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Effects of Plant Stress and Habitat Manipulation on Aphid Control in Greenhouse Sweet Peppers

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Interactions between sweet pepper, aphids, and natural enemies under greenhouses can be modified by management practices. An excess of salinity in the irrigation of sweet pepper, the effect of flowering plants on aphid density, and natural enemy diversity were evaluated. Aphids were more abundant on plants irrigated with high conductivity solutions and on sweet peppers without associated flowering plants. Parasitoids and predators were more diverse and abundant in presence of flowering plants. Greenhouse horticultural management practices that avoid stress conditions by means of appropriate irrigation, and increase local biodiversity with flowering plants, could improve aphid control by enhancing abundance and diversity of natural enemies.

KEYWORDS *Aphididae, saline stress, flowering plants, natural enemies, biodiversity*

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INTRODUCTION

A major challenge for sustainable agricultural systems is to control pests in a way that is economically profitable and environmentally sound. The need for minimizing the release of pesticides to the environment requires a better understanding of plant–pest–natural enemy interactions in order to design adequate management strategies. However, this is particularly difficult in intensive production systems such as those developed under greenhouses where biological control mechanisms are weak and plant growing conditions are not always physiologically appropriate.

Multitrophic interactions between crops and associated plants, herbivores (which under certain conditions can reach pest status), and natural enemies should be considered when selecting strategies to manage pests in agricultural systems. The relative importance of forces that control herbivore populations and community dynamics in the context of multitrophic interactions (Price et al. 1980) was an ecological discussion issue during the 80's and 90's, where bottom-up and top-down forces may affect the whole trophic chain as a cascade effect (Hunter and Price 1992). In recent years, interest in the significance of interactions between the three or four levels that characterize most agroecosystems has been increasing rapidly (Verkerk 2004; Chen et al. 2010).

Pest control techniques based on the manipulation of the upper trophic level (biological control) and the lower one (crop resistance) should complement each other in order to achieve the most valuable combination. Preventive practices in sustainable agriculture should also include the avoidance of stress conditions that may enhance plant susceptibility to insect pests and environmental management for conservation biological control (Ellsworth and Martínez-Carrillo 2001; Naranjo 2001).

Phytophagous insects depend on plants for surviving and are subjected to the outcomes of the interactions between plants and environment. Changes in environmental conditions can modify characteristics of plant palatability for herbivorous insects (Goranson et al. 2004). The plant-stress hypothesis formulated by White (1969, 1984) predicts that environmental stresses on plants decrease plant resistance to insect herbivory by altering plant source-sink resource allocations and foliar chemistry, thus changing food palatability (Huberty and Denno 2004; Joern and Mole 2005). Stress can alter the level of soluble proteins, the concentration of amino acids and the quantity of some critical solutes needed for insect development (Dale 1988; Holtzer et al. 1988; Huberty and Denno 2004). From an agronomic viewpoint, stress is a suboptimal crop growth condition that may be caused by common practices in horticulture, such as irrigation and fertilization in greenhouses, rarely attended as detrimental. Symptoms of stress induced physiological changes are not always evident in plants. Despite the absence of visible symptoms, the altered plant chemistry caused by stress can have profound effects on the quality and suitability of plants as hosts for insects

(Heinrichs 1988), which in turn could cause pest resurgence (Hardin et al. 1995; Slosser et al. 2004) and affect natural enemies. A widely expanded problem of horticultural management in greenhouses is salt stress caused by fertilization through irrigation water. Environmental stresses like salinity and water deficit induce a number of plant responses that modify the plant biochemistry and, thus, the quality and suitability of the plant as a host for insects.

Although natural pest control mechanisms has been lost as consequence of agricultural intensification (Altieri 2000), many agroecosystems have potentially diverse natural enemy communities that may produce biotic regulation mechanisms for pest control (Dennis and Fry 1992; Kromp and Steinberger 1992; Stary and Pike 1999). The management of vegetation patterns to enhance conservation biological control mechanisms, implies an increase in the abundance and diversity of natural enemies, and a negative impact on the herbivores in agroecosystems (Altieri and Whitcomb 1979; van Emden 1995; Ehler 1998; Murphy et al. 1998; Cortesero et al. 2000; Landis et al. 2000; Nicholls and Altieri 2002; Rebek et al. 2005; Wäckers and Fadamiro 2005; Begum et al. 2006). This poses a challenge from an agronomic and ecological perspective that requires a better understanding of relationships among agroecosystem components to manipulate the environment for natural enemies (Baggen and Gurr 1998; Lavandero et al. 2006). Removal or mitigation of adverse factors (i.e., nonselective pesticides), and the provision of resources for natural enemies (i.e., pollen, nectar, other preys and hosts) are desirable practices. Increasing plant diversity by means of the introduction of appropriate flowering plants can be an effective low-cost strategy to improve biological control in greenhouse systems (Polack and Brambilla 2000; Saini et al. 2001).

Horticultural production in the surroundings of Great Buenos Aires (NE Buenos Aires province, Argentina) is a highly intensive activity that comprises an area of approximately 200 ha of sweet pepper crops, *Capsicum annuum* L. (Solanaceae), mostly under greenhouse cultivation, and produces 10,000 tn/year (Ministerio de Asuntos Agrarios [MAA] 2006). The aphids *Myzus persicae* and *Aphis gossypii* (Hemiptera: Aphididae) are key pests of this crop (Polack and Mitidieri 2005a). The green peach aphid, *M. persicae* (Sulzer), is a polyphagous species that can spread virus (Raboudi et al. 2002) and cause indirect damage by producing a fungi complex that grows on aphid honeydew excretions. The fungi covers leaves and fruits with a black sooty mold, decreasing phothosynthetic capacity and diminishing quality and commercial value. The cotton aphid, *A. gossypii* (Glover), is also polyphagous (Capinera 2005). It causes the same kind of damage and transmits the same virus as *M. persicae* on sweet pepper crops (Raboudi et al. 2002).

