

# Regional abundance of a planthopper pest: the effect of host patch area and configuration

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## Abstract

The effect of host patch area and configuration on the abundance of dispersing individuals of *Delphacodes kuscheli* Fennah (Homoptera: Delphacidae), the vector of Río Cuarto disease in maize, was investigated in the main maize production area of Argentina. Actively dispersing *D. kuscheli* individuals were collected from 15 sampling sites during the spring seasons of 1999 and 2000, using sticky traps placed at 6 m above ground level. Host patches were detected and quantified using Landsat 5 TM images for the periods studied. The spatial pattern analysis program FRAGSTATS was used to estimate the total class area, largest patch index, mean proximity index, and patch cohesion index for patches of winter pastures (the main insect host during winter) as observed from the satellite images. Landsat 5 TM estimations showed local variability in the proportion of winter pastures, with patches bigger during 1999 than during 2000, but these patches represented only a very small part of the total landscape. Proximity between host patches was also variable between sites and higher values of cohesion occurred during the first sampling season. The relationship between host area and *D. kuscheli* mean abundance was adjusted to an exponential ( $R^2 = 77.5\%$ ) model. Host patch dominance, host patch isolation, and host patch connectivity all showed a positive relationship with *D. kuscheli* mean abundance, adjusting significantly to linear models ( $R^2 = 92\%$ ,  $R^2 = 90\%$ , and  $R^2 = 22\%$ , respectively). Outbreaks of Río Cuarto disease in the main maize production area of Argentina are related to high vector populations. The results indicate that the abundance of *D. kuscheli* depends on factors related to the abundance and configuration of its host patches.

## Introduction

*Delphacodes kuscheli* (Fennah) (Homoptera: Delphacidae) is the economically most important delphacid species in Argentina because of its ability to transmit what was initially thought to be a local strain of the maize rough dwarf virus (MRDV–RC) named Río Cuarto disease (Conci & Marzachi, 1993; March et al., 1995). The insect does not reproduce on maize, but it can transmit the virus when feeding on maize plants. If the infection occurs during the first 3 weeks after plant emergence, the disease can be severe and, in some cases, lead to plant death. After its most susceptible period, infection may occur but the effect on grain production is relatively minor (Lenardón, 1987).

*Delphacodes kuscheli* has a limited range of hosts, and can breed on winter cereals such as rye (*Secale cereale* L.) or

wheat (*Triticum aestivum* L.) and winter pastures such as oats (*Avena sativa* L.). The latter are the most important overwintering hosts as they are sown by the end of the summer and not harvested until spring, becoming the main source from which *D. kuscheli* migrates to maize fields (Tesón et al., 1986; Virla & Remes Lenicov, 1991; Ornaghi et al., 1993; Garat et al., 1999; Remes Lenicov et al., 1999). The species has a wide distribution, from the north of Argentina (Jujuy Province) to the south (Río Negro Province) (Remes Lenicov et al., 1999).

There are two wing forms among populations of *D. kuscheli*: long-winged macropters, which can fly, and short-winged brachipters, which are flightless (Ornaghi et al., 1993). Only macropters disperse and, in general, their dispersal range is from 1 to 3 km (Denno & Grissel, 1979; Denno et al., 1980, 1991). *Delphacodes kuscheli* is a multivoltine species, with three or four generations per year (Remes Lenicov et al., 1991). Most of the generations

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appear during late (southern hemisphere) spring and early summer (Garat et al., 1999), with a clear seasonal pattern, increasing during October and November, which roughly coincides with the senescence of the winter pastures, and peaking in December (Grilli & Gorla, 1999, 2002). Areas with high population densities are strongly associated with land use management (Grilli & Gorla, 1997, 1998), and the presence, condition, and distribution of host vegetation (Grilli & Gorla, 1997, 1998). The abundance of planthoppers is related to the distribution and abundance of host plants: the higher the environmental diversity in terms of crop species per unit area, the lower the abundance of individual planthopper species (Grilli & Gorla, 1999). But all these studies were performed at a regional level.

In the study area, farmers are very traditional in terms of when and what to sow in their farmland, and crop rotation in each field on the farm is a common practice. In general, it is thus very rare for a farm plot to have the same crop from one year to the next. The same place will show a changing pattern of land use, with larger or smaller areas dedicated to host and non-host-plant species, and this can be considered as the most important change observed in the land.

Many authors (Chen et al., 1995; Hunter et al., 1996, 2002; Collinge, 2000; Connor et al., 2000; Hanski & Singer, 2001; Biederman, 2002; Cronin, 2003) have emphasised the role of habitat patches in insect population ecology. Studies of patchily distributed populations showed the importance of patch size and isolation in determining their distributions (Hanski, 1999). The occurrence and density of planthoppers in a particular habitat patch may depend on the area, isolation, quality, and surrounding landscape structure of the patch (Biederman, 2002). In many cases immigration and emigration from habitat patches will be affected by patch size and distribution (Connor et al., 2000; Cronin, 2003).

The size, number, and distribution of patches are important aspects of a landscape (Forman & Godron, 1986). The spatial configuration of a landscape can be quantified using patch-based measures (Gustafson, 1998), including size, number, density, and connectivity of patches, computed for all classes at the same time or for a particular class of interest (Gustafson & Parker, 1992; Schumaker, 1996; Gustafson, 1998). The objective of this work was to examine the effects of host patch area and configuration on the abundance of the dispersing fraction of *D. kuscheli* populations.

## Materials and methods

### Study area

The study was performed in the most important maize production area of Argentina, which extends from the

south of the provinces of Córdoba and Santa Fé to the north of the province of Buenos Aires. There are 16 species of Delphacidae present in the study area, but *D. kuscheli* is the most abundant, with the highest 'relative weight index' (approximately 25) (Laguna et al., 2002). In other areas, insect abundance and disease incidence are variable.

