Arthropod Assemblage Related to Volatile Cues in Flowering Wheat: Interaction between Aphid Herbivory and Soil Conditions as Induction Factors

Author(s): Adriana E. Lenardis, Alfonsina Szpeiner and Claudio M. Ghersa
Source: Environmental Entomology, 43(2):448-457.
Published By: Entomological Society of America
URL: http://www.bioone.org/doi/full/10.1603/EN13235

Arthropod Assemblage Related to Volatile Cues in Flowering Wheat: Interaction Between Aphid Herbivory and Soil Conditions as Induction Factors

ADRIANA E. LENARDIS,[1,2] ALFONSINA SZPEINER,[3] AND CLAUDIO M. GHERSA[3]

Environ. Entomol. 43(2): 448–457 (2014); DOI: http://dx.doi.org/10.1603/EN13235

ABSTRACT Volatile cues released by plants play an important role in plant–insect interactions and are influenced by pests or soil conditions affecting plant metabolism. Field microcosm experiments were used to characterize arthropod spontaneous assemblies in homogenous unstressed wheat patches exposed to volatile cues coming from wheat plants with different levels of stress. The design was a factorial completely randomized block design with three replications. Source wheat pots combined two stress factors: 1) soil degradation level: high and low, and 2) aphid herbivory: with (A) and without (B). Eighteen experimental units consisted of source stressed wheat pots, connected by tubes conducting the volatile cues to sink wheat patches. These patches were located at the end of the tubes placed in a flowering wheat field. Arthropod assemblies on wheat sinks were different between years and they were associated to the source cues. Soil condition was the main discriminating factor among arthropods when a clear contrast between high and low soil degradation was observed, whereas aphid herbivory was the main discriminating factor when soil condition effects were absent. Main soil properties related with arthropods assembly were Mg and K in the first year and cation exchange capacity, total nitrogen, and pH in the second year of experiment. According to this study, spontaneous arthropod distributions in the homogeneous, unstressed wheat patch responded to the volatile cues coming from wheat sources growing in particular soil conditions. It is possible to suggest that soil–plant– herbivore interactions change wheat cues and this phenomenon produces significant differences in neighboring arthropod community structure.

KEY WORDS herbivory, soil degradation, volatile compound, arthropods community, plant defense

Volatiles released by plants play an important role in plant–insect interactions (Pichersky and Gershenzon 2002). Volatile organic compounds (VOCs) can act as constitutive defenses (Wittstock and Gershenzon 2002) or as induced defenses when they are released or synthesized in response to tissue damage (Paré and Tumlinson 1996). Both constitutive and induced volatile composition and concentration are influenced by stress factors, such as pests or soil condition affecting plant metabolism (Herms and Mattson 1992, Paré and Tumlinson 1999, Bezemer and van Dam 2005).

Herbivore-induced plant volatiles may directly influence herbivore development (Bernays and Chapman 1994, Karban and Baldwin 1997, Schoonhoven et al. 1998) and may indirectly attract herbivore's natural enemies (Bruin et al. 1995, de Moraes et al. 1998, Dicke 1999, Paré and Tumlinson 1999, Kessler and Baldwin 2001, Steidle and Van Loon 2003). For example, volatiles released from corn seedlings (*Zea mays* L.) infested by herbivores may function as chemical cues for parasitic wasps (Turlings et al. 1991). The same phenomenon was observed from wheat leaves wounded by aphid (*Sitobion avenae* F.; Zhao et al. 2009).

Intensive agricultural land use causes soil erosion and degradation as well as changes in plant and arthropods communities (de la Fuente et al. 2006). Lenardis et al. (2007) found that allogeneic VOCs emitted by plants (wheat and coriander winter crops) grown in soil with different degradation level played some role in the determination of spontaneous arthropod assemblies in crop plants growing without stress. Moreover, Szpeiner et al. (2009) showed that when the two stresses were acting simultaneously, the response to volatile emissions caused by aphid herbivory was greater than that caused by soil conditions. Despite these studies, there is no information on how the influence of allogeneic VOCs may affect crop arthropod assemblages along different growth stages. Significant morphological and physiological changes occur during crop development, and the effects of allogeneic plant VOCs on arthropods assemblage could be blurred by local plant VOCs emissions. Understanding how arthropods assemblages are affected

---

[1] Departamento de Producción Vegetal, Facultad de Agronomía, Universidad de Buenos Aires, Av., San Martín 4453, (1417) Buenos Aires, Argentina.

[2] Corresponding author, e-mail: lenardis@agro.uba.ar.

[3] Departamento de Recursos Naturales y Ambiente, Facultad de Agronomía, IFEVA, Av., San Martín 4453, (1417) Buenos Aires, Argentina.

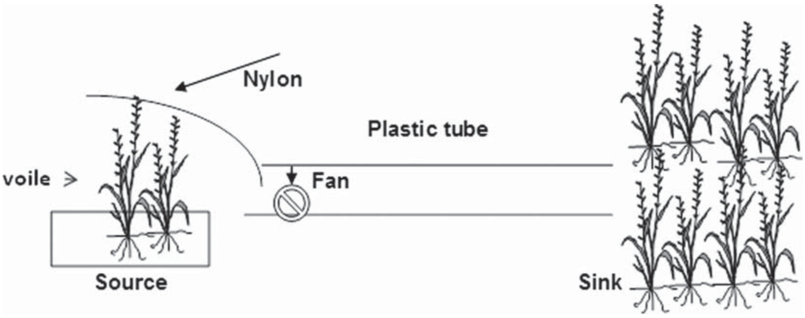

Fig. 1. Experimental area diagram.

by allogeneic plant VOCs during the crop reproductive stages is important, especially considering their potential impact during these stages that are critical for yield determination (Fischer 1985). For this reason, the aim of this study was to evaluate spontaneous arthropod assemblies in unstressed flowering wheat crop patches exposed to allogeneic cues coming from wheat plants growing under different levels of stress. Stress factors were generated by high and low level of soil degradation and with or without aphid herbivory.