Many natural enemies have been found in this region, not only on crops but also on wild plants (Carrizo 1995; Bertolaccini 1997; Saini et al. 2001, Paleologos et al. 2008). Particularly, *Aphidius colemani*, *Praon volucre*

(Hymenoptera: Braconidae) and *Aphelinus abdominalis* (Hymenoptera: Aphelinidae) are the main parasitoids of aphids (Polack et al. 2002), and *Chrysoperla externa* (Neuroptera, Crisopidae), *Eriopis connexa*, *Cycloneda sanguinea* and *Scymnus spp.* (Coleoptera, Coccinellidae) and *Allograpta exotica* (Diptera, Sirphidae) are the generalists predators (Saini and Alvarado 2000; Saini et al. 2001). Recommended management of *M. persicae* and *A. gossypii* on sweet pepper in greenhouses of the region combines monitoring nymphs and apterous adults with applications of selective insecticides (Polack and Mitidieri 2005a) based on an economic threshold (Polack et al. 2002). Nevertheless, chemical control with broad-spectrum insecticides is still the most common practice in this area leading to economic (high cost inputs) and environmental problems that make it unsustainable.

Sustainability is a multidimensional concept that includes socioeconomic and nature conservation goals. Interactions between sweet pepper, insect pests and natural enemies under greenhouse conditions may be modified by management practices in order to improve economic advantages for the farmer and increase agrobiodiversity and ecological functions. An appropriate irrigation and an increased local plant biodiversity could improve pest control, through the enhancement of top-down and bottom-up mechanisms. The objective of this research was to study trophic interactions that occur in sweet pepper crops, including two key pests, the aphids *M. persicae* and *A. gossypii,* and their natural enemies in greenhouses of the northeastern Buenos Aires province. First, we considered mechanisms that limit pest populations from the lower trophic level by means of changes in crop conditions produced by stress factors feasible to be managed with agronomic practices. Second, we account for mechanisms that limit pest populations from the upper trophic level through interactions between herbivores and natural enemies, and between plants (crop and associate plants) and natural enemies. The particular aims of this work were: 1) to assess an excess of salinity in the irrigation water of sweet pepper crop, on the performance of *M. persicae*; 2) to evaluate the effect of the association of flowering plants with sweet pepper plants on the abundance and diversity of natural enemies and the consequence on aphid abundance; and 3) to combine the effects of sweet pepper plants irrigated with high salinity water and the presence of flowering plants on the abundance of aphids and the diversity and abundance of natural enemies.

MATERIALS AND METHODS

Sweet Pepper Plants and Aphids

All the experiments were established under greenhouse conditions in San Pedro, Buenos Aires province (34° 41′S, 59° 41′W) in INTA Agricultural

Experimental Station. We used seedlings of a sweet pepper blocky red hybrid, var. Vergasa (Syngenta Seed SA), sowed in expanded polystyrene seedlings, with cells of 90 ml, in a commercial medium for seedlings. An aphid colony of *M. persicae* was reared on sweet pepper plants in a glasshouse, for many generations. New plants were added periodically as the damaged ones were removed.

Experiments

1. Effect of an agronomic practice on sweet pepper aphids

To assess the effect of stress caused by high conductivity irrigation water on the performance of *M. persicae*, an experiment was conducted in a metallic funnel greenhouse of 10 m × 50 m × 3.40 m (width × length × height). Sweet pepper plants were transplanted singly into pots of 10 l of black polyethylene, with a medium composed of 30% perlite and 70% soil from a noncultivated field. The side sprouts were periodically cut before overcoming 15 cm long to lead the plant in the apical sprout by means of a plastic thread. The following treatments were established: 1) Sweet pepper plants irrigated with high conductivity water by adding 50 g/hl NaCl (HC) and 2) control plants irrigated with low conductivity water (C). Both treatments were nutritionally balanced with a basic chemical composition in the irrigation solution of 17.1 g/hl NO_3K, 8.2 g/hl NO_3NH_4, 37.25 cc/hl H_3PO_4, and $pH = 6.3$. Electrical conductivity was 1.17mS/cm for the control and 2.11 mS/cm for HC treatment when the experiment was established. The irrigation system was designed with separate tanks and pumps for each treatment solution. Recharges were made by a caudalimeter to allow the addition of defined volumes with the concentrations of salts required in each treatment. Electrical conductivity was determined by a conductimeter with a 1:2 soil:water suspension, and pH measures were performed by a potentiometer with glass electrode and 1:2.5 soil:water suspension during the experiment. The frequency of irrigation changed according to phenological stages of the crop and meteorological conditions.

Complete randomized blocks along the greenhouse were established with four replications per treatment. Each replicate consisted of a line of 12 pots of sweet pepper plants of which the first and the last plants were discarded. From the remaining 10, 5 plants were used for the survey. Therefore, each treatment was comprised of 20 plants (4 replications × 5 pots). Two additional external lines of pots were used as borders in each replicate.

Plants were inoculated with 8–15 small nymphs/leaf from the *M. persicae* colony, on five marked leaves per plant. Leaves were monitored daily for apterous adult appearance. When detected, two apterous adults per leaf were left as a starting point for the experiment (day 1). At day 4 and day 10 the apterous adult fecundity (mean number of nymphs and adults of the following generation) was measured. The number of nymphs 1 (N_1), nymphs 2 (N_2), nymphs 3 (N_3) and apterous adults (AA) of *M. persicae* were measured for each leaf. Marked leaves with absence of aphids or migration evidence were discarded in the second counting. Mean temperature along the experiment period (April–May) was 22°C (minimum 8.5°C to maximum 35.7°C).

2. INTERACTION BETWEEN PLANTS AND NATURAL ENEMIES: EFFECTS ON APHIDS

To assess the effect of the association of flowering plants with sweet pepper crop on the abundance and diversity of natural enemies, and consequently on the abundance of *M. persicae,* we selected four different species of plants with flowers: fennel, *Foeniculum vulgare* Mill. (Apiaceae); coriander, *Coriandrum sativum* L. (Apiaceae); sow-thistle, *Sonchus oleraceus* L. (Asteraceae) and marigold, *Calendula officinalis* (L.) (Asteraceae). We took into account the following criteria for selection: 1) to produce high amounts of pollen or nectar, 2) to function as insectary plants for natural enemies, 3) to be compatible with the greenhouse environmental conditions under which the sweet pepper grows, 4) not to be host plants of the main pests of the crop, 5) to have an extended period of flowering in coincidence with the crop cycle, and 6) to be easily multiplied. Sweet pepper seedlings were transplanted at November, while the associated plants, a month later. Sow-thistle and marigold started to bloom in December. More than 50% of the plants had flowers by the beginning of January and maintained them until the end of the assay. Coriander flowered in January and fennel in February, and both retained flowers until the end of the experiment.