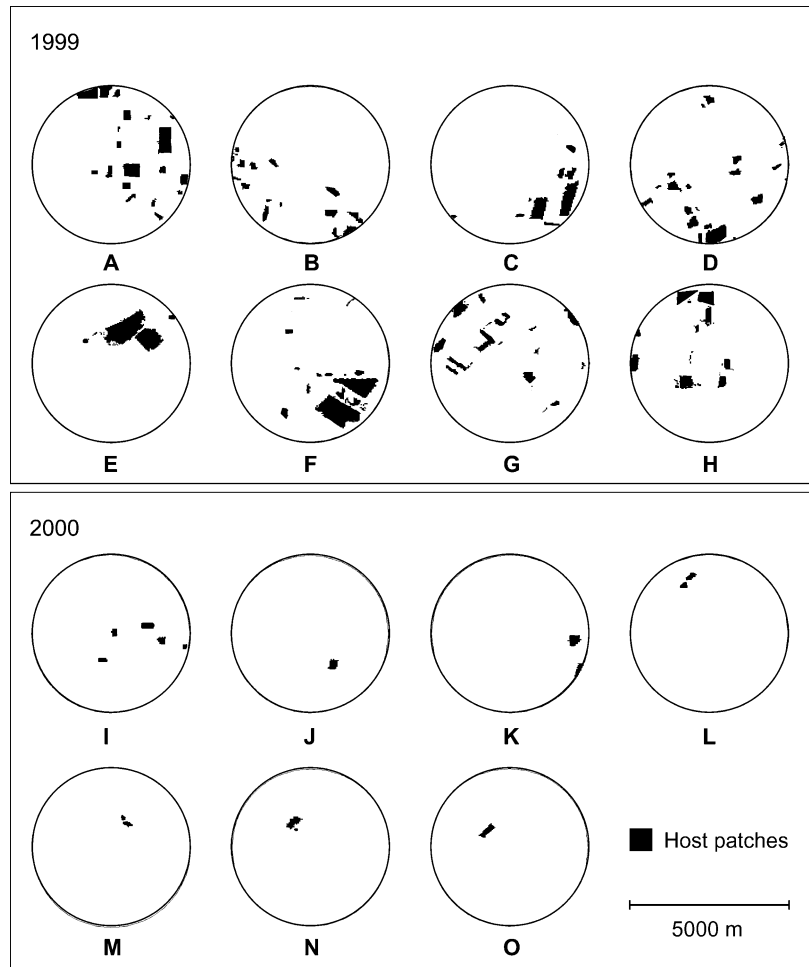
### Insect sampling

Data on insect abundance were derived from an 8-month field study that recorded flying *D. kuscheli* individuals using sticky traps. Insects were collected within a 59 113 km<sup>2</sup> area using sticky traps, as described in Grilli & Gorla (1997), replaced every 7 days during the spring and summer seasons of 1999 and 2000. This method has been shown to be useful for estimating the abundance of dispersing macropterous individuals (Grilli & Gorla, 1998). Sampling was conducted from the beginning of spring in order to detect flying *D. kuscheli* individuals leaving winter pastures, which are the only host available from the end of summer to the end of winter. Sampling was carried out at 15 sites, eight in 1999 (identified as A, B, C, D, E, F, G, and H) and seven in 2000 (identified as I, J, K, L, M, N, and O; Figure 1). Sites were 50 km apart and the sticky traps in each of them consisted of metal cylinders, supporting a plastic film coated with lithium grease (YPF® EP 62, Repsol-YPF, Argentina) as an adhesive, which were placed on the top of a 6-m mast. The plastic film was removed on each sampling date, replaced by a clean one and taken to the laboratory, where *D. kuscheli* were identified according to Remes Lenicov & Virla (1999). At each sampling site, three traps were placed to form a single set (maximum of 100 m and minimum of 25 m separation between the most distant traps of the set) with no special connection between them. Sites were selected within a uniform landscape, and special care was taken to avoid tree barriers in the area around the traps.

Insect abundance was expressed as insects/trap/day. Although the traps were in the field from September to December (the most critical period for Río Cuarto disease transmission), the mean insect abundance estimated considered only the spatial variation of the abundance with all the insects captured during this period (121 days) grouped in one mean value per site.

### Land-cover estimation

Winter pastures are sown at the end of the summer and are not harvested until spring. Eight Landsat TM 5 scenes were used to estimate the land cover of the study area during each year of the study. A supervised classification was used to estimate land use, based on spectral brightness, for six spectral bands in the visible and reflected infrared regions of the electromagnetic spectrum. We identified 300 training sites from site visits and considered three classes in the



**Figure 1** Areas around the sampling site with host patches extracted from Landsat 5 TM classified images. Sampling sites: A, B, C, D, E, F, G, and H were taken during 1999; I, J, K, L, M, N, and O during 2000.

analysis: winter pasture, perennial pasture, and stubble or naked soil (as one class).

Training site areas were digitized and signatures, describing each informational class, were created. We classified images using a minimum-distance-to-means classifier, which is less susceptible to training site problems than others (Eastman, 2003). Finally, accuracy was assessed by generating a random set of locations for verification of the true land-cover type. We applied an error matrix to compare the classes obtained with the real classes found in the field and to tabulate the overall proportional error (Congalton & Green, 1999). Based on the most common dispersal distances for planthoppers reviewed by Denno et al. (1991), a circular area of 5000 m in diameter around each insect sampling site was extracted from each classified image, and the area of patches classified as winter pastures was retained (Figure 1).

**Landscape metrics**

Using FRAGSTATS 3.3 (McGarigal & Marks, 1995), four landscape configuration measures were estimated for

the winter pastures obtained from the classified images (Figure 1). All of them are patch-based indices representing different landscape properties:

*Total class area* represents the total area of the host patches in each sampling site and approaches 0 as the patch type becomes increasingly rare in the landscape.

*Largest patch index* quantifies the percentage of the total landscape area included by the largest patch and is a simple measure of dominance.

*Mean proximity index* discriminates isolated patches from aggregated patches. This index will equal 0 if a patch has no neighbours of the same patch type; in our case the proximity index increases as the number of neighbour patches of the same class within the 5000 m searching diameter increases, and as those patches become closer and more contiguous. It is estimated by:

$$PROX = \sum_{s=1}^n \frac{a_{ijs}}{h_{ijs}^2},$$

where  $a_{ijs}$  = area ( $m^2$ ) of patch  $ijs$  within the specified neighbourhood ( $m$ ) of patch  $ij$ ,  $h_{ijs}$  = distance ( $m$ ) between

patch  $ij$ s and each of the patches of the same class, based on patch edge-to-edge distance, computed from cell centre to cell centre,  $i$  is the patch class,  $j$  is the patch number, and  $s$  is the number of patches within the specified neighbourhood. A mean value of the proximity index was calculated for each study site.

