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An area-wide model approach for the management of a disease vector planthopper in an extensive agricultural system

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ABSTRACT

The "Mal de Río Cuarto" disease in maize is a viral disease caused by a reovirus (MRCV) and transmitted by the delphacid planthopper *Delphacodes kuscheli* Fennah in a persistent manner. Although the disease is endemic in only one provincial department, when regional outbreaks occur the losses in maize production are very significant.

Actively dispersing *D. kuscheli* individuals were collected from 15 sampling sites during the 1999 and 2000 spring seasons using sticky traps placed at 6 m above ground level, designed to detect flying individuals.

Insect host patches were surveyed using Landsat 5 TM images for the periods studied. Two critical landscape metrics, total class area and mean proximity index, were calculated using FRAGSTATS 3.3 on the winter pasture satellite images.

A multiple regression model showed the relationship between host patch area, mean proximity index and D. kuscheli abundance to be highly significant ($R^2 = 0.96$, r = 0.98, P < 0.0001).

Spatial simulations of different host areas and different interpatch separations were created in order to test the effect of these metrics on the abundance of the dispersing individuals. The estimate of the insect's abundance showed that, although patch size is very important in determining mean insect abundance in an area, the separation of these patches is crucial to establish the effect of host patch area on the abundance of dispersing individuals.

Until now, disease management consisted in modifying sowing dates in order to avoid maximum *D. kuscheli* abundances and thus minimize risk of Mal de Río Cuarto Disease. Our results show that a rational area-wide management of host patches can keep populations of the vector at a very low level, diminishing the risk of a regional outbreak.

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1. Introduction

Mal de Río Cuarto Disease (MRCD) is the most important viral disease affecting maize in Argentina, causing significant yield losses in maize production (March et al., 1993; Lenardón et al., 1998). It was reported for the first time in 1976 in the southern area of Córdoba Province. This disease is caused by a reovirus (MRCV) which belongs to the Fijivirus family (Van Regenmortel et al., 2000). Although at the moment it is endemic only in Río Cuarto Department (Rodriguez Pardina

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Fig. 1 – Diagram showing the epidemiology of RCD (adapted from Laguna and Pecci y otros, 2000). * indicates those hosts in which the insect can reproduce and acquire the virus.

et al., 1998), it has gradually spread with a typical incidence of 1.5% per year (Lenardón et al., 1998). During the 1996–1997 season, the loss of maize production caused by MRCD cost USD 120,000,000, and the area affected extended far beyond the endemic region to three other Argentinean provinces (Lenardón et al., 1998).

The virus is transmitted by *Delphacodes kuscheli* Fennah (Homoptera: Delphacidae) in a persistent manner (Remes Lenicov et al., 1985; Ornaghi et al., 1993). The insect does not reproduce on maize and only the dispersive fraction of *D. kuscheli* populations arrives in maize fields (Trumper et al., 1996), transmitting the virus when feeding on maize plants. If the infection occurs during the first three weeks after plant emergence, the disease can be severe and, in some cases, lead to plant death. After this most susceptible period, infection may occur but the effect on grain production is relatively minor (Lenardón, 1987).

Some epidemiological studies have revealed the presence of the virus in different seasonal and perennial grasses: Panicum milliaceum L., Setaria italica (L.), Sorghum bicolour (L.), Zea mais L., Secale cereale L., Triticum aestivum L., Triticosecale, Hordeum vulgare L., Avena sativa L., among the cultivated grasses and Bromus unioloides, Arudo donas L., Cynodon dactylon (L.), Cyperus cayennensus (Lam.), Cyperus rotundus L., Sorghum halepense (L.), Cenchrus echinautus L., Cenchrus, Digitaria sanguinalis (L.), Echinocloa colonum (L.), Echinocloa crusgalli, Eleusine indica (L.), Eragrostis virescens, Setaria geniculata (L.) and Setaria verticillata (L.) among the natural grasses (Laguna and Pecci y otros, 2000). All these species are sources from which D. kuscheli individuals will potentially acquire the virus if feeding on them.

Not all these virus reservoirs are present throughout the year. Some of them are present during autumn and winter and others during spring and summer. This means the availability of virus sources is limited depending on the season.