Three treatments were defined: 1) sweet pepper plants associated with plants with flowers (WF: with flowers), 2) sweet pepper without associated flowering plants (NF: no flowers), and 3) sweet pepper without flowering plants nearby, but with flowers in the same greenhouse (AF: adjacent flowers). We used four metallic bitunnel greenhouses 18 × 25 m; each one divided in four sectors (9 × 12.5 m each). Two of the four greenhouses, had two sectors diagonally opposite with sweet pepper and associated plants (WF); sectors left without flowers in these greenhouses were considered AF (adjacent flowers) treatments. In the other two greenhouses, we planted sweet pepper plants without associated plants (NF), and took two sectors of the same diagonal for sampling. Limited availability of greenhouses required a nonrandomized block design with two replications. Each block consisted of one greenhouse without associated flowers (NF) and one with flowers (WF and AF).

Spontaneously colonizing aphids were sampled according to Protocol of Integrated Pest and Disease Management of Sweet Pepper (Polack and Mitidieri 2005b). Three sweet pepper plants were randomly selected per sector to count the number of aphid nymphs, apterous adults and aphid mummies on the lower face of four randomly selected leaves in the medium stratum of the plant. Mummies were identified as different species of aphid parasitoids. The cumulative abundance of apterous aphids was expressed as cumulative aphid-days (CAD) calculated by using the procedures of Hanafi et al. (1989). Parasitized aphid percentage was estimated by replacing aphids with aphid mummies and calculating the cumulative abundance of mummies. From the transplanting of the associated plants, aphids and mummies were monitored weekly.

In addition to the aphid sampling previously mentioned modified Malaise traps were used simultaneously for sampling flying natural enemies and aphids. Traps were metallic pyramidal structures, with 40 cm of side square base by 32 cm in height, covered by fabric of voile. In the top, a metallic ring supported a glass Portici trap with ethanol 70%. From the cross of the pyramidal base, a translucent plastic strip hung to the soil in order to intercept flying insects, which climbed up until reaching the glass trap. We placed a total of 36 traps, three per sector, at a height of 170 cm among the sweet pepper plants. Traps remained exposed for 14 days. After that period their contents were conserved in glass bottles containing ethanol 70% and were taken to the laboratory. A binocular microscope, taxonomic keys and guides (Ceballos 1941, DeBach 1964; Saini 1985) were used to identify species and count aphids and natural enemies found in samples. To assess density dependent mortality of aphids in each treatment, regressions of the mean number of coccinellids/trap on mean number of aphids/trap were performed. Alpha diversity was measured by species richness (S) (total number of species) and Shannon-Wiener index of diversity (H′) of predators and parasitoids of *M. persicae* (Moreno 2001).

3. Integration of an agronomic practice and plant diversity

Interactions between trophic levels were studied by assembling both effects described above: sweet pepper plants under salinity stress associated with flowering plants, and evaluating the outcome of this combination on aphids and natural enemies. The experiment was conducted during autumn and winter under similar greenhouse conditions. Additionally, the cultivation procedure used the same pots, irrigation system, and irrigation solutions. The pots watered with the HC solution, had already been irrigated in the previous trial. Sweet pepper plants were transplanted at the beginning of May. Sow-thistle, coriander and marigold plants flowered from the establishment of the experiment. With the exception of coriander, sow-thistle, and marigold maintained the flowers until the end. Fennel did not bloom at that time of the year. Average temperature along the trial was 21°C (mean minimum of 8.3°C to mean maximum of 33.7°C).

Treatments were defined by the irrigation water (with low or high conductivity) and the presence or absence of associate plants with flowers as follows: 1) low conductivity water without associate flowers (C), 2) low conductivity water with associate flowers (C-F), 3) high conductivity water without associate flowers (HC), and 4) high conductivity water with associate flowers (HC-F). All treatments had a nutritional balance of NPK. The experiment was a complete randomized block design with four replications per treatment. Sweet pepper pots were distributed in four blocks along the greenhouse; each one with two double lines of pots, with 6 m between them. An extra line of sweet pepper was placed in the middle of the double lines, in order to increase aphid inoculum. Within each block there were four replicates of eight pots. In treatments with associate flowering plants four pots (13 × 43 × 12 cm; width × length × depth) each one with one of the four flowering species (coriander, fennel, sow-thistle and marigold) were placed between two lines of sweet pepper.

Naturally infested plants (twelve per treatment and three per replicate) with *M. persicae* and *A. gossypii* were monitored weekly according to Polack and Mitidieri (2005b). The number of nymphs, apterous adults, and mummies in the lower face of four randomly selected leaves in the medium stratum of each sampled plant were counted.

Statistical Analysis

Data were analyzed using analysis of variance (ANOVA) and Duncan test ($p < 0.05$) to detect differences between treatments (Zar 1999). Values were transformed to logarithm and percentages to arcsin $\sqrt{x}$ for data normalization and homocedasticity assumptions. Differences between pairs of H' diversity values were measured with t test (Moreno 2001). We used ANOVA of repeated measures when sample dates were analyzed simultaneously and two-way ANOVA of repeated measures when high conductivity irrigation and presence of flowers were evaluated as different factors through time. The relationship between percentage of parasitism and the number of aphids were determined by linear regression, and differences between slopes were compared by confidence intervals.

RESULTS

1. Effect of an Agronomic Practice on Sweet Pepper Aphids

Significant differences were found among irrigation treatments for the specific electric conductivity (ANOVA: $F = 31.19$, $df = 1, 6$, $p = 0.0014$); it was higher in pots irrigated with the HC solution than in the other treatments (Table 1) at the beginning of the assay. No differences were found in pH

TABLE 1 Mean ± SE Soil Traits After Irrigation, in Sweet Pepper Pots at the Beginning of the Assay (Comparisons are within a column; values followed by the same letter are not significantly different at $p > 0.05$. HC: high conductivity.)