Materials and Methods

Microcosm Experiment. Two factorial experiments in a completely randomized block design with three replications were carried out in the Faculty of Agronomy, University of Buenos Aires (34° 35′5″ S latitude, 58° 29′ W longitude) during 2004 and 2005. Experimental units consisted of source pots with stressed wheat emitting cues, connected with sink patches with unstressed wheat receiving cues from the source (Lenardis et al. 2007). Source pots combined two factors: 1) soil conditions: control (CON) and high (D) and low (ND) degradation level and 2) aphid herbivory: with (A) and without (B). Wheat sink patches were chosen within a wheat field sown in winter and were structurally similar considering plants' phenology, density, and height.

Soil condition treatments consisted of different land use conditions of top soils from the Rolling Pampas' Mollisols, Argentina (34 and 36° S and 58 and 62° W). The top soil (20 cm) samples were collected randomly from cropping fields at several locations: Santa Juana$_m$ (M), Las Polvaredas (LP), and Santa Juana (SJ) in 2004 and La Matilde (LM), Las Polvaredas (LP), and Santa Juana (SJ) in 2005. In 2004, M consisted of soils sampled the previous year (2003) from an agricultural field (SJ). The levels of soil degradation were determined based on cropping histories, soil physic, and chemical analysis and weed communities (Cárcova et al. 1998, de la Fuente et al. 1999, Suárez et al. 2001) of fields belonging to a typical Agiudoll (Luvic Phaeozen) of the Arroyo Dulce soil series (INTA 1974). The fields of D group had many agricultural cycles (>10 yr), low (<20%) relative soil stability index, and absence of the floristic groups characteristic of the Sonchus–Bidens or Bidens–Stellaria weed communities, present in ND soils (de la Fuente et al. 1999, Suárez et al. 2001). ND fields had few agricultural cycles (<10 yr), high (>20%) relative soil stability index, and weed communities of the Sonchus–Bidens or Bidens–Stellaria type (de la Fuente et al. 1999, Suárez et al. 2001). CON for each year was commercial potting top soils.

Aphid herbivory treatments were carried out introducing 100 apterous aphids into source pots during tilling (Zadoks et al. 1974). Adult aphids were previously obtained from a greenhouse culture of *Sipha maydis* (Passerini) in wild *Sorghum halepense* (L.).

The whole experimental area and source pots were sown (330 seeds m^{-2}) with wheat (Guapo, cultivar) on 19 June 2004 and 1 July 2005. For each experiment, a block consisted of each of the three locations with two different levels of degradation (SJ, LP, and M in 2004 and SJ, LP, and LM in 2005) together with CON. Each treatment was repeated twice with herbivory (A) or without herbivory (B). Eighteen source pots consisted of plastic containers of 0.25 m^2 that were symmetrically placed 10 m (2004) or 5 m (2005) apart in the experimental area. Each source pot was protected by a metallic mesh covered with nylon (100 *u*) and voile to prevent undesirable arthropods and to concentrate the volatile cues emitted by the crops. Sinks consisted of wheat patches of 2 m^2 in the experimental area. At the beginning of the wheat spike emergence, source and sink were connected by a plastic tube of 0.2 m in diameter and 8 m (2004) or 4 m (2005) in length. Electric fans (12 V) installed inside each of the tubes gently forced air from source to sink (2.8 m^3/min). In this way, the volatile cues were conducted from the source wheat growing in different soil conditions and aphid herbivory to sink with homogeneous unstressed wheat patch (Fig. 1).

Measurements. *Soil Analysis.* On 2004 and 2005, before the sowing date, composite soil samples from source pots were taken for each soil condition and a homogenized subsample of 1 kg was analyzed. Organic C, total N (Nt), extractable P, pH, CE (electric conductivity), Ca, Mg, K, Na, CEC (cation exchange capacity), and Zn (Page et al. 1982) were quantified.

Arthropods Sampling and Determination. In both years, aerial arthropods were sampled on sink patches when wheat was at anthesis (Zadoks et al. 1974), using a small vacuum collector operated during 30 s in each

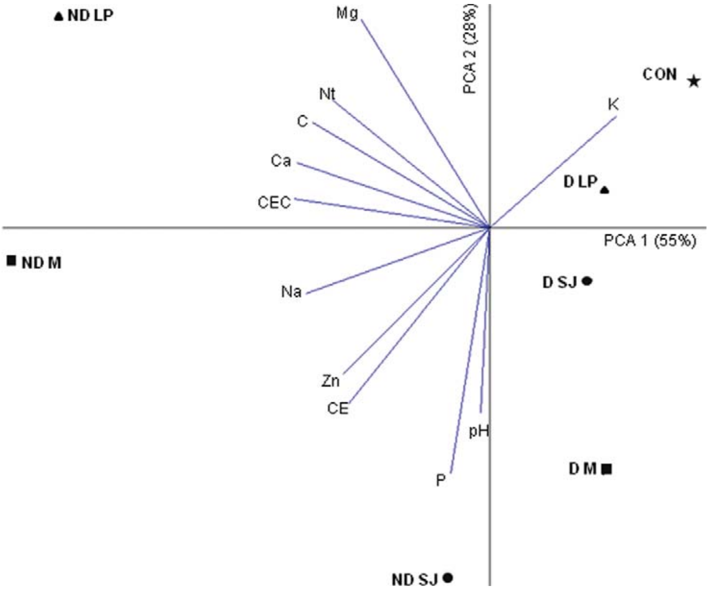

Fig. 2. PCA ordination of soil degradation treatments (2004) arranged by soil chemical variables. Source pots soil codes are: ND (low soil degradation), D (high soil degradation). Location codes are: triangle ▲ (Las Polvaredas, LP), circle ● (Santa Juana, SJ), square ■ (Santa Juanam, M), and star ★ (Control, CON). (Online figure in color.)

sink patch (Buffington and Redak 1998). The sampling was carried out under similar climatic conditions (sunny and without wind), at the same time of day between 10.00 a.m. and 15.00 p.m.