In Argentina D. kuscheli has a limited range of hosts during winter, breeding on winter cereals like rye (Secale cereale L.), barley (Hordeum vulgare L.) or wheat (Triticum aestivum L.), and winter pastures like oats (Avena sativa L.), which are the only gramineous species present in this period. Winter pastures are the most important overwintering hosts as they are sown by the end of the summer and last until spring, thus becoming the main source from which D. kuscheli migrates to maize fields (Fig. 1) (Garat et al., 1999; Remes Lenicov et al., 1999; Ornaghi et al., 1993; Virla and Remes Lenicov, 1991; Tesón et al., 1986).

The species has been found in many regions in Argentina, from the north of the country (Jujuy Province) to the south (Río Negro Province), probably only requiring the presence of its host species (Remes Lenicov et al., 1999). The populations are composed of individuals of two wing-forms: macropterous which have functional wings and can fly, and brachypterous which have short wings and are flightless (Ornaghi et al., 1993). Only the macropterous planthoppers disperse and generally over distances ranging from 1 to 3 km (Denno and Grisel, 1979; Denno et al., 1980, 1991). D. kuscheli has a seasonal life cycle, appearing during late spring and early summer (Garat et al., 1999), increasing from October and November, which roughly coincides with the senescence of the winter pastures (Grilli and Gorla, 1999, 2002). Areas with high population densities are strongly associated with land use management (Grilli and Gorla, 1997, 1998).

Landscape attributes, such as the size, shape and configuration of habitat patches, can affect spatial distribution of species (Beckler et al., 2005; Forman and Godron, 1981; Collinge and Forman, 1998). One way of quantifying the spatial configuration of a landscape is by the use of patch-based



Fig. 2 – Study area. Sampling sites: C1, C2, C3, SF1, SF2, BA1, BA2, and BA3 were taken during 1999; C4, C5, C6, SF3, BA4, BA5, BA6 during 2000. Squares represent approximately the area inside which the samples were taken.

measures (Gustafson, 1998) that include size, number, density and connectivity of patches. These measures can be computed for a particular class of interest (Gustafson and Parker, 1992; Gustafson, 1998; Schumaker, 1996) and are commonly known as "landscape metrics". Landscape metrics are indices based in algorithms that quantify specific spatial characteristics of patches, classes of patches or the entire landscape. There are two categories of these metrics: those that quantify the composition of the landscape and those that quantify the spatial configuration of the landscape, requiring spatial information for their calculation (McGarigal and Marks, 1995; Gustafson, 1998).

The role of habitat patches in insect population ecology has been widely described (Chen et al., 1995; Collinge, 2000; Hunter et al., 1996; Hunter, 2002; Hanski and Singer, 2001; Biedermann, 2002; Connor et al., 2000; Cronin, 2003). Many of these studies emphasize the importance of patch size and isolation in determining the distribution of local populations (Hanski, 1999). For example, 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 (Biedermann, 2002). In many cases, immigration to and emigration from habitat patches will be affected by patch size and distribution (Cronin, 2003; Connor et al., 2000).

The first step in the analysis of patch size and distribution is to detect the presence of these patches. This can be done by determining the land cover of an area using remote sensing techniques, which have the advantage that large areas can be surveyed quickly and repetitively with the degree of detail required, eliminating the problems and costs of ground surveys (Sabins, 1997). Image classification is one way to estimate land cover from a remote sensing source, essentially involving the transformation of remotely sensed measures of spectral radiance into information about the composition of the land surface (Alexander and Millington, 2000).

In this paper we explore the effect of host patch configuration on the abundance of the dispersing fraction of *D. kuscheli* population and its implication for area-wide management recommendations.

2. Methods

2.1. Study area

The study was performed in the most important maize production area of Argentina, which extends from the south of Córdoba and Santa Fe to the north of Buenos Aires. It is a flat land with similar agricultural activities (Fig. 2). The most abundant Delphacidae species in this region is *D. kuscheli* (Grilli and Gorla, 1998).