Treatment	Conductivity (mS/cm)	pH
HC	6.95 ± 0.91 a	6.81 ± 0.07 a
Control	1.75 ± 0.58 b	6.86 ± 0.13 a

measurements (ANOVA: $F = 0.25$, $df = 1, 6$, $p = 0.63$) between treatments (Table 1).

When *M. persicae* performance was analyzed nonsignificant differences were found in the number of N_1/leaf (ANOVA: $F = 3.08$; $df = 1, 106$; $p = 0.08$) between treatments in the first sample (day 4), although there was a trend toward a higher number of N_1 on plants irrigated with HC solution (Table 2). The number of N_2/leaf (ANOVA: $F = 0.99$; $df = 1, 106$; $p = 0.32$) and number of N_3/leaf (ANOVA: $F = 0.24$; $df = 1, 106$; $p = 0.63$) were not different between treatments (Table 2). In the second sampling date (Day 10) there were no differences between treatments for the number of nymphs: N_1/leaf (ANOVA: $F = 0.20$; $df = 1, 106$; $p = 0.66$). However, for N_2/leaf (ANOVA: $F = 5.59$; $df = 1, 106$; $p = 0.02$), N_3/leaf (ANOVA: $F = 4.35$; $df = 1, 109$; $p = 0.04$) and the number of apterous adults (AA/leaf: ANOVA: $F = 5.47$; $df = 1, 106$; $p = 0.02$) we found significantly more aphids on plants irrigated with HC solutions than in control plants (Table 2).

2. Interaction Between Plants and Natural Enemies: Effects on Aphids

Sweet pepper was infested spontaneously by one species of aphid, *M. persicae,* in a very irregular way at the beginning of the sampling period (November). By February this species reached a steady dissemination in the

TABLE 2 Number of Nymphs/Leaf at First Sampling (day 4) and Number of Nymphs and Apterous Adults/Leaf at Second Sampling (day 10) on Plants of HC and Control (Comparisons are within a column; values followed by the same letter are not significantly different at $p > 0.05$. HC: high conductivity, N_1: nymphs 1, N_2: nymphs 2, N3: nymphs 3, AA: apterous adults.)

	N_1	N_2	N_3	AA
Day 4				
HC	18.31 ± 2.79 a	1.73 ± 0.46 a	1.54 ± 0.31 a	—
control	11.69 ± 1.37 a	2.50 ± 0.63 a	1.25 ± 0.26 a	—
Day 10				
HC	28.81 ± 4.03 a	22.75 ± 3.18 a	15.73 ± 2.69 a	4.84 ± 0.56 a
control	20.85 ± 2.59 a	13.69 ± 1.93 b	9.64 ± 1.40 b	2.83 ± 0.22 b

TABLE 3 Cumulative Aphid-Days CAD/Leaf (± S.E.) and Total Aphids Captured in Malaise Traps (Comparisons are within a column; values followed by the same letter are not significantly different at $p > 0.05$. NF: no flowers, AF: adjacent to flowers, WF: with flowers.)

Treatment	CAD/leaf	Total aphids captured
NF	1137.96 ± 530.16 a	4.58 ± 0.41 a
AF	250.71 ± 198.71 b	2.76 ± 0.64 b
WF	220.34 ± 222.29 b	2.25 ± 0.58 b

four greenhouses. Although there was a great dispersion of data the cumulative aphid-days (CAD) from February to March showed that the number of aphids significantly increased on NF sweet peppers (ANOVA: $F = 5.70$; $df = 2, 8$; $p = 0.03$) compared with AF and WF treatments (Table 3). At the same time, total numbers of aphids captured with Malaise traps were significantly greater (ANOVA: $F = 7.05$; $df = 2, 32$; $P = 0.03$) in traps of sectors without flowers (NF) than in AF and WF ones (Table 3). *Aphis gossypii* was no detected during the entire crop cycle.

Aphid parasitism was evidenced through 363 aphid mummies on sweet pepper leaves along the sampling period. They belonged to three species of parasitoids: Golden mummies of *Aphidius colemani* (Hymenoptera: Braconidae) were the most abundant (80.44%), followed by black mummies of *Aphelinus abdominalis* (Hymenoptera: Aphelinidae) (16.53%), and mummies of *Praon volucre* (Hymenoptera: Braconidae), which built a basket with the parasitoid pupae below it (3.03%). Sweet pepper plants with associate flowers (WF) had a higher percentage of aphid mummies than in NF and AF treatments (ANOVA: $F = 4.73$; $df = 2, 8$; $P = 0.04$) (Table 4).

A total of 1,492 individuals belonging to more than 25 species of natural enemies were collected in Malaise traps on six collecting dates from January to April. From this total, 1,423 individuals of 20 species were aphid natural enemies. The total number of aphid natural enemies were different among treatments for the first three dates (ANOVA: $F = 3.83$; $df = 2, 32$; $p = 0.03$) with flower sectors (WF and AF) having significantly higher natural enemies than sectors without flowers (NF). However no differences were found for the last three dates between treatments (ANOVA: $F = 0.87$; $df = 2, 32$; $p = 0.43$) (Table 4). No significant differences were found in the total number of Coccinelids for the first three captures (ANOVA: $F = 2.99$; $df = 2, 32$; $p = 0.06$), nor for the three last ones (ANOVA: $F = 0.87$; $df = 2, 32$; $p = 0.43$). Nevertheless, a statistical significance of 6% in first captures, similar to those of total natural enemies, indicates a trend toward greater numbers of Coccinelids on AF and WF traps (Table 4). A density dependent number of Coccinelids of all species on *M. persicae* density was found on NF treatments by regression analysis ($y = 0.27 + 0.18\ x$; $R^2 = 0.87$; $F = 25.80$; $p = 0.007$). However, a weak or inexistent relationship was evaluated

TABLE 4 Percentage of Aphid Parasitism (± S.E.) (Cumulative Mummy-Days/Cumulative Aphid-Days + Cumulative Mummy-Days) on Leaves, and Total Mean Captures ± SE of Natural Enemies in Malaise Traps (Comparisons are within a column; values followed by the same letter are not significantly different at $p > 0.05$. NF: no flowers, AF: adjacent to flowers, WF: with flowers.)