*Patch cohesion index* quantifies the connectivity of a particular patch type. It is sensitive to the aggregation of the focal class (in our case winter pastures patches). Patch cohesion increases as the patch type becomes more clumped or aggregated in distribution (Gustafson, 1998). In our particular case, the index will approach 0 as the proportion of the landscape which consists of winter pastures decreases, becomes more subdivided and less physically connected. The cohesion index will approach the maximum value of 100 as the proportion of the landscape which includes winter pastures increases. It is estimated by:

$$PCI = \left[ 1 - \frac{\sum_{j=1}^n P_{ij}}{\sum_{j=1}^n P_{ij} \sqrt{a_{ij}}} \right] \left[ 1 - \frac{1}{\sqrt{A}} \right]^{-1} \cdot (100),$$

where  $p_{ij}$  = perimeter of patch  $ij$  in terms of number of cell surfaces,  $a_{ij}$  = area of patch  $ij$  in terms of number of cells, and  $A$  = total number of cells in the landscape.

#### Data analysis

The density of *D. kuscheli* was estimated as the mean number of macropterous individuals collected per trap

divided by the number of days, the plastic film was exposed to field conditions (insects/trap/day). The relationship between the landscape measures obtained with FRAGSTATS and the dispersive fraction of *D. kuscheli* were estimated by simple linear regression between each measure and insect abundance. To test normal distribution of regression residuals, the Shapiro–Wilk test was applied (Shapiro & Wilk, 1965). This test involves the calculation of a statistic  $W$  which is compared to a critical value of  $W$  provided in a table of critical values. The null hypothesis is rejected if  $W < W_c$  (with  $\alpha$  level of significance and  $n$  sample size).

#### Results

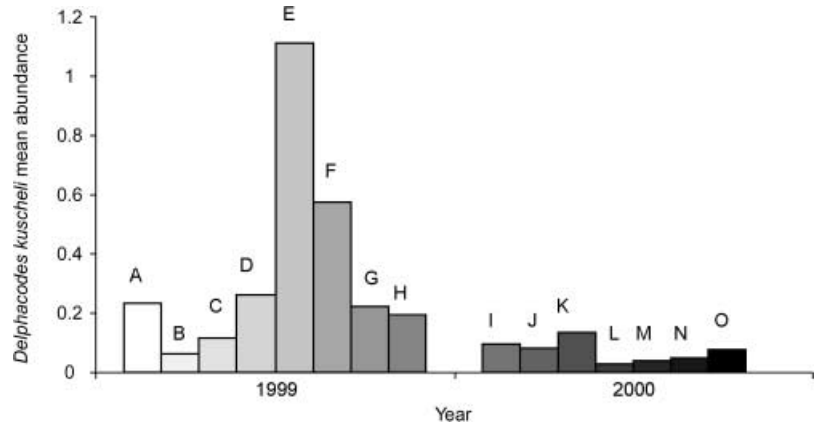
Land use in the studied area of Argentina has changed little in the last 20 years. Estimations from Landsat 5 TM showed that there is considerable local variability in land management, in particular regarding the proportion of winter pastures (primary host) (Figure 1). Land use mean area was variable, with respect to the area of host patches (Table 1). The error matrix accounted for 83 and 85% of overall accuracy of the land use classification for 1999 and 2000, respectively.

Mean abundance of *D. kuscheli* was variable in the different sites and years. The central area of the maize region showed the highest abundances during 1999 in sites E (Santa Fé province), F, and D (Buenos Aires Province). During the 2000 season, all the sites showed lower *D. kuscheli* mean abundance and the spatial pattern observed during 1999 was not repeated (Figure 2).

**Table 1** Total class area (ha), largest patch index expressed as percentage of the total area, mean patch proximity index (dimensionless) and patch cohesion index (expressed as the percentage of connectivity) of host patches, for each sampling site of *Delphacodes kuscheli* in the study area

Year	Sampling site	Total class area (ha)	Largest patch index (%)	Mean patch proximity index	Patch cohesion index (%)
1999	A	81.27	0.2941	2.9216	73.3775
	B	41.4	0.1886	2.2264	68.3799
	C	37.17	0.617	2.381	87.816
	D	82.35	0.7467	3.4646	79.9924
	E	94.14	2.2944	75.7466	96.0703
	F	104.4	1.2855	30.0849	93.5224
	G	67.86	0.1598	3.5662	81.6506
	H	60.57	0.2639	4.324	77.0125
2000	I	13.41	0.124	0.9941	73.9613
	J	6.39	0.0805	0	88.43
	K	9.9	0.0275	0.1507	86.677
	L	4.14	0.0199	3.1265	76.6366
	M	9	0.0766	13.1382	88.6944
	N	3.78	0.018	0.2689	81.7815
	O	8.19	0.0555	0	89.7388

**Figure 2** Mean *Delphacodes kuscheli* abundance/trap/day during both sampling periods in each sampling site. A, B, C, D, E, F, G, and H were taken during 1999, I, J, K, L, M, N, and O during 2000.



Host area ranged from 3.78 to 104 ha within the study area (5000 m in diameter) at each sampling site. During 1999 there were larger patches than during 2000, but these patches represented a small amount of the total landscape as revealed by the largest patch index. Proximity between host patches also was very variable, with the highest values occurring in 1999. Finally, host patches were clumped but higher values of cohesion occurred during 1999 (Table 1).