2.2. Insect sampling

Insects were collected within a 59,113 km² area using sticky traps which were replaced every 7 days during the spring and summer seasons of 1999 and 2000. Sampling was carried out at 15 sites identified as C1, C2, C3, SF1, SF2, BA1, BA2, BA3 in 1999 and as C4, C5, C6, SF3, BA4, BA5, BA6 in 2000 (Fig. 2). Sampling sites were 50 km apart from each other and in each of them insects were collected at 6 m above ground. At each site, three traps were placed close to each other forming 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 these traps. Special care was taken to avoid tree barriers in the area surrounding the traps. Sticky traps consisted of metal cylinders, supporting a plastic film which was coated with grease as an adhesive, and placed on the top of a 6 m mast. The plastic film was replaced by a clean one on each sampling date. In the laboratory, D. kuscheli on the films were identified according to Remes Lenicov and Virla's (1999) identification key.

2.3. Land cover estimation

Winter pastures are sown at the end of the summer and last until spring. Sixteen Landsat TM 5 scenes were used to estimate the land cover of the study area. Eight winter scenes, frames 229/83, 228/83, 227/84, 226/84 were employed to assess 1999 and 2000 land cover. A supervised classification was used to perform the estimate of land use.

The classification of land use by remote sensing is based on the fact that, in Landsat TM images, spectral brightness is recorded for six spectral bands in the visible and reflected infra-red regions of the electromagnetic spectrum. A pixel may be characterized by its spectral signature, which is determined by the relative reflectance in the different wavelength bands (Sabins, 1997). The first step in undertaking a supervised classification is to define the areas that will be used as training sites for each land cover class. This was done by visiting the sites. Three hundred training sites were recorded for the classification. Three classes were considered in the analysis: winter pasture, perennial pasture, and stubble or naked soil (as one class). Once the training site areas were digitized, a description of each informational class was created. The informational classes are called signatures.

The final step was to classify the images. This was done using a Minimum-Distance-to-Means classifier. This classifier is very strong and less susceptible to training site problems than others (Eastman, 2003). Finally, an accuracy assessment was made by generating a random set of locations for verification of the true land-cover type. This was done by applying an error matrix to compare the classes obtained with the real ground classes found in the field and to tabulate the overall proportional error (Congalton and Green, 1999).

Considering the most common dispersing distances for planthoppers reviewed by Denno et al. (1991), a 5000 m diameter circular area surrounding each insect sampling site was



Fig. 3 – Areas around the sampling site with host patches extracted from Landsat 5 TM classified images during both sampling seasons.

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extracted from each classified image, and the area of patches classified as winter pastures was retained (Fig. 3).

2.4. Landscape metrics

Two landscape configuration measures were estimated using FRAGSTATS 3.3 (McGarigal and Marks, 1995) for the winter pastures obtained from the classified images (Fig. 3). Both of them are patch-based indices and represent different landscape properties:

2.5. Total class area (TCA)

Total class area is a measure that indicates how much of the landscape is comprised of a particular patch type. In our case, class area represents the total area of the host patches in each sampling site. This measure approaches 0 as the patch type becomes increasingly rare in the landscape. It is estimated by;

$$TCA = \sum_{i=j=1}^{n} a_{ij} \left(\frac{1}{10,000} \right)$$
(1)

where a_{ij} = area (m²) of the ith–jth patch.

2.6. Mean proximity index (MPI)

Proximity index discriminates isolated patches from those which are part of a complex of patches. This index will equal 0 if a patch has no neighbours of the same patch: in our case, if a host patch does not have neighbouring host patches within the 5000 m diameter area. The proximity index increases as the neighbourhood within the 5000 m diameter searching area is more occupied by patches of the same class, and as those patches become closer and more contiguous or less fragmented in distribution. The index is dimensionless, so the absolute value of the index has little interpretive value; it is used as a comparative index (Gustafson and Parker, 1992). Each patch in the 5000 m diameter area has its own proximity index. A mean value of this specific measure was estimated by summing all the proximity indexes obtained and dividing the sum by the total number of patches in the area. MPI is estimated by;

$$MPI = \frac{\sum_{i=j=1}^{m} \left(\sum_{i=j=s=1}^{n} a_{ijs} / h_{ijs}^{2} \right)}{N}$$
(2)

where a_{ijs} = area (m²) of the ith's–jth's patch within a specified neighbourhood (m) of the ith–jth patch. h_{ijs} = distance (m) between ith's–jth's patches, based on patch edge-to-edge distance, computed from cell centre to cell centre. N = total number of patches.