Arthropods were taxonomically determined at order level in all cases and at suborder or families when was possible. Morphospecies were considered as a group of biological organisms that differ in some morphological characteristics from all other groups, considering that differences between morphospecies and taxonomic species are very small in many cases (Derraik et al. 2002). Although detailed taxonomy usually improves the interpretation of results, the determination work at species level is usually time consuming, if not impossible, because of lack of taxonomic expertise available for some orders. Each suborder or family was represented by only one morphospecies. Each arthropod morphospecies was classified into herbivores and nonherbivores according to its habits and food preferences in/during the crop cycle, based on anatomical characteristics and bibliography (Richards and Davies 1984, Arroyo Varela and Viñuela Sandoval 1991). The arthropods that document the observations are available in the author's personal arthropod collection at the Faculty of Agronomy, University of Buenos Aires.

Although defining functional groups in such a way is not a perfect approach, it is an efficient and useful step forward to relate diversity and agroecosystems function (Perner et al. 2005).

Data Analyses. Soil data of source pots was analyzed using indirect gradient analyses, principal component analyses (PCA; ter Braak 1987a). Using PC-ORD Multivariate analysis of ecological data version 5.0 (McCune and Grace 2002, Mjm Software Design, Gleneden Beach, OR).

A correlation matrix was used in the PCA because the soil variables were not measured on the same scale (James and McCulloch 1990).

The presence–absence data of arthropods on sink patches was classified using a cluster analyses (McCune and Grace 2002). Classification provides a useful summary of large data matrices. A Sorensen coefficient version modified by Bray and Curtis (Magurran 1988) was used as a distance measure. Farthest neighbor (complete linkage) was used as a similarity measure (van Tongeren 1987).

Cluster of arthropods and treatments from the classification were presented in a table for each year, where faunistic groups of arthropods are shown in rows and communities are shown in columns. Constancy (proportion of sink samples in which a given morphospecies occurs in the survey) was calculated for each arthropod morphospecies (Mueller-Dombois and Ellenberg 1974).

Table 1. Principal components scores of soil properties (2004)

Variables	Scores	
	PCA 1	PCA 2
Ca	−0.39	0.13
Mg	−0.26	0.43
Na	−0.37	−0.13
K	0.26	0.23
CEC	−0.40	0.06
Zn	−0.30	−0.30
C	−0.36	0.22
N	−0.32	0.26
P	−0.08	−0.50
pH	−0.02	−0.38
CE	−0.29	−0.36

Distance based in biplot was used for scoring soil properties.

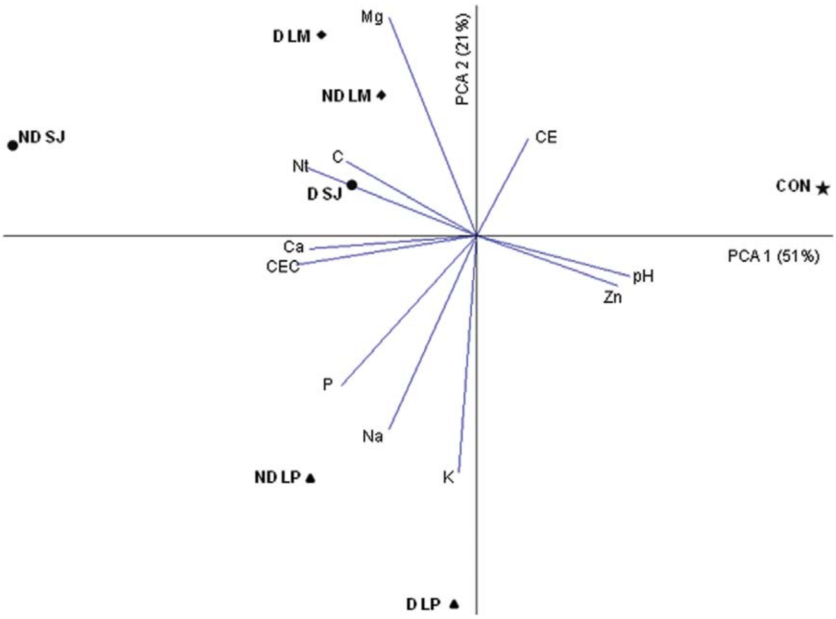

Fig. 3. PCA ordination of soil degradation treatments (2005) arranged by soil chemical variables. Source pots soil codes are: ND (low soil degradation), D (high soil degradation). Location codes are: triangle ▲ (Las Polvaredas, LP), circle ● (Santa Juana, SJ), rhombus ◆ (La Matilde, LM), and star ★ (Control, CON). (Online figure in color.)

The relationship between arthropods presence–absence on sink patches and soil properties on source pots was analyzed using a direct gradient analysis, canonical correspondence analysis (CCA) by PC-ORD Multivariate analysis of ecological data version 5.0 (McCune and Grace 2002). CCA constructs those linear combinations (axes) of explanatory variables along which the distribution of the morphospecies are maximally separated (ter Braak 1987b), and has a great potential for examining the response of communities to diverse variables (Kenkel et al. 2002). The explanatory variables used were soil properties. To determine association between arthropods data and explanatory variables, a biplot from CCA was obtained by overlaying a vector diagram based on coefficients from the canonical functions describing each canonical axis. In the resulting ordination diagram, treatments and arthropods are represented by points and soil properties by arrows.

Results

In 2004, PCA Axis 1, explaining 55% of the variance, revealed a contrast between soils from fields with different agricultural history (ND left part of diagram and D right part of diagram) regardless the location. CON was similar to D in Axis 1. Axis 2, which explained 28% of the variance, presented a contrast between soils within each location (Fig. 2). Main soil properties related with Axis 1 were CEC, Ca (left part of diagram), and K (right part of diagram). Mg (top part of diagram) and P (bottom part of diagram) were related with Axis 2. The soil properties related with axis were represented by vectors (Fig. 2; Table 1).

