the effect of plant-mediated aphid-aphid interactions (intra- and interspecific effects), five-leaf seedlings were randomly assigned to the following treatments ($n = 20$ per treatment): 1) infested with *S. flava*, 2) infested with *R. maidis*, and 3) not infested (control). In treatments 1 and 2, each seedling was infested with 15 aphids (second or third instar). The initial number of aphids was constant during the 5-d induction period. After this time, all aphids were removed, and plants were carefully cleaned with distilled water. Twenty-four hours later, half of the seedlings in each treatment (10 seedlings/treatment), were infested with *S. flava* and the other half with *R. maidis* (10 adult aphids/seedling). Eighteen days later, aphids were transferred to ethanol containing vials for later counting. One-way ANOVA was used for comparisons of means for each aphid species.

Effect of abiotic conditions (temperature/photoperiod) on some life history traits of S. flava and R. maidis

We evaluated the time to first reproduction, number of nymphs produced, and longevity of each aphid species on *S. halepense* seedlings in a growth chamber at two temperature/photoperiod conditions simulating the mean climatic conditions during fall and spring: 1) 10°C, L:D 10:14 ("fall") and 2) 20°C, L:D 12:12 ("spring"). Aphids were synchronized within 12 h. In each replicate, a recently born test aphid was placed inside a clip cage (2 cm diameter, 2 cm height) attached to the second or third leaf of a four-leaf seedlings of *S. halepense* ($n = 10$ per treatment). Nymphs produced by the test aphid until its death were counted. Nymphs were removed daily and *S. halepense* seedlings were changed approximately every 10 d. Two-way ANOVA (temperature/photoperiod and aphid species) was used to compare means for each variable of aphid performance.

Results

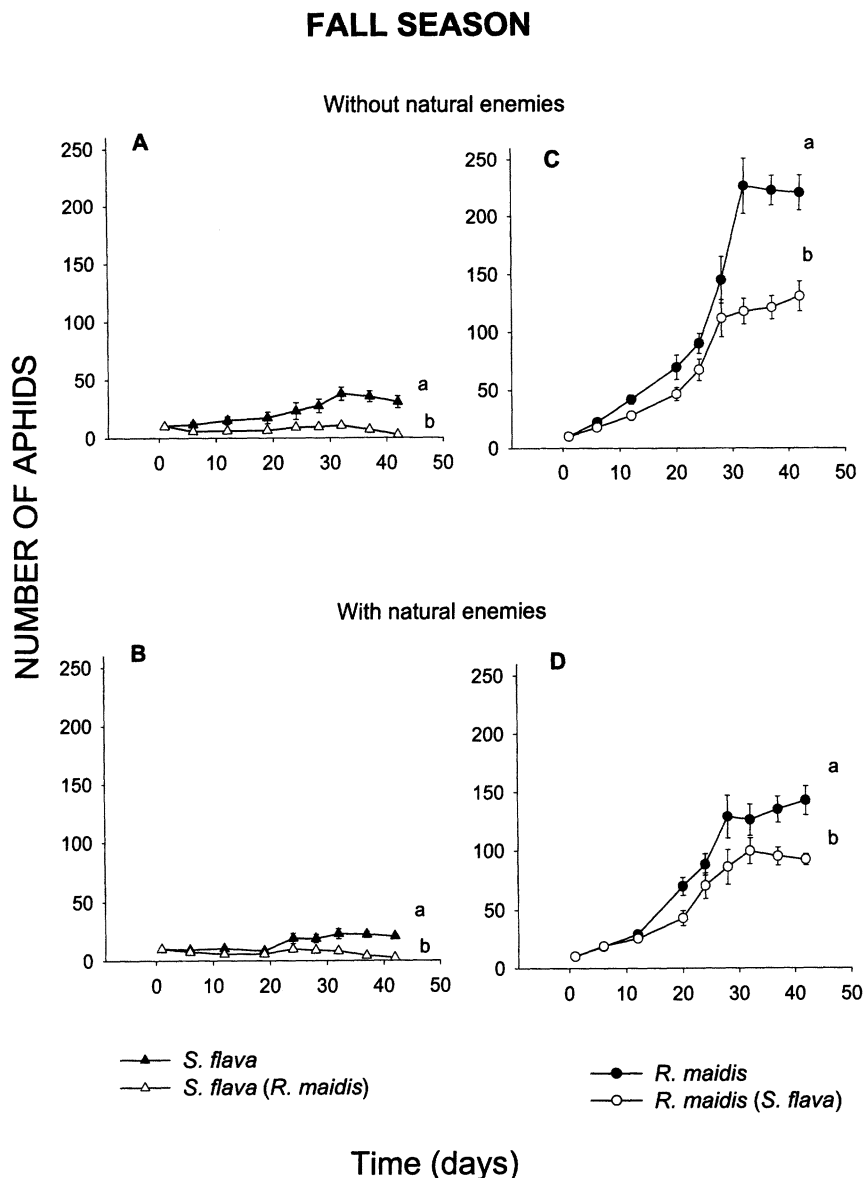## Interspecific competition and exclusion of natural enemies during fall and spring seasons