2.7. Data analysis

D. kuscheli density 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 3.3 (McGarigal and Marks,

1995) and the abundance of dispersive D. kuscheli was estimated by a multiple regression model between both measures and the insect abundance. Before running regressions on multiple variables, we tested the multicollinearity of the landscape variables estimating the tolerance and the variance inflation factor (VIF). The tolerance of a variable is defined as 1 minus the squared multiple correlation of this variable with all other independent variables in the regression equation. Therefore the smaller the tolerance the more redundant is its contribution to the regression (StatSoft, 2002). The reciprocal of the tolerance is known as the variance inflation factor (VIF). A commonly given rule of thumb is that VIF's of 10 or higher (this is tolerances of 0.1 or less) may be reason for concern. To test normal distribution of regression residuals, the Shapiro-Wilk test was applied to all the regression analyses performed (Shapiro and Wilk, 1965). This test involves the calculation of a W statistic which is compared to a critical value of W provided in a table of critical values. The null hypothesis is rejected if $W < W_{(with \alpha \text{ level of significance and } N \text{ sample size})}$.

2.8. Landscape simulation

Considering that proximity index is dimensionless, we were interested in quantifying the relationship between the distance separating host patches and the mean proximity index value. To do this, images with a total area of 2500 ha were created and in each image patches of different sizes and different interpatch separations were represented. The total area of the images created was equivalent to the 5000 m diameter circular area that surrounded each insect sampling site in hectares. Two possible scenarios were simulated: one in which the total patch area (class area) was 225 ha (9% of the total landscape) and a second one in which the total patch area (class area) was 500 ha (20% of the landscape). In each of these scenarios the total patch area was divided into patches of two possible sizes; small patches of 6.25 ha and big ones of 25 ha. The interpatch separations ranged from 50 to 500 m. A total of 40 simulated landscapes were created (Fig. 4). Finally, MPI was estimated using FRAGSTATS for each of the simulated landscapes (Fig. 5).

2.9. D. kuscheli abundance simulation

Using a multiple regression equation (Table 2) and the parameters obtained from the landscape simulation, *D. kuscheli* mean abundances were estimated for all the 40 different landscape scenarios, simulating the effect that different total host patch area, mean patch size and interpatch separations would have on the overall population of the vector.

Finally, the mean abundance of *D. kuscheli* was estimated for different total class areas, different mean patch size and different interpatch separation using the interpolated function described in Table 2 (Fig. 6).

3. Results

3.1. Land cover estimation

In the central area of Argentina, because of its climate and soil, land use has a spatial and temporal uniformity. Nev-



5000 metres

Fig. 4 – Example of patch distribution with different interpatch distances. In this study, 225 ha as total class area, 25 ha (a) and 6.25 ha (b) patches, and 50, 100 and 500 m of interpatch separation.



Fig. 5 – Relationship between mean patch separations obtained from the simulated landscapes and mean proximity index values for simulated landscapes. (●) 500 ha total class area, patches of 25 ha each. (●) 225 ha total class area, patches of 25 ha each. (□) 500 ha total class area, patches of 6.25 ha each. (■) 225 ha total class area, patches of 6.25 ha each.

ertheless, the estimates made from Landsat 5 TM showed that there is considerable local variability in the management of the land, in particular as regards the spatial arrangement of plots of the primary vector host (winter pastures) at a farm scale. Land cover-land use mean area was very variable in the different sites and years, in particular with respect to the surface of host patches within the areas where sticky traps were placed (Fig. 3). The error matrix accounted for 83 and 85% of overall accuracy of the land use classification for 1999 and 2000 (Congalton and Green, 1999).

Host area and configuration were very variable between sites and changed from 1 year to the next. This variability





Table 1 – Total class area (expressed in ha) and mean patch proximity index (dimensionless) values for each sampling site

Sampling site	Total class area (ha)	Mean patch proximity index	
C1	81.27	2.9216	
C2	41.4	2.2264	
C3	37.17	2.381	
C4	13.41	0.9941	
C5	6.39	0	
C6	9.9	0.1507	
SF1	82.35	3.4646	
SF2	94.14	75.7466	
SF3	4.14	3.1265	
BA1	104.4	30.0849	
BA2	67.86	3.5662	
BA3	60.57	4.324	
BA4	9	13.1382	
BA5	3.78	0.2689	
BA6	8.19	0	

ranged from 104 to 3.78 ha within the constant 5000 m diameter area in each sampling site.