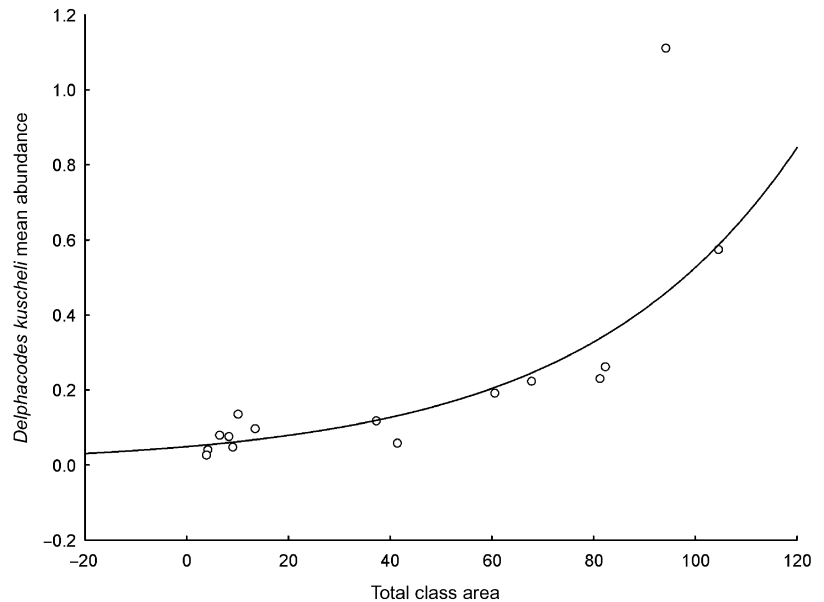
The effect of patch configuration on *D. kuscheli* populations was tested by simple regressions. Different models were tested and in all cases *D. kuscheli* mean abundance was used as the dependent variable. Normal distribution of the residuals applying the Shapiro–Wilk test (Shapiro & Wilk, 1965) could not be rejected. The relationship between total class area and *D. kuscheli* mean abundance fitted the exponential model ( $R^2 = 77.5\%$ ;  $r = 0.88$ ,  $P < 0.001$ ;

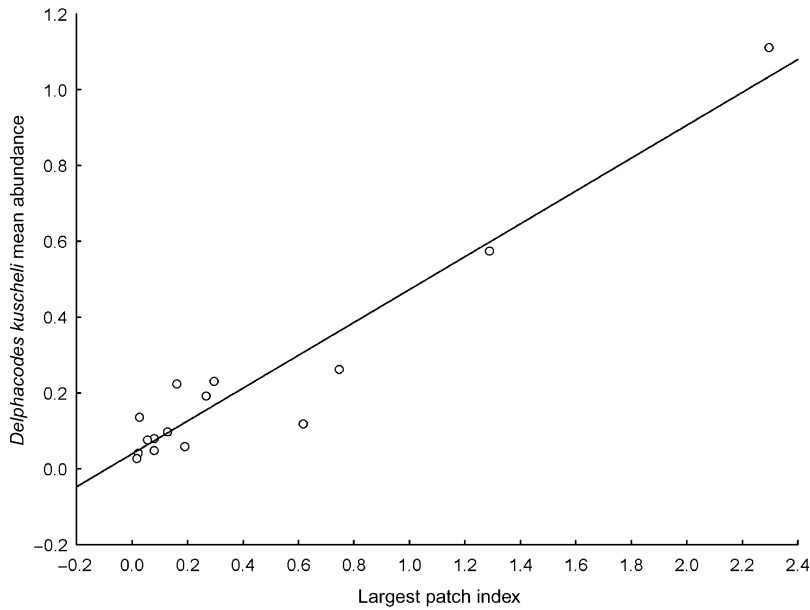
Figure 3). Host patch dominance, expressed by the largest patch index, showed a positive relation with *D. kuscheli* mean abundance, and it adjusted significantly to a linear model ( $R^2 = 92\%$ ;  $r = 0.96$ ,  $P < 0.001$ ; Figure 4). Host patch isolation, estimated by using the mean proximity index, showed a positive relationship with *D. kuscheli* mean abundance and it significantly fitted a linear model ( $R^2 = 90\%$ ;  $r = 0.95$ ,  $P < 0.001$ ) (Figure 5); and finally, host patch connectivity represented by the patch cohesion index also showed a positive relationship with *D. kuscheli* mean abundance, significantly fitting a linear model ( $R^2 = 22\%$ ;  $r = 0.52$ ,  $P < 0.04$ ; Figure 6).

**Discussion**

More than 80% of the maize produced in Argentina is sown in the study area (Indec, 1995). As Río Cuarto disease

**Figure 3** Relationship between *Delphacodes kuscheli* mean abundance and total class area for host patches in the 5000 m around each sampling site.  $R^2 = 77.5\%$ ;  $r = 0.88$ ,  $P < 0.001$  for exponential model (fitted).



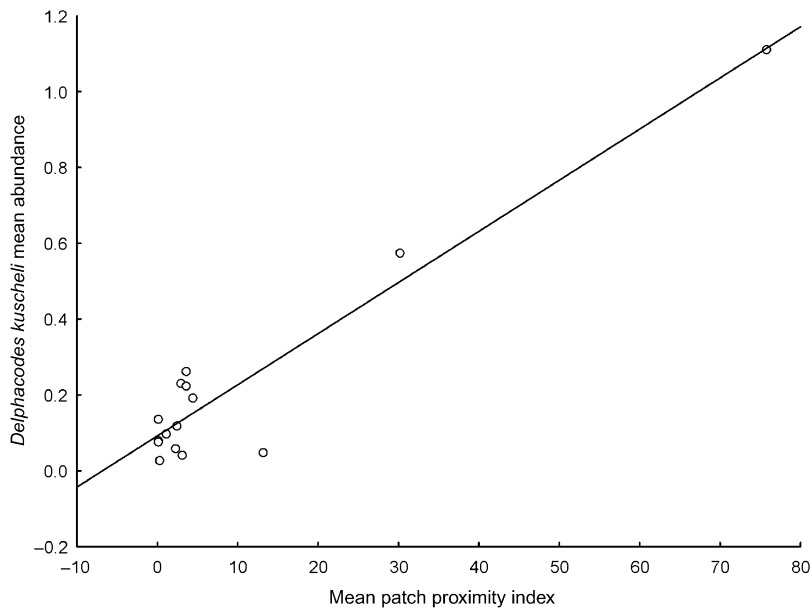


**Figure 4** Relationship between *Delphacodes kuscheli* mean abundance and largest patch index, extracted from host patches in the 5000 m around each sampling site.  $R^2 = 92\%$ ;  $r = 0.96$ ,  $P < 0.001$  for linear model (adjusted).