The population size of the two aphid species was significantly affected by each of the three main factors: season, natural enemies, and competition (three-factor repeated-measures ANOVA, $P < 0.0001$ for each factor). Statistical interactions between pairs of main factors were significant in almost all treatments ($P < 0.023$, except for the *S. flava* season × natural enemies interaction, $P = 0.073$, see Table 1). A significant statistical interaction implies that the effect of one factor on a level depends on another factor. This interaction could express a change in the direction or relative magnitude of the expected effects of the additive combinations of factors (Sokal and Rohlf 1995). In our study, for *S. flava* the outcome of competition with *R. maidis* was affected by season and natural enemies. Thus, signifi-

cant interactions between competition and season and natural enemies like factors (see Table 1), expressed changes in the magnitude and direction of the combinated effects. During the fall, the population size of *S. flava* was reduced by *R. maidis* in all treatments (a posteriori LSD test, $P < 0.001$ in each contrast; Fig. 1A, B), but different results were obtained during the spring, where *S. flava* was not affected by *R. maidis* in the natural enemies exclusion treatment (LSD test, $P = 0.37$; Fig. 2A), and was positively affected by *R. maidis* in the treatments with natural enemies (LSD test, $P < 0.05$, Fig. 2B). On the other hand, the population size of *R. maidis* was negatively affected by *S. flava* under all treatments (LSD test, $P < 0.05$ for every contrast, Fig. 1C, D and Fig. 2C, D). In spite of the statistical interactions between the effect of competition, season, and natural enemies being significant (Table 1), changes in the magnitude of the interacting factors did not affect the outcome of competition for *R. maidis*.

Table 1. Repeated-measures ANOVA on aphid density per plant (*S. flava* and *R. maidis*) for season (fall/spring) and competition treatments, with absence/presence of natural enemies.

Source of variation	df	MS	F	P
S. flava				
Competition	1	25.97	51.12	<0.0001
Season	1	911.30	1793.93	<0.0001
Natural enemies	1	13.85	27.26	<0.0001
Competition × season	1	36.35	71.56	<0.0001
Competition × natural enemies	1	2.75	5.42	0.0225
Season × natural enemies	1	1.68	3.30	0.0731
Competition × season × natural enemies	1	0.24	0.47	0.4955
Error (treatment)	76	0.51		
Time	8	29.07	376.95	<0.0001
Competition × time	8	1.59	20.63	<0.0001
Season × time	8	20.49	265.74	<0.0001
Natural enemies × time	8	1.03	13.33	<0.0001
Competition × season × time	8	2.93	38.07	<0.0001
Competition × natural enemies × time	8	0.11	1.47	0.1647
Season × natural enemies × time	8	0.12	1.51	0.1497
Competition × season × natural enemies × time	8	0.19	2.44	0.0131
Error (individual)	608	0.07		
R. maidis				
Competition	1	40.40	96.04	<0.0001
Season	1	172.08	409.12	<0.0001
Natural enemies	1	16.05	38.15	<0.0001
Competition × season	1	3.81	9.05	0.0036
Competition × natural enemies	1	4.21	10.01	0.0022
Season × natural enemies	1	2.87	6.82	0.0109
Competition × season × natural enemies	1	8.23	19.56	<0.0001
Error (treatment)	76	0.42		
Time	8	93.34	1279.79	<0.0001
Competition × time	8	1.71	23.47	<0.0001
Season × time	8	2.90	39.71	<0.0001
Natural enemies × time	8	1.47	20.12	<0.0001
Competition × season × time	8	0.44	6.07	<0.0001
Competition × natural enemies × time	8	0.17	2.29	<0.0200
Season × natural enemies × time	8	0.40	5.51	<0.0001
Competition × season × natural enemies × time	8	0.20	2.68	0.0067
Error (individual)	608	0.07		