		Natural enemies		Coccinelids		Heteroptera
	% Parasitism (mummies on leaves)	First three captures	Last three captures	First three captures	Last three captures	total
NF	0.30 ± 0.28 b	1.69 ± 0.15 b	3.18 ± 0.29 a	1.31 ± 0.19 a	3.10 ± 0.29 a	1.13 ± 0.16 b
AF	2.44 ± 1.60 b	2.29 ± 0.29 a	2.98 ± 0.24 a	1.88 ± 0.32 a	2.75 ± 0.27 a	1.72 ± 0.25 ab
WF	7.55 ± 2.09 a	2.28 ± 0.24 a	3.29 ± 0.17 a	1.90 ± 0.24 a	2.97 ± 0.16 a	2.19 ± 0.27 a

for AF ($R^2 = 0.40$; $F = 2.67$; $p = 0.18$) and WF ($R^2 = 0.00$; $F = 0.00$; $p = 0.96$), respectively. Total number of Heteroptera captures along all sampling dates showed significant differences (ANOVA: $F = 5.95$; *df* = 2, 32; $p = 0.006$). The number of heteroptera captured in the WF traps was greater than in NF ones with intermediate values for AF traps (Table 4). Among aphid natural enemies captured by Malaise traps, Coleoptera: Coccinellidae comprised 70 to 90% of species (Figure 1), being the most important: *Eriopis connexa* (35–50%), *Scymnus argentinicus* (35–42%), and *Hyperaspis festiva* (10–15%). Then, we found Heteroptera: Anthocoridae, Miridae and Geocoridae (6–27% of the species), Neuroptera (1.2–2.1% of the species), and finally Diptera: Syrphidae (0.4–1.1% of the species). No Hymenoptera parasitoids of aphids were found in the Malaise traps.

Aphid natural enemy species richness (S) ranged from 5 to 12 species in all the treatments. A statistical analysis that included all sampling dates showed significant differences in species richness per trap among treatments (repeated-measures ANOVA: *df* = 2, 32; $F = 4.61$; $p = 0.017$): it was higher in WF traps (mean = 2.97 species), lower in NF traps (mean = 2.07 species), and intermediate in AF traps (mean = 2.67 species). Shannon-Wiener index of diversity (H′) were compared by pairs of treatments (*t* test, $p < 0.05$). A greater diversity of aphid natural enemies in AF treatment (H′ = 1.81), intermediate value for WF treatment (H′ = 1.74) and a lower diversity in NF traps (H′ = 1.50) were found (Figure 1). Diversity was also analyzed for each sampling date. Only in the second sampling period at the beginning of February were natural enemies more diverse in NF, lower in AF and intermediate in WF treatments (Student's *t* test $P < 0.05$). All the other dates

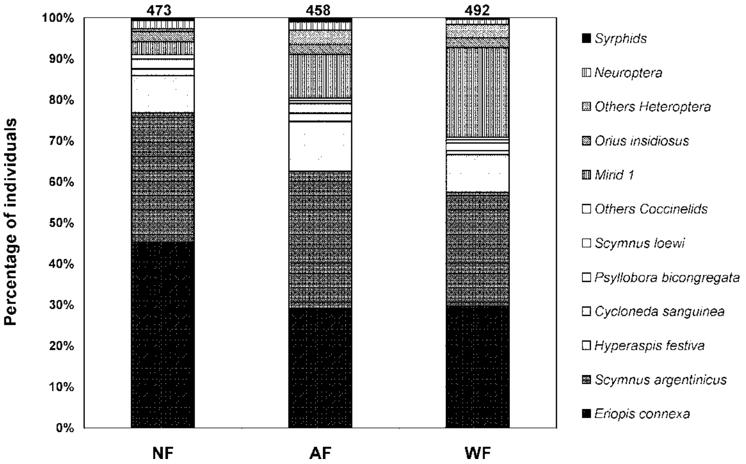

FIGURE 1 Percentage of individuals of aphid natural enemies found in Malaise traps. Numbers above columns indicate total number of individuals captured. NF: without flowers, AF: adjacent flowers, and WF: with flowers.

showed greater diversity in Malaise traps of AF and WF treatments (Student *t* test, $p < 0.05$).

3. Integration of an Agronomic Practice and Plant Diversity

Significant differences were observed among four treatments for the electrical specific conductivity (ANOVA: $F = 10.82$; $df = 1, 25$; $p = 0.0001$): treatments with high conductivity with (HC-F) and without flowers (HC) had a higher electrical conductivity than the control ones (Table 5). The pH followed the same trend: pots irrigated with saline solution (HC and HC-F) had a higher pH than the control without flowers (C), whereas the control with flowers (C-F) had an intermediate value (ANOVA: $F = 5.11$; $df = 1, 25$; $p = 0.007$) (Table 5).

Total number of aphids (nymphs and apterous adults of *A. gossypii* + *M. persicae*) per leaf were analyzed for all twelve sampling dates. Significant differences were found for the effect of the irrigation solution (high conductivity vs. control), however, there was no significant effect of the flower factor (with vs. without flowers; Table 6). The same analysis for the first through sixth dates, showed significant differences for both factors: irrigation and plants with flowers. Through the seventh through twelfth dates, only difference in conductivity effect was noticed (Table 6). This means that high conductivity treatments supported higher density of aphids along the whole experiment, while the presence of flowers was particularly important during the first period; aphid abundance was lower in treatments with flowers (HC-F and C-F). When *M. persicae* was analyzed separately similar patterns in total aphids were found: effect of high conductivity along twelve dates, and effect of flowers during the first six dates. Neither the plants with flowers nor the irrigation solution factor had significant effects on *A. gossypii*. No interactions between conductivity and flowers were found in the analysis (Table 6).

TABLE 5 Mean ± SE Values of Electrical Conductivity and pH of Soil in Pots, After Irrigation, During The Experiment (Comparisons are within a column; values followed by the same letter are not significantly different at $p > 0.05$. HC: high conductivity water without associate flowers, HC-F: high conductivity water with associate flowers, 2) C-F: low conductivity water with associate flowers, and C: low conductivity water without associate flowers.)

Treatment	Conductivity (mS/cm)	pH
HC	1.01 ± 0.07 a	7.61 ± 0.09 a
HC-F	0.96 ± 0.14 a	7.60 ± 0.16 a
C-F	0.57 ± 0.03 b	7.44 ± 0.10 ab
C	0.58 ± 0.03 b	7.35 ± 0.04 b

TABLE 6 Effects of Soil Conductivity and Flowering Plants on the Abundance of Aphids (Two-way repeated-measures ANOVA. Degrees of freedom (1, 41) in all cases. C: high conductivity water; F: with flowers.)