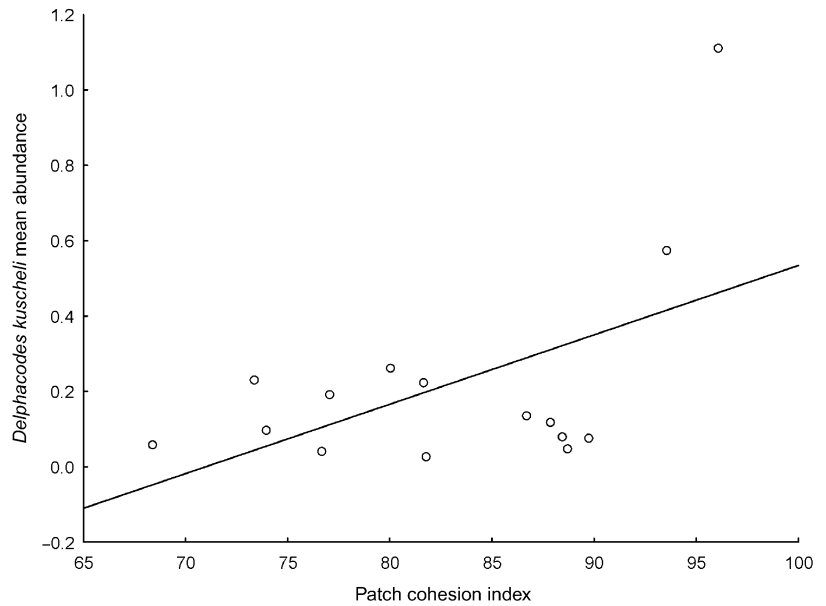
is the most important disease affecting maize and as *D. kuscheli* does not breed in maize but migrates to it from other sources (Ornaghi et al., 1993), this study area was chosen in order to compare these dispersive populations (macropterous) of *D. kuscheli*.

Previous analyses of *D. kuscheli* showed that the species is affected by the condition and distribution of the vegetation (Grilli & Gorla, 1997). They also showed that its abundance is related to the distribution and abundance of host plants at a regional level (Grilli & Gorla, 1999). In nature, the distribution of plants is more or less aggregated, forming

discrete patches. This situation is more evident in agricultural landscapes, and it can be considered as a regional-scale experiment, in which the distribution, abundance, and fragmentation of those plant patches will inevitably affect the distribution and abundance of insect pests. For specialist herbivorous insects with a restricted range of hosts, habitat in an agricultural landscape will be distributed in patches (crop fields) of different sizes, at varying distances from each other, with varying frequencies of disturbance from farming operations, and with increased environmental stochasticity caused by the disappearance



**Figure 5** Relationship between *Delphacodes kuscheli* mean abundance and mean patch proximity index for host patches in the 5000 m around each sampling site.  $R^2 = 90\%$ ;  $r = 0.95$ ,  $P < 0.001$  for linear model (adjusted).



**Figure 6** Relationship between *Delphacodes kuscheli* mean abundance and patch cohesion index for host patches in the 5000 m around each sampling site.  $R^2 = 22\%$ ;  $r = 0.52$ ,  $P < 0.04$  for linear model (adjusted).

of patches whenever a field is used for a different crop type (Hanski & Gilpin, 1997; Fahrig & Jonsen, 1998).

The sampling technique employed ensured that only macropterous insects were collected as they are the only ones capable of flying at 6 m above the ground. Although *D. kuscheli* populations are made up of long-winged and short-winged individuals, only the macropterous ones disperse to maize and transmit Río Cuarto disease (Ornaghi et al., 1993; Grilli & Gorla, 1997). Over the 2-year study period, the average population density was higher and more variable during 1999 than during 2000, with the highest abundance in site E, located in Santa Fé province in 1999 (Figure 2).

Although the study was performed in an almost homogeneous agricultural region, local differences in land use were observed in the area farmers sow with host and non-host species. When analysing the land cover using Landsat images, different proportions of areas with host and non-host crops were found (Figure 1).

Studies of patchily distributed insect populations have made clear the importance of host patch size and degree of isolation in determining the distribution of insect populations (Hanski, 1999). Planthopper occurrence and density in a particular habitat patch may depend on the area, isolation, quality, and surrounding landscape structure of the patch (Biederman, 2002). Host area and configuration was very variable during the period of this study (Table 1). The area, cohesion, connectivity, and the dominance of host patches have a direct effect on the *D. kuscheli* population. Dispersing individuals of *D. kuscheli* are positively affected by the total host area immediately surrounding the sampling traps (Figure 3). In many cases a positive relationship has been

found between planthopper population density and the area of host plant patches (Lawton, 1978; Raup & Denno, 1979; Denno et al., 1981). There are many conceptual explanations for the relationship between insect species abundance and the area of its host. The area requirements of planthopper populations differ among species (Biederman, 2002) based on population dynamics or life history traits. Species that can build up high densities in their patches can reach sufficient population sizes to reduce the risk of extinction due to environmental stochasticity (Lande, 1993). Higher probabilities of finding mates, winter survival, or annual recolonization because of demographic or environmental stochasticity may lead to populations in larger patches persisting at higher mean densities than populations in small patches (Raupp & Denno, 1979; Denno et al., 1981; Møller, 1991, 1995). Additionally, a positive correlation between population density and patch area may arise from a number of mechanistic explanations (Connor et al., 2000) acting individually or collectively, and the mechanisms may differ depending on the species. For example, the resource concentration hypothesis (Risch, 1981; Kareiva, 1983) predicts that specialist herbivores should have higher densities in large patches of their host plants because insects move from small to big habitat patches (Root, 1973). Another possible explanation which is not incompatible with the movement hypothesis is the 'enemies hypothesis'. This suggests that predators are more effective in smaller patches than in large ones (Root, 1973; Raupp & Denno, 1979; Kareiva, 1983), keeping densities of prey populations lower in small patches (Denno et al., 1981; Ambuel & Temple, 1983; Askins et al., 1987; Rolstad & Wegge, 1987; Møller, 1991, 1995; Paton, 1994).