Fig. 1. Population dynamics of *S. flava* and *R. maidis* during the fall season without natural enemies (A and C) and with natural enemies (B and D). In each graph, one species was represented without interaction (filled symbols), and with interaction with the other aphid species (open symbols). Curves followed by different letters are significantly different (a posteriori LSD test, $P < 0.001$).

FALL SEASON

Without natural enemies

With natural enemies

—▲— S. flava
—△— S. flava (R. maidis)

—●— R. maidis
—○— R. maidis (S. flava)

Time (days)

NUMBER OF APHIDS

Effect of parasitism by *L. testaceipes* on the *S. flava–R. maidis* interaction

S. flava population size was affected negatively only when this species was exposed to parasitoids. The other treatments in the factorial experiment did not affect *S. flava* population size (a posteriori Tukey test, $P > 0.05$ for every contrast, Fig. 3a). On the other hand, *R. maidis* population size was reduced by the presence of *S. flava* or the parasitoid, and a stronger reduction was found on the treatment with these combinated factors (*S. flava* plus parasitoid). The population size of *R. maidis* differed among treatments (Table 2, a posteriori Tukey test, $P < 0.05$, for every contrast, Fig. 3b).

Oviposition behavior and developmental success of *L. testaceipes* toward *S. flava* and/or *R. maidis*

The parasitoid showed higher preference and oviposition success on *R. maidis* than on *S. flava*. The time to first attack by *L. testaceipes* to *S. flava* was higher (*S. flava*: 370.7 ± 37.1 s; *R. maidis*: 177.7 ± 33.6 s; $t_{18} = -3.85$, $P < 0.01$), and the number of attacks lower (*S. flava*: 5.5 ± 0.6; *R. maidis*: 37.8 ± 2.6, $t_{18} = 11.9$, $P < 0.0001$) than to *R. maidis*. In the treatment with a mixed group of aphids, *R. maidis* suffered more frequently the first parasitoid attack (10 of 12 replicates; sign test, $Z_{12} = 2.02$, $P < 0.05$), and experienced a higher number of attacks than *S. flava* (36.5 ± 3.07 s

and 2.2 ± 0.6 s; Wilcoxon matched pairs, $Z_{12} = 3.06$, $P < 0.01$). Additionally, *L. testaceipes* showed a higher infection success on *R. maidis* than on *S. flava* ($\bar{x} = 10.6 \pm 0.6$ mummies for *R. maidis*, no mummies for *S. flava*, per initial group of 15 aphids)

Effect of the previous infestation of *S. halepense* on *S. flava* or *R. maidis*

Host plants previously infested by either conspecific or heterospecific aphids did not affect *S. flava* population size (MS = 605.5, $F_{2,30} = 1.42$, $P = 0.258$). However, *R. maidis* population size on *S. halepense* previously infested with heterospecific aphids (*S. flava*) was significantly lower than the control without previous

infestation (Tukey test, $P = 0.04$). No significant difference was found between the number of *R. maidis* in plants previously infested by conspecific aphids (Tukey test, $P = 0.85$), in relation to the control without previous infestation (Table 3).