	Sampling dates	Factor	*F*	*P*
Total aphids	All 12 dates	Conductivity (C)	8.79	0.005
		Flowers (F)	0.49	0.49
		Interaction (C × F)	0.23	0.64
	1st–6th dates	Conductivity (C)	14.03	0.0005
		Flowers (F)	6.41	0.015
		Interaction (C × F)	2.94	0.09
	7th–12th dates	Conductivity (C)	4.83	0.034
		Flowers (F)	0.12	0.73
		Interaction (C × F)	0.05	0.82
Mysus persicae	All 12 dates	Conductivity (C)	9.28	0.004
		Flowers (F)	0.98	0.33
		Interaction (C × F)	0.15	0.70
	1st–6th dates	Conductivity (C)	12.12	0.001
		Flowers (F)	4.38	0.04
		Interaction (C × F)	1.92	0.17
	7th–12th dates	Conductivity (C)	9.28	0.005
		Flowers (F)	0.98	0.33
		Interaction (C × F)	0.15	0.70
Aphis gossypii	All 12 dates	Conductivity (C)	2.50	0.12
		Flowers (F)	0.04	0.84
		Interaction (C × F)	0.05	0.82
	1st–6th dates	Conductivity (C)	2.71	0.11
		Flowers (F)	0.55	0.46
		Interaction (C × F)	0.94	0.34
	7th–12th dates	Conductivity (C)	2.04	0.16
		Flowers (F)	0.59	0.45
		Interaction (C × F)	0.06	0.81

Aphid parasitism of *M. pericae* + *A. gossypii,* was analyzed by a two-way repeated measures ANOVA for six sampling dates from June to July. No significant differences were observed for the effect of irrigation (ANOVA: $df = 1, 41$; $F = 2.42$; $p = 0.13$), for the effect of associated flowers (ANOVA: $df = 1, 41$; $F = 0.53$; $p = 0.47$), and for the interaction between them (ANOVA: $df = 1, 41$; $F = 0.48$; $p = 0.49$) among treatments. Percentage of parasitism of both species together was also evaluated as a function of aphid density (total number of aphids/leaf) by means of regression analysis. An increase in the number of hosts was accompanied with an increase in the proportion of parasitism. Nevertheless, for the same number of aphids/leaf the percentage of parasitism was higher in the controls (C and C-F) than in HC and HC-F treatments (Figure 2); regression slopes were lower in HC and

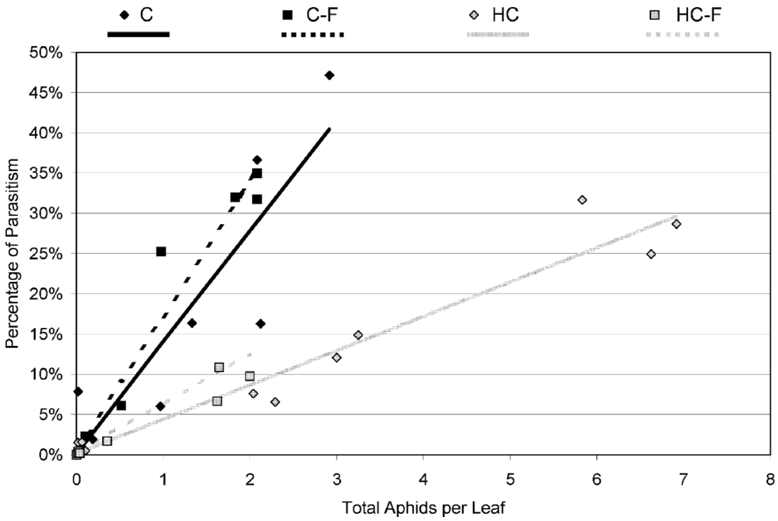

FIGURE 2 Relationship between percentage of parasitized aphids and total aphids (*M. persicae* + *A. gossypii*) per leaf in four treatments. C: low conductivity water without associate flowers (entire black line), C-F: low conductivity water with associate flowers (dotted black line), HC: high conductivity water without associate flowers (entire gray line) and HC-F: high conductivity water with associate flowers (dotted gray line). Each point represents a sample date. Significances of lines are shown in Table 7.

TABLE 7 Regression Analysis Between Percentage of Parasitism and Total Number of Aphids/Leaf (a intercept, b slope. C: low conductivity water without associate flowers, C-F: low conductivity water with associate flowers, HC: high conductivity water without associate flowers and HC-F: high conductivity water with associate flowers.)

	R^2	a	Inf. 95%	Sup.95%	P	b	Inf.95%	Sup.95%	*P*
C	0.86	0.0007	−0.0481	0.0494	0.98	0.1385	0.0991	0.1780	0.0000
C-F	0.96	0.0041	−0.0208	0.0290	0.72	0.1677	0.1440	0.1913	0.0000
HC	0.95	0.0013	−0.0234	0.0260	0.91	0.0426	0.0358	0.0495	0.0000
HC-F	0.76	0.0026	−0.0209	0.0261	0.81	0.0612	0.0369	0.0855	0.0002

HC-F treatments. No overlap was found between confidence intervals of C and C-F, and HC and HC-F ones (Table 7).

DISCUSSION

Multitrophic interactions between crops and associated plants, herbivores, which under certain conditions can reach pest status and natural enemies, should be considered when selecting strategies to manage pests in sustainable agricultural systems. Several factors can alter these interactions, leading to an increase or decrease of pest populations. Farmers of this region reported that due to the large expansion of greenhouses, despite the application of large amounts of pesticides, the pest problem has augmented. This suggests that greenhouse system may alter certain environmental conditions that increase crop susceptibility to pests. It is well known that changes in environmental conditions can modify plant suitability for insect pests (Goranson et al. 2004). Stressed plants in particular could be more likely to be attacked and damaged to a greater extent by herbivores than healthy ones.