In 2005, PCA Axis 1 and Axis 2 explained 72% of the variance (51 and 21% respectively). Most of the variation in Axis 1 was caused by the large difference of soils from different locations (left part of diagram) and CON soil (right part of diagram). Variation in Axis 2 was related to differences between LP soils (bottom part of diagram) and LM soils (top part of diagram; Fig. 3). Location soils were related to high levels of CEC (left part of diagram) and CON was related to high levels of pH (right part of diagram); whereas in Axis 2, LP was related to high levels of K (bottom part of diagram) and LM and SJ to high levels of Mg (top part of diagram) The soil properties related with axis were represented by vectors (Fig. 3; Table 2).

The classification of 33 arthropod morphospecies and 18 experimental units from 2004 experiment resulted in four communities (columns) and six arthro-

Table 2. Principal components scores of soil properties (2005)

Variables	Scores	
	PCA 1	PCA 2
Ca	−0.39	−0.03
Mg	−0.20	0.50
Na	−0.20	−0.44
K	−0.04	−0.55
CEC	−0.42	−0.07
Zn	0.33	−0.12
C	−0.30	0.17
N	−0.40	0.16
P	−0.31	−0.34
pH	0.35	−0.09
CE	0.12	0.22

Distance based in biplot was used for scoring soil properties.

Table 3. Order, suborder or family, function, and constancy of arthropod morphospecies and units (faunistic groups and communities) resulting from the cluster analysis of sink wheat arthropods exposed to cues coming from source plants under soil and herbivory treatments (2004)

Faunistic groups	Communities						
	Order	Suborder or family	Function	Source cues			
				CON		Level of degradation	
				A	B	D	ND
				Constancy (%)			
I	Diptera	Chloropidae	h/nh		33	33	33
	Hymenoptera	Chalcidoidea	nh	67	67		33
	Hymenoptera	Braconidae	nh	100	33	67	17
	Coleoptera	Lathrididae	nh	100	33	50	50
	Diptera	Cynipidae	h/nh	33		17	17
	Thysanoptera		h	33	33	17	17
II	Diptera	Brachycera	nh		33	67	
	Coleoptera	Lygaeidae	h/nh		33	17	
	Diptera	Cryptochaetidae	nh		33	17	
	Hemiptera	Delphacidae	h		33	17	
	Hymenoptera	Entedontidae	h/nh		33	17	
III	Diptera	Chironomidae	nh				50
	Hemiptera						33
	Aracnida	Araneae	nh				17
	Diptera	Helomyzidae	nh				17
	Neuroptera	Chysopidae	nh				17
IV	Hymenoptera	Tetrastichidae	h/nh	33			
	Diptera	Nematocera		33			
	Hymenoptera	Eulophidae	h/nh	33			
	Coleoptera	Curculionidae	h	33			
V	Hymenoptera	Scelionidae	nh			17	
	Hymenoptera	Aphidiinae	nh			17	
	Diptera					17	
	Diptera	Dolichopodidae	nh			17	
	Diptera	Bibionidae	nh			17	
	Coleoptera		nh			17	
	Aracnida	Araneae	nh			17	
	Lepidoptera					17	
	Hymenoptera		nh			17	
VI	Hemiptera	Aphididae	h	67		17	
	Diptera	Agromycidae	h	33		17	
	Coleoptera	Cantharidae	nh	33			17
	Coleoptera	Coccinelidae	nh			17	17
Total morphospecies richness				12	10	22	13
Nonherbivores morphospecies richness				4	5	12	9
Herbivores morphospecies richness				4	2	4	1
Morphospecies whose function was not determined				1	–	2	1

Codes: control soil (CON) with (A) and without (B) herbivores, high (D) and low (ND) levels of soil degradation. h, herbivores; nh, non-herbivores.

pods groups (rows; Table 3). In 2005, five communities (columns) and six arthropods groups (rows) became apparent after classification of 23 arthropods and 18 experimental units (Table 4).

Four arthropod communities were identified according to source cues in 2004. Two communities were from CON with and without herbivores (A and B) and two communities from soil with different levels of degradation (D and ND), regardless of the location (Table 3). Five arthropod communities were identified according to source cues in 2005. Two communities were from LM and LP with and without herbivore (A and B), regardless of the location, and two communities come from SJ with different levels of degradation (D and ND) and a community from CON.

In both years, Group l was common to all arthropod communities. In 2004, the arthropod community related to CON (A) was characterized by Groups I, IV, and VI and the arthropod community related to CON (B) was characterized by the presence of Groups I and II. The community related to level of degradation (D) was characterized by Groups I, II, V, and VI, and the level of degradation (ND) was characterized by Groups I, III, and VI. Thus, Group III was present only in ND, Group IV in CON (A), and Group V only in D (Table 3), whereas in 2005, the arthropod community related to locations (LM–LP; A) was characterized by Groups I, IV, V, and VI, (B) was characterized by Groups I and II. The SJ (D) was characterized by Groups I and IV; SJ (ND) was characterized only by Groups I and VI. The arthropod community related to CON was characterized by Groups I, III, and V. Thus, Group II was only present in locations without herbivores and Group III was only present in CON (Table 4). Arthropod morphospecies were different between years and arthropod richness was higher in 2004 than in 2005. The mor-

Table 4. Order, suborder or family, function, and constancy of arthropod morphospecies and units (faunistic groups and communities) resulting from the cluster analysis of sink wheat arthropods exposed to cues coming from source plants under soil and herbivory treatments (2005)