Effect of abiotic conditions (temperature/photoperiod) on some life history traits of *S. flava* and *R. maidis*

Table 4 shows that for *S. flava* under "fall" conditions, time to first reproduction and longevity were higher, and number of nymphs was lower (Tukey test, $P < 0.001$ for each contrast) than under "spring" condi-
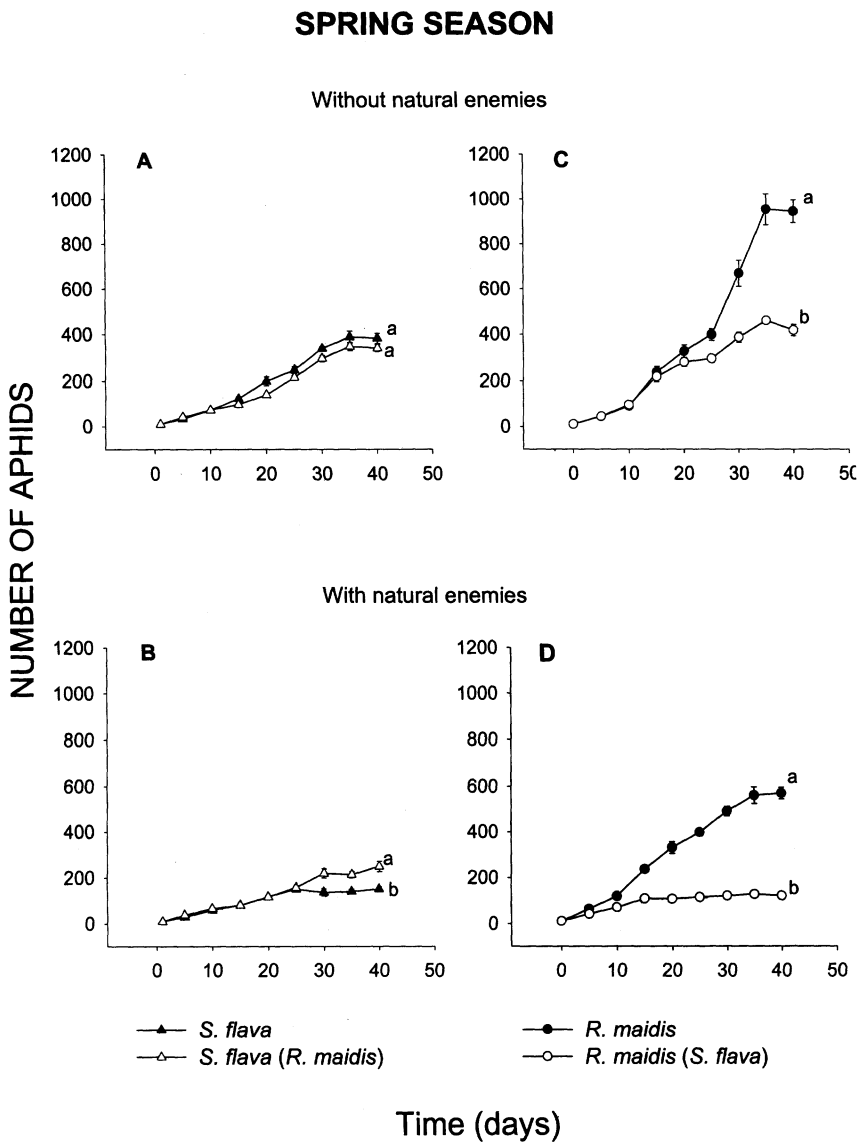