There is evidence that positive correlations between density and patch area occur more frequently in patch systems embedded in highly fragmented landscapes (Andren, 1994). This seems to be the case in this study system. We found that *D. kuscheli* populations are positively affected by the cohesion of the host patches (Figure 6), with *D. kuscheli* more abundant in less fragmented host patches. The first intuitive thought is that, for insects that are habitat specialists and unable to use the matrix, fragmentation will reduce the density because of an increase in demographic stochasticity or the disruption of metapopulation dynamics (Debinski & Holt, 2000). *Delphacodes kuscheli* can be considered as a specialist species as it has a very limited range of hosts (Remes Lenicov & Virla, 1999). In an exhaustive survey, Debinski & Holt (2000) showed that, in at least half of the analysed cases, the abundance of insect populations decreased with habitat fragmentation, especially for specialist species (Vandewoestijne et al., 2005). In specialist insect species, even small scale habitat fragmentation causes a significant decrease in population abundance (Zabel & Tscharrantke, 1998). In species with high dispersal ability such as *D. kuscheli*, there is a higher probability of all patches being reached (Biedermann, 2002), but patch connectivity is a critical factor affecting patterns of patch occupancy and regional dynamics in patchily distributed populations (Hanski, 1994, 1999; Stacey et al., 1997). Host patch proximity has a direct effect on the abundance of dispersive *D. kuscheli* populations (Figure 5). Patch isolation is frequently predicted to have a negative effect on population density since isolated patches will have lower immigration, reducing rescue and recolonization rates (Sjögren Gulve, 1994; Dunning et al., 1995; Enoksson et al., 1995; Hinsley et al., 1995). A possible explanation for this is that greater interpatch separation will lead to an increase in the dispersing insects' mortality rate due to a lower probability of finding a suitable host patch. Mortality during dispersal is often ignored in spatial population studies, but this cause of mortality may be, in certain cases, very important (Matter et al., 2004; Hanski et al., 2000).

Finally, a positive relationship was found between host dominance, represented by the largest patch index, and *D. kuscheli* abundance (Figure 4). One major requisite of the planthoppers' habitat is the presence of the host plant (Biedermann, 2002). It is essential to the planthoppers' nutrition (Backus, 1985), as a shelter for their eggs (Claridge et al., 1977), and as a transmission means for bioacoustic signals (Michelsen et al., 1982). The loss of plant diversity causes higher insect abundance, in particular of specialist insect pests (Root, 1973; Kareiva, 1983; Risch et al., 1983; Strong et al., 1984), which in general have higher reproductive rates in monocultures (Kareiva, 1985; Elmstrom et al., 1988; Haddad et al., 2001).

Among the many methods used to manage Río Cuarto disease, we can mention the use of tolerant (but not resistant) maize hybrids to diminish the economic incidence of the disease (Prescello et al., 1991), or the avoidance of the maximum abundance of dispersive vectors in the field (Lenardón, 1987; Remes Lenicov et al., 1999), by sowing maize at the beginning of spring (September) or at the beginning of summer (end of December).

A more general approach could be the use of area-wide pest management, limiting or managing the spatial distribution of winter host patches. The objective of area-wide pest management is the suppression of key pest populations by applying uniform tactics on large geographic areas (Kogan, 1998). This technique has been applied to slow the spread of insect pests that are highly mobile and occupy a large geographic area (Sharov et al., 2002), or to reduce their numbers to densities below the economic injury level (Tollefson, 1998; Vargas et al., 2001; Chandler, 2003). This approach is particularly useful in those cases in which the insect pest species can escape from fields where control measures are applied, and can colonize available non-treated areas of host plants. *Delphacodes kuscheli* seems to qualify for this approach because the ecological requirements of *D. kuscheli* are basically related to the presence and configuration of its host patches. The migratory tactics of *D. kuscheli* are similar to those noted by Denno (1979) for some of the families of Auchenorrhyncha, especially delphacids in unstable habitats. The mechanism of dispersion is triggered by the condition of the host (Ornaghi et al., 1993). In spring (end of September), winter pastures decline and *D. kuscheli* begins its activity to escape from this declining resource. By the beginning of the summer, all winter pastures patches disappear, so the individuals trapped in the sticky traps are those leaving the patches. The number of dispersing individuals will vary according to the abundance of the populations in the patches around each sticky trap. Population densities of dispersing individuals in a certain area are strongly affected not only by host area but also by proximity, dominance, and connectivity of the host patches. Areas with bigger, closer, and less fragmented host patches will have larger amounts of dispersing *D. kuscheli* individuals. Río Cuarto disease outbreaks in the main maize production area of Argentina are generally related to an unusually high vector population (Lenardón et al., 1998). Previous studies indicate that agroecosystem management and the amount of green vegetation in a region can have some effect on *D. kuscheli* populations present in that region (Grilli & Gorla, 1997, 1998). The results presented here show that the distribution and abundance of *D. kuscheli* in a region depends on many factors related to the presence and configuration of host patches. It is very probable that the concurrence of all these



factors is the ultimate cause for the unusually high numbers of dispersive individuals that finally cause area-wide outbreaks of Río Cuarto disease in Argentina.