Faunistic groups	Communities							
	Order	Suborder or family	Function	Source cues				
				Locations				CON
				(LM_LP)		(SJ)		
				A	B	D	ND	
				Constancy (%)				
I	Thysanoptera		h	75	25		100	100
	Hymenoptera	Braconidae	nh	25	75	100	100	17
	Hemiptera	Aphididae	h	50	25			83
	Hymenoptera	Serphidae	nh	50	50	100		50
	Hemiptera	Velidae		50	50		50	
	Hymenoptera	Chalcididae	nh	50	25	100		33
	Diptera	Lonchopteridae	nh	50		50		67
	Hemiptera				25	50		17
	Hemiptera	Corixidae	h		25	50		17
II	Diptera	Scaptophagidae	nh		25			
	Hemiptera	Ceratocombidae	h		25			
	Aracnidae	Philodromidae	nh		25			
III	Hemiptera	Thaumastocoridae	h					17
	Hemiptera	Nabidae	nh					33
	Diptera	Culicidae	nh					17
	Coleoptera	Carabidae	nh					17
IV	Hemiptera	Ochteridae	nh	50		50		
	Hemiptera	Gerridae	nh			50		
	Diptera	Phoridae	nh	25		50		
V	Diptera	Empetidae	nh	25				17
	Coleoptera	Scarabaeidae	nh	25				17
VI	Diptera	Dolichopodidae	nh	50			50	
	Coleoptera	Coccinelidae	nh				50	
Total morphospecies richness				12	11	9	5	14
Nonherbivores morphospecies richness				9	5	7	3	9
Herbivores morphospecies richness				2	4	1	1	4
Morphospecies whose function was not determined				1	2	1	1	1

Codes: locations (LM–LP) with (A) and without (B) herbivore, location SJ with high (D) and low (ND) level of degradation and control soil (CON). h, herbivores; nh, non-herbivores.

phospecies functions were determined in >90 and 80% of morphospecies in 2004 and 2005 respectively. Among them, between 8 and 33% were herbivores and 33 and 69% of morphospecies were nonherbivores in 2004 (bottom of Table 3), whereas in 2005, between 17–36% were herbivores and 45–77% of morphospecies were nonherbivores (bottom Table 4).

The first two axes of CCA explained 20% in 2004 and 37% in 2005 of the total variance in arthropod data. In both years, a high correlation of soil properties with first two axes (Pearson correlation coefficient: 0.863 for Axis 1 and 0.907 for Axis 2 during 2004; and −0.850 for Axis 1 and 0.747 for Axis 2 during 2005) was observed, supporting the association of sink arthropods with source soil properties.

In 2004, a contrast between LP and SJ D (right part of figure) and M and SJ ND (left part of figure) was evident in Axis 1. Axis 2 presented a contrast between LP and SJ ND (below part of figure) and LM and SJ D (top part of figure). In general, CON was located near to origin, indicating no effect (or an average effect equal zero) of the main ordination variables involved in CCA. In 2005, Axis 1 presented a contrast between SJ D (right part of figure) and SJ ND (left part of figure). In Axis 2, LP was separated according to levels of soil degradation and LM was separated according to herbivory treatments. CON was located near to origin (right and below part of figure). The main chemical soil properties with highest correlation with both axes are presented in Figs. 4 and 5: Mg and K in 2004 and CEC, Nt, and pH in 2005.

Discussion

Experiments used in this study demonstrated that the spontaneous arthropod communities' arrangements in the sink patches with wheat flowering plants were changed by the air flows coming from the source pots. The change in arthropod assemblies was influenced by the volatile cues related to both the herbivory (biotic) and soil condition (abiotic) stress factors influencing the wheat plants growing in the source pots (Szpeiner et al. 2009).

In both years, Community A was associated with cues coming from source pots with aphids and Community B without aphids. Cues coming from pots with wheat plants feeding aphids had a strong influence on the assembly of arthropod communities in both years. However, in 2004, A was associated with cues from source wheat growing in CON, and in 2005, it was associated with cues from source wheat growing in LM and LP.

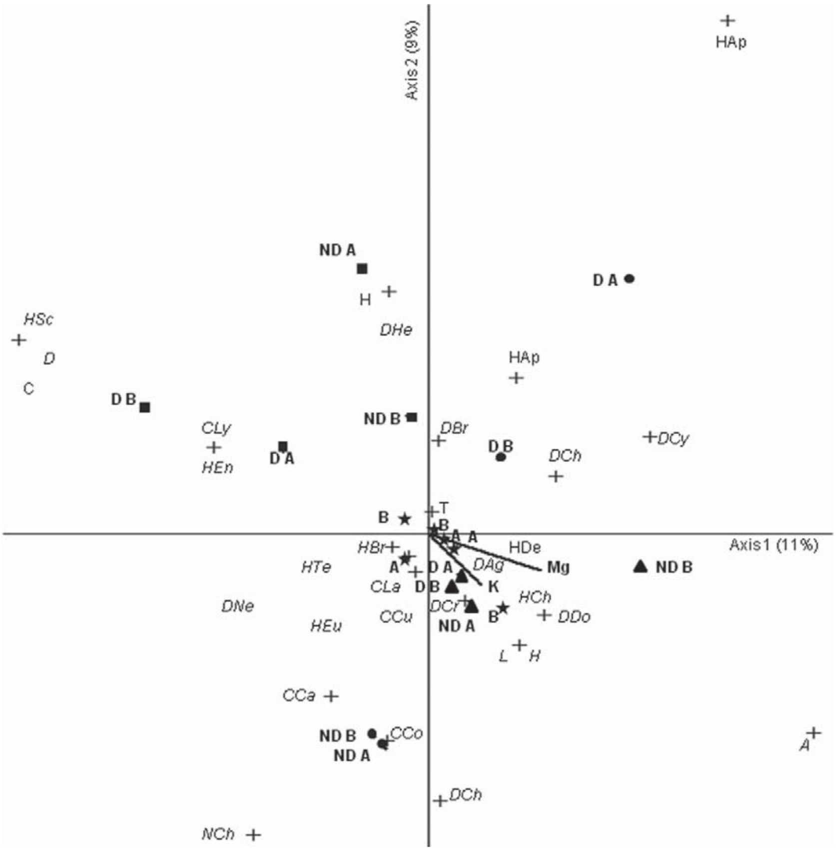

Fig. 4. CCA ordination diagram of arthropods from sink patches receiving cues of source pots and experimental units (2004). Source soil codes are: ND (low soil degradation), D (high soil degradation). Location symbols are: triangle ▲ (Las Polvaredas, LP), circle ● (Santa Juana, SJ), square ■ (Santa Juanam, M) and star ⋆ (Control, CON). Herbivory codes are: A (with herbivore) and B (without herbivore). Arthropods codes are: first letter of the order name and the following two letters of the suborder or family name. The relative length vectors indicate the importance of soil properties.