Modern agricultural systems have been designed to maximize crop yield by means of harvest index increase and the supply of large quantities of inputs (water, pesticides, fertilizers). These production practices may stimulate physiological changes that generate stress within plants. Even some common agricultural practices that may have little impact on yield could produce asymptomatic stress that reduces plant resistance to pests. A widespread problem of horticultural management in greenhouses is soil salinization produced by irrigation water that can cause plant stress. This experiment showed that the simulation of soil salinization altered the susceptibility of sweet pepper for *M. persicae*. Plants subjected to HC treatment, which represents a saline type stress, allowed aphids to perform better and this response is related to the stress hypothesis (White 1974; Mattson and Haack 1987; Louda and Collinge 1992; Huberty and Denno 2004, Joern and Mole 2005). After four days the number of small nymphs in HC treatment was similar than in the control. However, at the day 10, we found a greater number of N_2, N_3, and apterous adults (AA) in the HC treatment. Offspring reached adulthood at day 10, which is considered approximately the generation time for *M. persicae* on other host plants (Davis et al. 2006). From the two progenitors /leaf placed in the previous generation at the beginning of the experiment, the number of AA/leaf reached about ~5 in the next generation. HC treatment had a positive effect on *M. persicae* that consequently could allow a faster development, a higher fecundity, and an increasing population growth.

Water stress has two possible effects on herbivory (Huberty and Denno 2004). It can support herbivores due to an increase in nitrogen concentration, but can also harm them because the turgor pressure of cells diminishes. When the stress is temporal or by pulses, plants suffer a brief period (few hours) of stress, and then rapidly restore the turgor of their tissues. Even under optimal irrigation conditions crops suffer temporary stress. At this time a higher concentration of nitrogen remains available improving herbivore performance. Stress and restore conditions are part of a crop under greenhouse conditions in this horticultural area, that also support high radiation and temperature favorable for pest outbreaks. In this experiment plants of HC treatment had a lower water potential and were more prone to stress than others thus favoring the performance of aphids.

Horticultural crops in greenhouses are characterized by low diversity and poor structural complexity (Cédola et al. 2001) due to the confinement conditions that prevent migration of some arthropods, the mechanical removal of weeds, and the use of mulches that avoid weeds. Therefore, conservation biological control is impaired in crops under greenhouse environments (Landis and Menalled 1998; van Lenteren and Manzaroli 1999). However, this experiment and one performed by Saini et al. (2001) observed high levels of parasitism and predation in pepper in greenhouses due to an important presence of natural enemies in the agroecosystem. A higher percentage of parasitism, more predators, a greater diversity, and a trend toward increased species richness of natural enemies in the presence of flowering plants were also observed in this experiment. All these variables enhanced aphid control. Although greenhouse crop production represent poor conditions for natural enemies, high levels of predation and parasitism were achieved even in the treatment without flowers (NF). Additionally, the environment surrounding greenhouses is conformed by diverse cultivated and spontaneous plants that act as a reservoir of natural enemies which if properly managed could be used as an ecological service in agroecosystems (Collins and Qualset 1999; Paoletti and Pimentel 1992, Paleologos et al. 2008). Future research should address in more depth the role of landscape ecology and its associated ecosystem services surrounding greenhouses for designing greenhouse pest management strategies.

Eriopis connexa and *S. argentinicus* were the most abundant predators in sweet pepper, and *A. colemani* was the main parasitoid of *M. persicae*. *A. colemani* is also the primary parasitoid of this aphid in tobacco (Kavallieratos et al. 2005) and is commercialized for *M. persicae* and *A. gossypii* control (Vasquez et al. 2004). Calvo and Belda (2004) observed that percentages of parasitism of *M. persicae* reached 95% on pepper in a greenhouse when *A. colemani* was introduced through oat plant reservoirs. Malaise traps in WF treatments had the largest number of natural enemies depicted by a high number of Coccinellids in the first three samplings and Heteroptera along all the period sampled. Among the Heteroptera, one species of Miridae represented 22% of individuals captured in the WF treatment (Figure 1). Mirids are omnivorous arthropods along a continuum between zoophagy and fitophagy; they are commonly found on Asteraceae (Logarzo et al. 2005), the family to which sow-thistle and marigold belong. Coccinellidae was the most abundant predator taxon. Coccinellids are considered voracious predators with a consumption capacity eight times greater than generalists ones when fed *M. persicae* on potatoes (Ro and Long 1998).

Malaise traps did not catch the parasitoids recorded on leaves as mummies (*A. colemani*, *A. abdominalis*, and *P. volucre*) probably because parasitism did not exceed 8%. We found a trend toward a higher richness of natural enemy species in WF plots, as well as more diversity in AF and WF treatments on most of the sampling dates. Plots WF seemed to show more evenness while *E. connexa* accounted for 45% in NF treatments and less than 30% in WF ones. The remaining taxa except *E. connexa* and *S. argentinicus* reached less than 25% in this treatment.

Studies of the significance of increasing crop diversity on pest control confirm that habitat management is beneficial for natural enemies and contribute to reduce herbivore abundance (Gurr et al. 1998; Langelotto and Denno 2004; Shrewsbury et al. 2004). The density of *M. persicae* was lower in the higher plant diversity treatment and there were higher parasitism and more predators in plots with diverse vegetation. These results agree with those of Polack and Brambilla (2000) and Saini et al. (2001), revealing that conservation biological control could be a successful and low-cost strategy for aphid control of greenhouse horticultural crops in northeastern Buenos Aires province.

Nevertheless, improper manipulation of adjacent plant diversity can increase pest problems. Colonization of aphids in sweet pepper showed an irregular pattern of infestation until populations reached a steady dispersion in the greenhouse. However, we could find significant differences in aphid abundance between treatments on leaves as well as Malaise traps. Narváez and Notz (1995) found an aggregated distribution of *M. persicae* in a potato crop on the borders. Habitat management for conservation biological control should consider a risk of pest colonization (Landis et al. 2000) by providing alternative sources of food (Lavandero et al. 2006). Additional research is required to minimize the chance of undesired effects when certain plants are selected in control strategies.