Fig. 2. Population dynamics of *S. flava* and *R. maidis* during the spring season without natural enemies (A and C) and with natural enemies (B and D). In each graph, one species was represented without interaction (filled symbols), and with interaction with the other aphid species (open symbols). Curves followed by different letters are significantly different (a posteriori LSD test, $P < 0.001$).
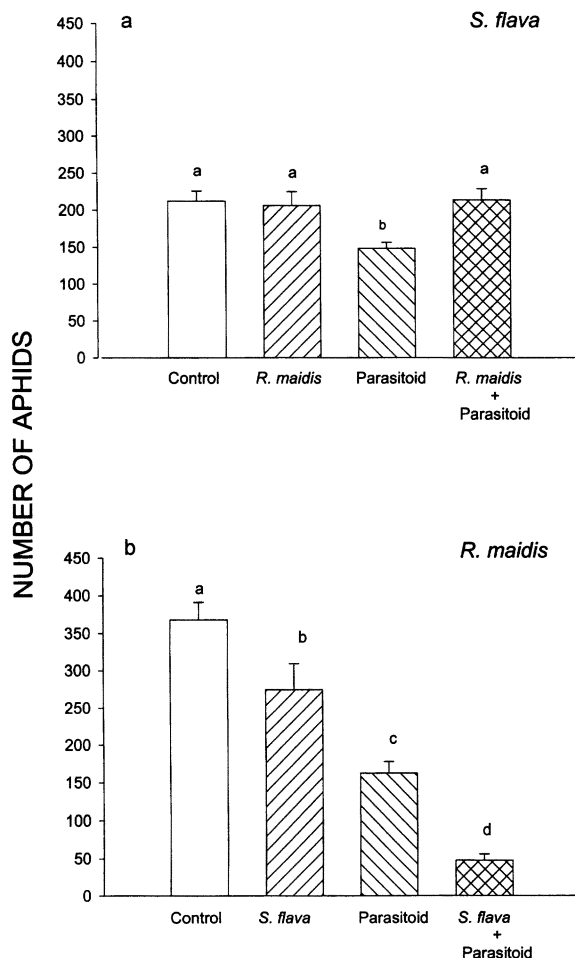
Fig. 3. Effect of parasitoid *L. testaceipes* and of the competitor on populations of (a) *S. flava* and (b) *R. maidis* under laboratory conditions. In each figure, different letters above bars are significantly different (a posteriori Tukey test, $P < 0.05$).

tions. Time to first reproduction and longevity in *R. maidis* under "fall" conditions were higher (Tukey test, $P < 0.001$ for each contrast) than under "spring" conditions; however, the number of nymphs was not significantly different (Tukey test, $P = 0.69$). Under "fall"

Table 2. ANOVA results for the effects of parasitism by *L. testaceipes* on the interaction between *S. flava* and *R. maidis* under laboratory conditions.

	df	MS	F	P
Sipha flava				
R. maidis	1	5251.04	4.14	0.055
Parasitoid	1	4732.04	3.73	0.068
R. maidis × parasitoid	1	7597.04	5.99	0.024
Error	20	1267.84		
Rhopalosiphum maidis				
S. flava	1	65208.37	21.26	<0.001
Parasitoid	1	28058.37	91.51	<0.001
S. flava × parasitoid	1	672.04	0.21	0.645
Error	20	3066.15		

Table 3. Effect of previous infestation of *S. halepense* by *S. flava* or *R. maidis* on aphid population growth. Means within a column followed by different letters are significantly different, ANOVA test ($P < 0.05$). Ten aphids were present at the beginning of the experiment. Mean ± SE ($n = 10$ replicates per treatment).

Treatments	*S. flava* (number of aphids)	*R. maidis* (number of aphids)
Previous infestation by *S. flava*	36.3 ± 5.4 a	58.5 ± 8.3 a
Previous infestation by *R. maidis*	39.9 ± 6.5 a	87.0 ± 12.1 ab
No previous infestation	45.6 ± 8.5 a	94.7 ± 9.2 b

conditions, time to first reproduction and longevity were lower and number of nymphs was higher for *R. maidis* than for *S. flava* (Tukey test, $P < 0.01$ for each contrast). Under "spring" conditions, these parameters did not show significant differences between the two aphid species (Tukey test, $P > 0.10$ for each contrast).