Soil condition treatments used in this study to generate different levels of stress expressed a detectable contrast in variables related to soil degradation levels (Michelena et al. 1989, Maddonni et al. 1999, Lenardis et al. 2007). However, other sources of variation related to location or year also contributed to differences in the soil environments available to the wheat plants. In 2004, contrast between soil degradation levels was observed regardless of the locations, while in 2005, soil degradation levels contrasts became evident within each location. Soil chemical properties that best explain differences between soil degradation levels were not the same between years. With the exception of CEC, K, Mg; Ca, and P were found as good indicators of level of soil degradation in 2004 and pH in 2005.

Despite all the variability found in soil conditions related to year and location, Communities D and ND come from soil with high and low degradation level, respectively, caused by agricultural activities. But, both communities were associated with cues from wheat regardless of the location in 2004, whereas in 2005, they were associated with cues from wheat growing in SJ. In 2004, Community D had the highest species richness.

In this study, soil condition was a discrimination factor of arthropods when a clear contrast between D and ND was observed. In 2004, this contrast was observed regardless of the location, whereas in 2005, the contrast between D and ND was observed only within SJ. Aphid herbivory appeared as a discrimination factor when soil condition effects were not present, for example within CONs in 2004 or within LM and LP soils in 2005.

In both years, a community resulted from cues coming from wheat growing in CON. In addition, CCA ordination showed that spontaneous arthropod distributions in the homogeneous unstressed wheat patches responded to the volatile cues from wheat source, growing in particular soil conditions. These results are in accordance with previous ones, suggesting that soil conditions induce change in crop's arthropod assemblies (Liddell 1999, Perner et al. 2005).

Variations in Mg and K (2004) and CEC, Nt, and pH (2005) in the soil of source pots were strongly associated with differences in arthropod assemblies in the

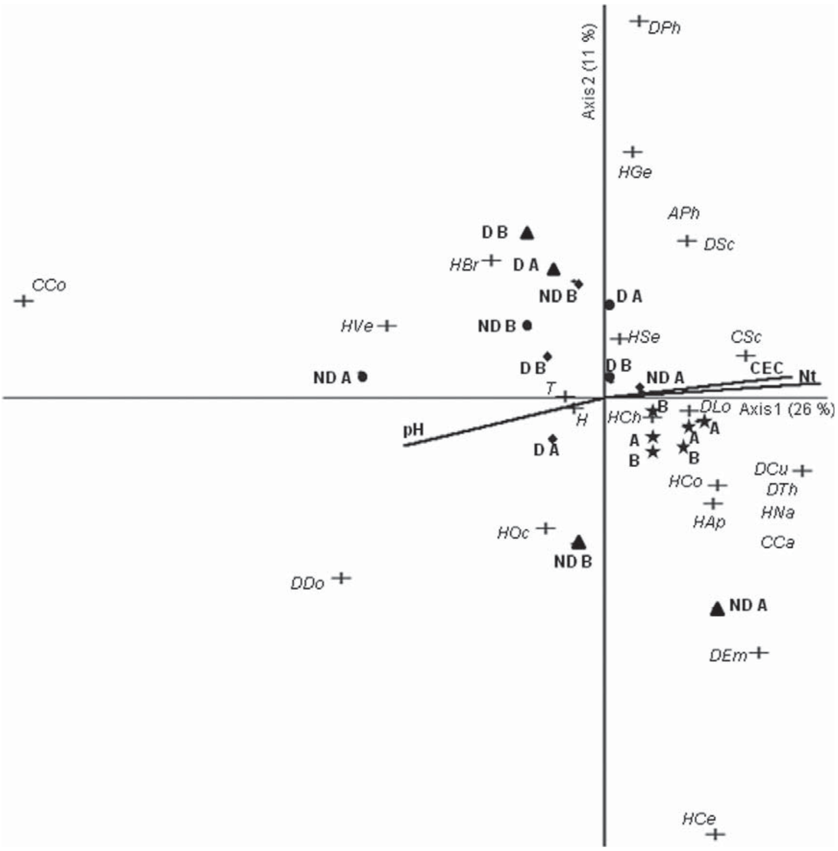

Fig. 5. CCA ordination diagram of arthropods from sink plots receiving cues of source pots and experimental units (2005). Source soil codes are: ND (low soil degradation), D (high soil degradation). Location symbols are: triangle ▲ (Las Polvaredas, LP), circle ● (Santa Juana, SJ), rhombus ◆ (La Matilde, LM), and star ⋆ (Control, CON). Herbivory codes are: A (with herbivore) and B (without herbivore). Arthropods codes are: first letter of the order name and the following two letters of the suborder or family name. The relative length vectors indicate the importance of soil properties.

sink wheat plants. CEC, Ca, K, P, Mg, and pH were related to levels of soil fertility and some of these soil factors; for example, K, P, and pH, were related to wheat's yield without herbivory (Szpeiner et al. 2009). Interestingly, this overlap in soil factors associated with soil fertility (CEC, K, Mg, and pH), wheat's yield (K and pH), and arthropod assembly variations (Mg, K, CEC, and pH) contrast with findings by Lenardis et al. (2007), showing that variation of micronutrients (Mn, Na, and Fe) rather than macronutrients in the soil of source pots had a strong relationship with differences in arthropod assemblies in the sink pots, but were unrelated to the crop's yield or biomass. The discrepancy with this previous work may be caused by nutrient unbalances, which can produce changes in physiological response of plants and consequently other nutrients can be more important for controlling arthropod assemblies (Dias et al. 2009, Sarfraz et al. 2009). Other possibility is differences in yield variation range of the experiments. Lenardis et al. (2007) showed that source wheat produced more biomass and grain yield in soil with ND, whereas no differences have been found across treatments in Szpeiner et al. (2009).