Under greenhouse conditions, variations in both plant stress and plant diversity can occur simultaneously, affecting plant–pest–natural enemy interactions. When high conductivity (HC) irrigation and flowers were combined, sweet pepper plants of HC treatments did affect the abundance of total aphids along the whole period. The effect of increase salinity followed the same trend as the previous experiment. The presence of flowers influenced aphids in the first half of the sampling period. This means that the number of total aphids increased due to HC in sweet pepper plants, while the existence of flowers reduced numbers and delayed aphid appearance, generating significant differences between treatments (HC and HC-F) in the first six samplings. Total aphids (*A. gossypii* + *M. persicae*) followed a similar pattern to that of *M. persicae* which displayed differences between treatments better than *A. gossypii* where populations were not affected by HC nor by flowers treatments. Flowering plants could have interfered in the host plant searching process. Associated plants are known to affect abundance and oviposition mechanisms of other pests: *Delia radicum* and *D. antiqua* (Diptera: Anthomyiidae) on cauliflower and onion (Finch et al. 2003), *Tetranychus urticae* (Acari; Tetranychidae) on strawberry (Greco et al. 2005), and whiteflies and aphids on zucchinis (Frank and Liburd 2005).

When the percentage of parasitism was evaluated as a function of host densities, no statistical difference between HC and HC-F treatments were noted. Moreover, there were no differences between C and C-F, indicating that the effect of associated plants was negligible for parasitism. Although the average number of aphids was higher in HC and HC-F treatments, parasitoids seemed to respond better to aphid densities of C and CF treatments. Direct density dependent effect of *A. colemani* on *M. persicae* on pepper plant scale was also found by Jarošík and Lapchin (2001). A minor effect of flowers was probably due to the experimental design where parasitoids could move among areas with and without flowers for finding hosts and food resources. The parasitoid *A. colemani* can travel 16 m after 24 hours of release (Langhof et al. 2005). Knowledge about parasitoids movement is important for designing the distribution of associated flowers with crop plants because replacing part of the crop with these plants utilizes resources such as space that could otherwise be used for crop production. In order to compatible economic and ecological goals, the associated plants should occupy the smallest area for ensuring the provision of this service under agroecological management. The absence of predators in the third experiment may be due to the season when this experiment was conducted (fall–winter), as the greenhouse remained closed longer and hindered the entry of predators.

Management practices such as excessive irrigation (or low quality water) that enhances salinity and conductivity, even without an appreciable effect on crop yield may negatively affect sweet pepper physiology and consequently increase aphid abundance. Soil variations as changes in the salinity that affect pH (Table 5) interact complexly and should be considered when formulating irrigation regimes. The pH can influence the availability of nutrients (Bandel et al. 2002; Kelley and Boyhan 2006) and therefore, affect the relation between them. This complexity needs more in depth research to establish the ideal relationship between optimum production and crop resistance to pests and diseases.

Responses of herbivorous insects to changes in plant quality vary within and among guilds (Awmack and Leather 2002; Huberty and Denno 2004). Phloem amino acid composition determines the nutritional quality of plants for sucking insects like aphids (Karley et al. 2002; Voelckel et al. 2004). Salinity and water stress can cause an increment in amino acids concentration in the phloem (Girousse et al. 1996; Hale et al. 2003) generating beneficial changes in plant quality for aphids. In addition they have short generation times, low mobility, and all stages of development eat phloem. In this case, the effect of HC stress on sweet pepper plant quality was manifested during the following generation that remained on the same plant.

For equal aphid density there was a higher percentage of parasitism in the nonstressed treatments (C and C-F) which may indicate a favorable relationship between crop resistance (i.e., decreased susceptibility) and natural biological control. Those management practices that avoid increasing crop susceptibility (like C and C-F treatments) will slow down the growth of aphid populations, while natural enemies will produce greater mortality. *Aphidius colemani* parasitized proportionally more aphids on control plants (C) where aphid abundance was lower compared to more susceptible ones (HC). Many papers explain the advantage of combining plant resistance and biological control (Benrey and Denno 1997; Messina and Sorenson 2001; Du et al. 2004). Verkerk (2004) remarked that the outcome of combining the effect of nonstressed plants and biological control show interactions ranging from synergistic to disruptive or antagonist. Our results showed a positive combination among those effects.

First, trophic level heterogeneity given by the crop as a principal resource and the associated flowering plants may influence aphids by generating repellence or confusion expressed in a delay in the colonization when associate plants were present. The quality of the first trophic level resources also affected natural enemy control on the aphids. This demonstrates that pest management needs to be focused from a multitrophic perspective, considering top-down as well as bottom-up processes

Horticultural growers of NE of Buenos Aires province consider irrigation and fertilization as usual practices not related to pest problems in greenhouses. Our results suggest that irrigation or fertilization can be manipulated not only for improving crop yield but also for reducing high levels of broad spectrum pesticide use, a critical aspect in terms of sustainability. They do not perceive the benefits of biological control yet, and distrust of the role of spontaneous plants which are considered weeds (Vicente et al. 2006).

Greenhouse horticultural crops constitute very simplified agroecosystems due to low diversity and structural complexity in this region (Cédola et al. 2001). Production of vegetables under these conditions is similar to that of temperate zones of Europe (van Lenteren 2000) where ventilation allows continue migration of the organisms (Gabarra et al 2004). Crops are exposed to high pest pressure due to favorable environmental conditions, but at the same time, they are colonized by numerous natural enemies from the outside. In our study, this movement was noticed even in NF treatment, where parasitoids and abundant predators were found. The surrounding areas are relatively undisturbed and provide the existing natural enemies with resources such as refuge, alternative hosts, preys, and food sources that make conservation biological control feasible in the greenhouses (Paleologos et al 2008). Natural enemy conservation is a potentially useful method of biological control for these systems that allow a reduction of pesticides releases to the environment. It requires a better understanding of tritrophic interactions in order to design adequate management strategies, a future research on habitat manipulation, and the identification of key plant species to enhance abundance and diversity of parasitoids and predators, particularly to conserve *E. connexa*, *S. argentinicus*, and *A. colemani*.

The design and management of sustainable agroecosystems should consider the importance of supporting adequate levels of plant biodiversity, both within the farms and the semi-natural environments, for the maintenance of ecological functions. Greenhouse horticultural management practices that avoid increasing soil salinity and promote an increment of local biodiversity with flowering plants could improve aphid control. The results of this work raise the need to examine the importance of different components of the IPM, in terms of preventive techniques, and the possibility to explore new alternatives and concepts for greenhouse horticultural crops in the context of a sustainable agriculture.

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