Discussion

The results of our study showed that *S. flava* and *R. maidis* established competitive interactions. The outcome of competition was asymmetrical, as often occurs in interspecific competition between insects (Lawton and Hassell 1981, Denno et al. 1995); interestingly, the direction of outcome was affected by season and natural enemies. Thus, during the fall, the two aphid species were reciprocally and negatively affected by the other species in all treatments (Fig. 1), but *S. flava* was strongly affected by *R. maidis* (Fig. 1A, B). This result may be explained, at least in part, by the lower performance parameters shown by *S. flava* in comparison to *R. maidis* under "fall" conditions (Table 4). These differential responses to environmental conditions between both aphid species may be related to their respective origins: tropical in the case of *S. flava* (Medina-Gaud et al. 1965, Smith and Cermeli 1979), and temperate in the case of *R. maidis* (Blackman and Eastop 2000). Previous reports have shown that low temperature limits the competitive ability of some insects, apparently due to their differential tolerance to temperature changes (Waloff 1968, Valle et al. 1989). This suggests that *S. flava* may experience a physiological constraint in some critical life history traits relevant to fitness during the fall season (Stearns 1992), and under these abiotic conditions this aphid was very susceptible to competitive effect of *R. maidis* in the shared host plant.

During the spring, a strong asymmetrical effect between both aphid species was also found (Fig. 2A, C). While *R. maidis* was negatively affected in all treatments, the consequences for *S. flava* population parameters were different. First, under natural enemies exclusion, *S. flava*

was not affected by interspecific competition. *Sipha flava* achieved higher population sizes in the spring than in the fall (Fig. 2A), which is consistent with better performance in the growth chamber under "spring" conditions than under "fall" conditions (Table 4). Thus, apparently *S. flava* did not experience physiological constraints, being able to increase its population size and overcome the potential adverse effect occasioned by *R. maidis*. Second, under the presence of natural enemies, surprisingly, the population of *S. flava* diverged ca 25 d after the start of the experiment and was higher when *R. maidis* was present (Fig. 2B). This result suggests that the presence of *R. maidis* in the shared host plant somehow diluted the negative effect of natural enemies on *S. flava* population size. Some mechanistic approaches could explain this result. Differential resistance/susceptibility of phytophagous insects to predators and parasitoids, either physiological (Blumberg 1997, Asgari et al. 1998), or behavioral (Losey and Denno 1998a, b, Hatle and Faragher 1998), as well as differences in foraging behavior of natural enemies, or host plant "tritrophic effects" (Carter et al. 1984, Gardner and Dixon 1985, Kareiva and Sahakian 1990, Grevstad and Klepetka 1992, Kauffman and Laroche 1994, Messina et al. 1997, Clark and Messina 1998), may affect natural enemy preference or performance, resulting in differential impact on phytophagous insect populations (Bergeson and Messina 1997).

Our laboratory experiments designed to assess the possible underlying mechanisms showed that parasitoids mediate interspecific interactions between these studied aphids, sustaining the hypothesis that during the spring season *R. maidis* diluted the negative effect of natural enemies (i.e. parasitoids) on *S. flava*, via differential preference and oviposition success of the parasitoid on a particular host herbivore. *Lysiphlebus testaceipes* showed higher attack intensity on *R. maidis* than on *S. flava*, when these aphids were available together. In addition, *L. testaceipes* attacked and disturbed *S. flava* when this aphid was offered alone as potential host, although this parasitoid was not able to successfully oviposit or develop on it. This result agrees with the fact that *S. flava* is not parasitized in the field (Starks and Mirkes 1979, Elliott et al. 1994, Webster et al. 1994). Moreover, previous work has shown that within-plant distribution of *R. maidis* colonies (upper part of the plants) suits well the foraging behavior of *L. testaceipes*, thus increasing the probability of host-parasitoid encounter (Städler and Völkl 1991, Gonzáles et al. 2001). Therefore, the preference of natural enemies for some insect species could result in a differential impact, which facilitates the establishment of a non-preferred species in novel environments (Settle and Wilson 1990).

Induced plant response by herbivory may mediate interspecific competition in insects (Faeth 1992, Hougen-Eitzman and Karban 1995, Denno et al. 2000). Previous evidence suggests that herbivory by some insects affect negatively the fitness of other insect species feeding on the same host plant (Hanhimäki 1989,

Table 4. a. Effect of abiotic conditions on the performance of *S. flava* and *R. maidis* ("fall condition": 10°C, L:D 10:14, and "spring condition": 20°C, L:D 12:12). Means within a column followed by different letters are significantly different, two-way ANOVA test ($P < 0.001$). Mean $\pm$ SE shown.