Despite that there are many studies showing that environmental conditions and herbivores may affect other arthropods behavior directly or indirectly (Städler 1992, Liddell 1999, Pedgley 1999, Kessler and Baldwin 2001, Myers and Gratton 2006) as well as arthropod community structure (Karban and Baldwin 1997, de Moraes et al. 1998, Dicke 1999, Liddell 1999, Price 2002, Arimura et al. 2005, de la Fuente et al. 2006, Lenardis et al. 2007), there are no studies evaluating the impact of soil–plant–herbivore interactions on cues affecting arthropod assemblies in flowering cereal crops. According to this study, it is possible to suggest that soil–plant–herbivore interactions change wheat cues and this phenomenon produces significant differences in neighboring arthropod community structure.

It should be remarked that the major difference in community structure was the richness of nonherbivorous arthropods. This suggests the existence of bottom-up effects on cues acting as attractants or repellents toward arthropods (Price 1981, 2002), which may control arthropod colonization in cropping fields before herbivore attack occurs. In future studies, it would be important to evaluate how these effects of volatile cues on arthropod community structure may relate with crop yields, considering soil heterogeneity and herbivory variability scenarios in cropping field conditions.

Acknowledgments

This research was financially supported by FONCyT; PICT/2003 N° 15007 (2003-2008) and FONCyT; PICT/2000 N°8-8370 (2003-2004).

References Cited

Arimura, G., C. Kost, and W. Boland. 2005. Herbivore-induced, indirect plant defences. BBA-Lipid Lipid Met. 1734: 91–111.

Arroyo Varela, M., and E. Viñuela Sandoval. 1991. Introducción a la Entomología. Ediciones Mundi-Prensa Madrid, España.

Bernays, A., and R. Chapman. 1994. Behavior: the process of host-plant selection, pp. 95–205. *In* A. E. Bernays and R. F. Chapman (eds.), Host-plant selection by phytophagous insects. Chapman & Hall, New York, NY.

Bezemer, T. M., and N. M. van Dam. 2005. Linking aboveground and belowground interactions via induced plant defenses. Trends Ecol. Evol. 20: 617–624.

Bruin, J., M. W., Sabelis, and M. Dicke. 1995. Do plants tap SOS signals from their infested neighbours? Trends Ecol. Evol. 10: 167–170.

Buffington, M. L., and R. A. Redak. 1998. A comparison of vacuum sampling versus sweep-netting for arthropod biodiversity measurements in California coastal sage scrub. J. Insect Conserv. 2: 99–106.

Cárcova, J., G. A. Maddonni, and C. M. Ghersa. 1998. Crop water stress index of three maize hybrids grown in soils with different quality. Field Crop Res. 55: 165–174.

de la Fuente, E. B., S. A. Suárez, C. M. Ghersa, and R.J.C. León. 1999. Soybean weeds community: relationship with cultural history and crop yield. Agron. J. 91: 234–241.

de la Fuente, E. B., A. E. Lenardis, S. A. Suárez, A. Gil, and C. M. Ghersa. 2006. Insect communities related to wheat and coriander cropping histories and essential oils in the Rolling Pampa, Argentina. Eur. J. Agron. 24: 385–395.

de Moraes, C., J. Lewis, P. Paré, T. Alborn, and J. Tumlinson. 1998. Herbivore infested plants selectively attract parasitoids. Nature 393: 570–573.

Derraik, J.G.B., G. P. Closs, K.J.M. Dickinson, P. Sirvid, B.I.P. Barratt, and B. H. Patrick. 2002. Arthropod morphospecies versus taxonomic species: a case study with Araneae, Coleoptera, and Lepidoptera. Conserv. Biol. 16: 1015–1023.

Dias, A. S., F. C. Lidon, and J. C. Ramalho. 2009. Heat stress in *Triticum:* kinetics of Fe and Mn accumulation. Braz. J. Plant Physiol. 21: 153–164.

Dicke, M. 1999. Direct and indirect effects of plants on performance if beneficial organisms, pp. 105–145. *In* J. R. Ruberson (ed.), Handbook of pest management. Marcel Decker, Inc., New York, NY.

Fischer, R. A. 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. J. Agric. Sci. 105: 447–461.

Herms, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. Q. Rev. Biol. 67: 283–335.

James, F. C., and C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? Annu. Rev. Ecol. Syst. 21: 129–166.

Karban, R., and I. T. Baldwin. 1997. Induced responses to herbivory. University of Chicago Press, Chicago, IL.

Kenkel, N. C., D. A. Derksen, A. G. Thomas, and P. R. Watson. 2002. Multivariate analysis in weed science research. Weed Sci. 50: 281–292.

Kessler, A., and I. T. Baldwin. 2001. Defensive function of herbivore-induced plant volatile emissions in nature. Science 291: 2141–2143.

Lenardis, A., C. van Baren, P. Di Leo Lira, and C. Ghersa. 2007. Plant-soil interactions in wheat and coriander crops driving arthropod assemblies through volatile compounds. Eur. J. Agron. 26: 410–417.

Liddell, C. M. 1999. Soil effects on pest populations, pp. 35–55. *In* J. R. Ruberson (ed.), Handbook of pest management, Marcel Decker, Inc., New York, NY.

Maddonni, G., S. Urricarriet, C. Ghersa, and R. Lavado. 1999. Assessing soil quality in the Rolling Pampa, using soil properties and maize characteristics. Agron. J. 91: 280–287.