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### References

- Ambuel B & Temple SA (1983) Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* 64: 1057–1068.
- Andren H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355–366.
- Askins RA, Philbrick MJ & Sugeno DS (1987) Relationship between the regional abundance of forest and the composition of forest bird communities. *Biological Conservation* 39: 129–152.
- Backus EA (1985) Anatomical and sensory mechanisms of leafhopper and planthopper feeding behaviour. *The Leafhoppers and Planthoppers* (ed. by LR Nault & JG Rodriguez), pp. 163–194. Wiley and Sons, New York, NY, USA.
- Biedermann R (2002) Leafhoppers (Hemiptera, Auchenorrhyncha) in fragmented habitats. *Denisia* 4: 523–530.
- Chandler LD (2003) Corn rootworm areawide management program: United States Department of Agriculture. Agricultural Research Service. *Pest Management Science* 59: 605–608.
- Chen J, Franklin JF & Spies TA (1995) Growing season microclimatic gradients from clearcut edges into old growth Douglas-fir forests. *Ecological Applications* 5: 74–86.
- Claridge MF, Reynolds WJ & Wilson MR (1977) Oviposition and food plant discrimination in leafhoppers of the genus *Oncopsis*. *Ecological Entomology* 2: 19–25.
- Collinge SK (2000) Effects of grassland fragmentation on insect species loss, colonization and movement pattern. *Ecology* 81: 2211–2226.
- Conci LR & Marzachi C (1993) Avances en la caracterización molecular del genoma del virus causal del 'Mal de Río Cuarto'. *Actas Workshop 'Mal de Río Cuarto del Maíz'* (ed. by INTA), pp. 27–28. Instituto Nacional de Tecnología Agropecuaria, Córdoba, Argentina.
- Congalton RG & Green K (1999) *Assessing the Accuracy of Classifications of Remotely Sensed Data: Principles and Practices*. Lewis Publishers, New York, NY, USA.
- Connor EF, Coutney AC & Yoder JM (2000) Individuals–area relationship: the relationship between animal population density and area. *Ecology* 81: 734–748.
- Cronin JT (2003) Movement and spatial population structure of a prairie planthopper. *Ecology* 84: 1179–1188.
- Debinski DM & Holt RD (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14: 342–355.
- Denno RF (1979) The relation between habitat stability and the migratory tactics of planthoppers (Homoptera: Delphacidae). *Miscellaneous Publications of the Entomological Society of America* 11: 41–69.
- Denno RF & Grissel EE (1979) The adaptiveness of wing dimorphism in the salt marsh inhabiting planthopper, *Prokelisia marginata* (Homoptera: Delphacidae). *Ecology* 60: 221–236.
- Denno RF, Raupp M & Tallamy D (1981) Organization of a guild of sap-feeding insects: equilibrium vs. nonequilibrium coexistence. *Insect Life History Patterns: Habitat and Geographic Variation* (ed. by RF Denno & F Dingle), pp. 151–181. Springer-Verlag, New York, NY, USA.
- Denno RF, Raupp M, Tallamy D & Reichelderfer CF (1980) Migration in heterogeneous environments: differences in habitat selection between the wing forms of the dimorphic planthopper *Prokelisia marginata* (Homoptera: Delphacidae). *Ecology* 61: 859–867.
- Denno RF, Roderick GK, Olmstead KL & Döbel HG (1991) Density related migration in planthoppers (Homoptera: Delphacidae): the role of habitat persistence. *The American Naturalist* 138: 1513–1541.
- Dunning JB, Borgella R, Clements K & Meffe GK (1995) Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conservation Biology* 9: 542–550.
- Eastman RJ (2003) *IDRISI Kilimanjaro Guide to GIS and Image Processing*. ClarkLabs Clark University, Worcester, MA, USA.
- Elmstrom KM, Andow DA & Barclay WW (1988) Flea beetle movement in a broccoli monoculture and diculture. *Environmental Entomology* 17: 299–305.
- Enoksson B, Angelstam P & Larsson K (1995) Deciduous forest and resident birds: the problem of fragmentation within a coniferous forest landscape. *Landscape Ecology* 10: 267–275.
- Fahrig L & Jonsen I (1998) Effect of habitat patch characteristics on abundance and diversity of insects in an agricultural landscape. *Ecosystems* 1: 197–205.
- Forman RTT & Godron M (1986) *Landscape Ecology*. John Wiley and Sons, New York, NY, USA.
- Garat O, Trumper EV, Gorla DE & Perez-Harguindeguy N (1999) Spatial pattern of the Río Cuarto corn disease vector, *Delphacodes kuscheli* Fennah (Hom., Delphacidae), in oats fields in Argentina and design of sampling plans. *Journal of Applied Entomology* 123: 121–126.
- Grilli M & Gorla D (1997) The spatio-temporal pattern of *Delphacodes kuscheli* (Homoptera: Delphacidae) abundance in central Argentina. *Bulletin of Entomological Research* 87: 45–53.
- Grilli MP & Gorla DE (1998) The effect of agroecosystem management on the abundance of *Delphacodes kuscheli* (Homoptera: Delphacidae), vector of the Maize Rough Dwarf virus, in central Argentina. *Maydica* 43: 77–82.
- Grilli MP & Gorla DE (1999) The distribution and abundance