Treatments	Time to first reproduction (d)	Number of nymphs	Longevity (d)
S. flava (fall)	38.6 ± 1.0 a	18.6 ± 2.3 b	81.3 ± 4.1 a
R. maidis (fall)	19.5 ± 0.4 b	46.2 ± 5.5 a	63.7 ± 4.1 b
S. flava (spring)	9.9 ± 0.3 c	37.1 ± 3.4 a	45.8 ± 2.7 c
R. maidis (spring)	8.1 ± 0.5 c	39.9 ± 4.5 a	37.1 ± 2.2 c

b. ANOVA results for the effects of abiotic conditions on time to first reproduction, number of nymphs, and longevity of *S. flava* and *R. maidis*

	Df	MS	F	P
Time to first reproduction				
Aphid species	1	1114.48	359.19	<0.001
Season	1	4090.21	1318.27	<0.001
Aphid species × season	1	764.62	246.43	<0.001
Error	37	3.10		
Number of nymphs				
Aphid species	1	2182.40	13.82	<0.001
Season	1	347.39	2.20	0.1472
Aphid species × season	1	1451.45	9.19	<0.005
Error	34	157.86		
Longevity				
Aphid species	1	1632.68	16.04	<0.001
Season	1	9166.31	90.07	<0.001
Aphid species × season	1	185.73	1.82	0.1856
Error	34	101.76		

Karban 1993, Karban and Baldwin 1997, Denno et al. 2000). Our results under laboratory conditions showed asymmetrical interspecific effects on previously infested shared host plants. Only *R. maidis* was negatively affected by host plants previously infested by heterospecific aphids (*S. flava*), but the reciprocal effect did not occur (Table 3). The leaves of *S. halepense* attacked by *S. flava* showed a reddish appearance and chlorotic symptoms both in fall and spring seasons (Costa-Arbulú et al. 2001, pers. obs.), such as previously reported for other *Sorghum* host plants (Long and Hansley 1972, Breen and Teetes 1986a); in contrast, no evidence of strong leaf damage by *R. maidis* was found. These results may help explain, at least in part, the negative effect of *S. flava* on *R. maidis* in all treatments (Fig. 1, 2). Thus, it is possible that intensive damage produced by a *S. flava* attack on the bottom part of the plant affects negatively the growth of the host plant, through nutrient translocation (from the senescing plant parts), hence reducing the nutritional value of younger leaves (new plant tissues), where *R. maidis* establishes. Even though we did not evaluate the changes in quality of top and bottom plant parts (e.g. nutritional value, chemical defense) after aphid attacks, asymmetrical impacts on insect populations may be mediated by changes in amino acid composition produced by feeding of different insects on distant plant tissue (Master and Brown 1992).

We should acknowledge that our experimental design lacked a control for the effect of interspecific competition (Bergeson and Messina 1997). Higher number of conspecifics could have produced the same outcome as observed in the heterospecific treatment designed to assess interspecific effect (Underwood 1998). The interspecific effect per se is confounded with differences in initial aphid density. However, our results suggest interspecific interaction because, in the presence of both aphid species located on their natural and different feeding sites, the performance of each of the species was negatively affected by the other (Moran and Whitham 1990, Gianoli 2000).

Our results show that season and natural enemies affect the *S. flava–R. maidis* relationship on *S. halepense*. Under all treatments, *R. maidis* was negatively affected by *S. flava*. Parasitoids and *R. maidis* benefited *S. flava* under favorable abiotic conditions. Furthermore, induced plant response and parasitoids mediate the *S. flava–R. maidis* interaction. Further work should address the possible role of other biotic factors, such as the consequence of other aphid species associated with this host plant, alternative host plants, intraspecific competition, and generalist predators, on this aphid–aphid relationship.

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