Magurran, A. E. 1988. A variety of diversities, pp. 81–99. *In* A. E. Magurran (ed.), Ecological diversity and its measurement. Princeton University Press, Princeton, NJ.

McCune, B., J. B. Grace, and D. L. Urban. 2002. Analysis of ecological communities. Mjm Software Design, Gleneden Beach, OR.

Michelena, R. O., C. B. Irurtia, F. A. Vavruska, R. Mon, and A. Pittaluga. 1989. Degradación de suelos en el Norte de la Región Pampeana. INTA Publ. Técnica. 6.0. Instituto Nacional de Tecnología Agropecuaria (INTA), Centros regionales de Buenos Aires Norte, Córdoba, Entre Ríos y Santa Fe. Proyecto de Agricultura Conservacionista, Buenos Aires, Argentina.

Mueller-Dombois, D., and H. Ellenberg. 1974. Causal analytical inquiries into the origin of plant communities, pp. 335–370. *In* D. Mueller-Dombois and H. Ellenberg (eds.), Aims and methods of vegetation ecology. Wiley, New York, NY.

Myers, J. H., and C. Gratton. 2006. Influence of potassium fertility on soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), population dynamics at a field and regional scale. Environ. Entomol. 35: 219–227.

Page, A. L., R. H. Miller, and D. R. Keeney. 1982. Methods of soil analysis chemical and microbiological properties. American Society of Agronomy, Madison, WI.

Paré, P. W., and J. H. Tumlinson. 1996. Plant volatile signals in response to herbivore feeding. Fla. Entomol. 19: 93–103.

Paré, P. W., and J. H. Tumlinson. 1999. Plant volatiles as a defense against insect herbivores. Plant Physiol. 121: 325–331.

Pedgley, D. A. 1999. Weather influences on pest movement, pp. 57–78. *In* J. R. Ruberson (ed.), Handbook of pest management. Marcel Decker, Inc., New York, NY.

Perner, J., C. Wytrykush, A. Kahmen, N. Buchamann, I. Egerer, S. Creutzburg, N. Odat, V. Audorff, and W. W. Weissser. 2005. Effects of plant diversity, plant productivity and habitat parameters on arthropod abundance in montane European Grasslands. Ecography 28: 429–442.

Pichersky, E., and J. Gershenzon. 2002. The formation and function of plant volatiles: perfumes for pollinator attraction and defense. Curr. Opin. Plant Biol. 5: 237–243.

Price, P. W. 1981. Semiochemicals in evolutionary time, pp. 251–271. *In* D. A. Nordlund, R. L. Jones, and W. J. Lewis (eds.), Semiochemical, their role in pest control. Wiley, New York, NY.

Price, P. W. 2002. Resource-driven terrestrial interaction webs. Ecol. Res. 17: 241–247.

Richards, O. W., and R. G. Davies. 1984. Tratado de Entomología. Clasificación y Biología. Editorial Omega, S. A. Barcelona, España.

Sarfraz, M., L. M. Dosdall, and B. A. Keddie. 2009. Host plant nutritional quality affects the performance of the parasitoid *Diadegma insulare.* Biocontrol 51: 34–41.

Schoonhoven, L. M., T. Jermy, and J.J.A. Van Loon. 1998. Insect- plant biology: from physiology to evolution. Chapman & Hall, London, United Kingdom.

Städler, E. 1992. Behavioral responses of insects to plant secondary compounds, pp. 45–88. *In* G. Rosenthal and M. Berenbaum (eds.), Herbivores. Their interactions with secondary plant metabolites. Academic, San Diego, New York, NY.

Steidle, J.L.M., and J.J.A. Van Loon. 2003. Dietary specialization and infochemical use in carnivorous arthropods: testing a concept. Entomol. Exp. Appl. 108: 133–148.

Suárez, S. A., E. B. de la Fuente, and C. M. Ghersa, and R.J.C. León. 2001. Weed community as an indicator of summer crop yield and site quality. Agron. J. 93: 524–530.

Szpeiner, A., M. A. Martinez Ghersa, and C. M. Ghersa. 2009. Wheat volatile emissions modified by top-soil chemical characteristics and herbivory alter the performance of neighbouring wheat plants. Agric. Ecosyst. Environ. 134: 99–107.

ter Braak, C.J.F. 1987b. Ordination, pp. 91–173. *In* R.H.G. Jongman, C.J.F. ter Braak, and O.F.R. van Tongeren (eds.), Data analysis in community and landscape ecology, 1st ed. Pudoc, Wageningen, The Netherlands.

ter Braak, C.J.F. 1987b. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69: 69–77.

Turlings, T.C.J., J.H. Tumlinson, R. R. Heath, A. T. Proveaux, and R. E. Doolittle. 1991. Isolation and identification of allelochemicals that attract the larval parasitoid, *Cotesia marginiventris* (Cresson), to the microhabitat of one of its hosts. J. Chem. Ecol. 17: 2235–2251.

van Tongeren, O. F. 1987. Cluster analysis, pp. 174–206. *In* R.H.G. Jongman, C.J.F. ter Braak, and O.F.R. van Tongeren (eds.), Data analysis in community and landscape ecology. Pudoc, Wageningen, The Netherlands.

Wittstock, U., and J. Gershenzon. 2002. Constitutive plant toxins and their role in defense against herbivores and pathogens. Curr. Opin. Plant Biol. 5: 300–307.

Zadoks, J. C., T. T. Chang, and C. F. Konzak. 1974. A decimal code for the growth stage of cereals. Weed Res. 14: 415–421.

Zhao, L. Y., J. I. Chen, D. F. Cheng, J. R. Sun, Y. Liu, and Z. Tian. 2009. Biochemical and molecular characterizations of *Sitobion avenae*-induced wheat defense responses. Crop Prot. 28: 435–442.

Received 16 August 2013; accepted 27 January 2014.