- of Delphacidae (Homoptera) in central Argentina. *Journal of Applied Entomology* 123: 13–21.
- Grilli MP & Gorla DE (2002) Variación geográfica de la abundancia poblacional de *Delphacodes kuscheli* (Fennah) en la región central de Argentina. *Ecología Austral* 12: 187–195.
- Gustafson EJ (1998) Quantifying landscape spatial pattern: what is the state of the art. *Ecosystems* 1: 143–156.
- Gustafson EJ & Parker GR (1992) Relationships between landcover proportion and indices of landscape spatial pattern. *Landscape Ecology* 7: 101–110.
- Haddad NM, Tilman D, Haarstad J, Ritchie M & Knops JMH (2001) Contrasting effects of plant richness and composition on insect communities: a field experiment. *The American Naturalist* 158: 17–35.
- Hanski I (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63: 151–162.
- Hanski I (1999) *Metapopulation Ecology*. Oxford University Press, New York, NY, USA.
- Hanski I, Alho J & Miolani A (2000) Estimating the parameters of survival and migration in metapopulations. *Ecology* 81: 239–251.
- Hanski I & Gilpin ME (1997) *Metapopulation Biology*. Ecology, Genetics, and Evolution. Academic Press, San Diego, CA, USA.
- Hanski I & Singer MC (2001) Extinction-colonization dynamics and host plant choice in butterfly metapopulations. *American Naturalist* 158: 341–353.
- Hinsley SA, Bellamy PE, Newton I & Sparks TH (1995) Habitat and landscape factors influencing the presence of individual breeding bird species in woodland fragments. *Journal of Avian Biology* 26: 94–104.
- Hunter MD (2002) Landscape structure, habitat fragmentation, and the ecology of insects. *Agricultural and Forest Entomology* 4: 1569–1166.
- Hunter MD, Malcom SB & Hartley SE (1996) Population level variation in plant secondary chemistry and the population biology of herbivores. *Chemoecology* 7: 45–56.
- Indec (1995) *Atlas Estadístico República Argentina*. Instituto Nacional de Estadísticas y Censos. Buenos Aires, Argentina.
- Kareiva PM (1983) Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. *Variable Plants and Herbivores in Natural and Managed Systems* (ed. by RF Denno & MS McClure), pp. 259–289. Academic Press, New York, NY, USA.
- Kareiva PM (1985) Finding and losing host plants by *Phyllotreta*: patch size and surrounding habitat. *Ecology* 66: 1809–1816.
- Kogan M (1998) Integrated pest management: historical perspectives and contemporary developments. *Annual Review of Entomology* 43: 243–270.
- Laguna IG, de Remes Lenicov AM, Virla EG, Avila AO, Gimenez Pecci MP et al. (2002) Difusión del virus del Mal de Río Cuarto (MRCV) del maíz, su vector, delfácidos asociados y huéspedes alternativos en la Argentina. *Revista de la Sociedad Entomológica Argentina* 61: 87–97.
- Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist* 142: 911–927.
- Lawton JH (1978) Host plant influences on insect diversity: the effects of space and time. *Diversity of Insect Faunas* (ed. by LA Mound & N Waloff), pp. 105–125. Blackwell Publishing, Oxford, UK.
- Lenardón S (1987) Mal de Río Cuarto. *Revista CREA* 1987: 6–15.
- Lenardón SL, March GJ, Nome SF & Ornaghi JA (1998) Recent outbreak of ‘Mal de Río Cuarto’ virus on corn in Argentina. *Plant Disease* 82: 448.
- March G, Balzarini M, Ornaghi J, Beviacqua J & Marinelli A (1995) Predictive model for ‘Mal de Río Cuarto’ disease intensity. *Plant Disease* 79: 1051–1053.
- Matter SF, Roland J, Moilanene A & Hanski I (2004) Migration and survival of *Parnasus smintheus*: detecting effects of habitat for individual butterflies. *Ecological Applications* 14: 1526–1534.
- McGarigal K & Marks BJ (1995) FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure. General Technical Report PNW-GTR-351, USDA Forest Service, Pacific Northwest Research Station, Portland, OR, USA.
- Michelsen A, Fink F, Gogala M & Traube D (1982) Plants and transmission channels for insects vibrational songs. *Behavioural Ecology and Sociobiology* 11: 269–281.
- Møller AP (1991) Clutch size, nest predation, and distribution of avian unequal competitors in a patchy environment. *Ecology* 72: 1336–1349.
- Møller AP (1995) Developmental stability and ideal despotic distribution of blackbirds in a patchy environment. *Oikos* 72: 228–234.
- Ornaghi J, Boito G, Sanchez G, March G & Beviacqua J (1993) Studies on the population of *Delphacodes kuscheli* Fennah in different years and agricultural areas. *Journal of Genetics and Breeding* 47: 227–282.
- Paton PWC (1994) The edge effect on avian nest success: How strong is the evidence? *Conservation Biology* 8: 17–26.
- Prescello DA, Solari L & Ferrer M (1991) Identificación de fuentes de resistencia genética al Mal de Río Cuarto. *Taller de Actualización Sobre Mal de Río Cuarto* (ed. by INTA), pp. 67–72. Pergamino, Buenos Aires, Argentina.
- Raupp MJ & Denno RF (1979) The influence of patch size on a guild of sap-feeding insects that inhabit salt marsh grass *Spartina patens*. *Environmental Entomology* 8: 412–417.
- Remes Lenicov AM, Laguna IG, Rodríguez Pardina P, Mariani R, Virla E et al. (1999) Diagnóstico del virus del ‘Mal de Río Cuarto’ y sus vectores en maíz en Argentina. *Manejo Integrado de Plagas* 51: 36–46.
- Remes Lenicov AM & Virla E (1999) Delfácidos asociados al cultivo de maíz en la República Argentina (Insecta – Homoptera – Delphacidae). *Revista de la Facultad de Agronomía, La Plata* 104: 1–16.
- Remes Lenicov AM, Virla E & Dagoberto E (1991) Cambios estacionales en las poblaciones del vector del Mal de Río Cuarto (*Delphacodes kuscheli* Fennah) en cultivos de avena y sus malezas circundantes en Sampacho, Córdoba. *Taller de Actualización sobre Mal de Río Cuarto* (ed. by INTA), pp. 116–122. Pergamino, Buenos Aires, Argentina.
- Risch SJ (1981) Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. *Ecology* 62: 1325–1340.

- Risch SJ, Andow D & Altieri MA (1983) Agroecosystem diversity and pest control: data, tentative conclusions, and new research directions. *Environmental Entomology* 12: 625–629.
- Rolstad J & Wegge P (1987) Distribution and size of capercaillie leks in relation to old forest fragmentation. *Oecologia* 72: 389–394.
- Root RN (1973) Organization of a plant arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43: 95–124.
- Schumaker NH (1996) Using landscape indices to predict habitat connectivity. *Ecology* 77: 1210–1225.
- Shapiro SS & Wilk MB (1965) An analysis of variance test for normality (complete samples). *Biometrika* 52: 591–611.
- Sharov AA, Leonard D, Liebhold AM & Clements NS (2002) Evaluation of preventative treatments in low-density gypsy moth populations using pheromone traps. *Journal of Economic Entomology* 95: 1205–1215.
- Sjögren Gulve P (1994) Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. *Ecology* 75: 1357–1367.
- Stacey PB, Johnson VA & Taper ML (1997) Migration within metapopulations: the impact upon local population dynamics. *Metapopulation Biology: Ecology, Genetics, and Evolution* (ed. by IA Hanski & ME Gilpin), pp. 267–291. Academic Press, San Diego, CA, USA.
- Strong DR, Lawton JH & Southwood R (1984) *Insects on Plants: Community Patterns and Mechanisms*. Harvard University Press, Cambridge, MA, USA.
- Tesón A, Remes Lenicov A, Dagoberto E & Paradel S (1986) Estudio de las poblaciones de delfácido sobre maíz, avena y malezas circundantes (Homoptera, Fulgoridae). *Gaceta Agronómica* 7: 507–517.
- Tollefson JJ (1998) Rootworm areawide management program in Iowa. *Journal of Agricultural Entomology* 15: 351–357.
- Vandewoestijne S, Polus E & Baguette M (2005) Fragmentation and insects: theory and application to calcareous grasslands. *Biotechnology, Agronomy, Society and Environment* 9: 139–142.
- Vargas RA, Peck SL, McQuate GT, Jackson CG, Stark JD & Armstrong JW (2001) Potential for areawide integrated management of Mediterranean fruit fly (Diptera: Tephritidae) with a braconid parasitoid and a novel bait spray. *Journal of Economic Entomology* 94: 817–825.
- Virla EG & Remes Lenicov AM (1991) Ciclo de vida de *Delphacodes kuscheli* sobre diferentes hospedantes en condiciones de laboratorio. *Taller de Actualización sobre Mal de Río Cuarto* (ed. by INTA), pp. 104–116, Pergamino, Buenos Aires, Argentina.
- Zabel J & Tschardt T (1998) Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? *Oecologia* 116: 419–425.