During 1999, winter pastures patches were larger and had higher mean proximity index values than during 2000 (Table 1). Site E, in Santa Fe province, was the one with the highest mean proximity index (75.74), while site F in Buenos Aires, which is very close to site E, showed the highest total class area (104 ha), also during the 1999 sampling season (Table 1).

3.2. Insect abundance

Mean abundance of *D. kuscheli* (insects/trap/day) was very variable in the different sites and years. During 1999, the highest abundances occurred in the centre of the study area with a maximum value of 1.11 insects/trap/day for the whole spring. During the 2000 season, all the sites showed lower mean abundances and the spatial pattern observed during 1999 did not repeat during this period (Fig. 7).

The effect of patch area and configuration on *D. kuscheli* populations was tested by a multiple regression model between total class area and mean proximity index against *D. kuscheli* mean abundance expressed as insects/trap/day. This relationship was highly significant ($R^2 = 0.96$, r = 0.98, P < 0.0001). The partial correlation for class area was r = 0.79 (P < 0.001, n = 15) and for the mean proximity index it was r = 0.96 (P < 0.001, n = 15). Normal distribution of the residu-



Fig. 7 – Mean Delphacodes kuscheli abundance/trap/day during both sampling periods in each sampling site and province. C1, C2, C3, SF1, SF2, BA1, BA2, and BA3 were taken during 1999; C4, C5, C6, SF3, BA4, BA5, BA6 during 2000.

als applying the Shapiro–Wilk test (Shapiro and Wilk, 1965) could not be rejected. No multicollinearity of the independent variables was observed (Table 2).

3.3. Winter host patches configuration

The MPI is affected by both patch area and the proximity of other patches of the same class (Eq. (2)). Simulation results show that MPI is affected mostly by the separation of patches (represented by mean patch distance), and then by patch size and total class area (Fig. 5). On the one hand, interpatch separation causes a very rapid reduction of MPI values, i.e., as mean patch distance increases, MPI values diminish until a minimum close to zero (Fig. 5). On the other hand, mean patch size is very important in determining the maximum MPI value. For 225 ha of TCA, the maximum MPI for 25 ha mean patch size was 169, but for 6.25 ha mean patch size it was only 60.

When interpatch separation changed from 59 to 100 m, MPI varied from 169 to 52, for a total host area (TCA) of 225 ha and a mean patch size of 25 ha. If mean patch size was set in 6.25 ha, MPI varied from 60 to 20. When TCA was set at 500 ha, very little change was observed in the dynamics of the model. The absolute value of total host area, represented by TCA, had little effect on MPI values compared to the effect of the other two parameters described in this section. For 25 ha mean patch size, if TCA was 225 ha, MPI showed a value of 169, but if TCA was set at 500 ha, MPI showed a value of 208. This variation was lower if the mean patch size was 6.25 ha, show-

Table 2 – Multiple Linear regression analysis y = a + b(TCA) + c(MPI), between the average abundance of Delphacodes kuscheli in each sampling site and the total class area (TCA) and the mean patch proximity index (MPI) within an area of 5000 m diameter around the sampling site

Independent variable	Coefficient	Partial correlation	Tolerance	Variance inflation factor	T statistic
Constant Total class area Mean proximity index	0.01995 0.00225 0.01116	0.79 [*] 0.96*	0.69 0.69	1.449 1.449	0.85409 4.43613 11.82752
* Denotes significant t					

ing an MPI value of 60 for a 225 ha TCA and 66 for a 500 ha TCA (Fig. 5).

3.4. Effect of landscape configuration on the abundance of dispersive D. kuscheli individuals

The *D.* kuscheli mean abundance estimate, obtained using the multiple regression model (Table 2) for different patch sizes and simulated configurations showed that, although patch size is very important in determining the insect mean abundance in an area, the separation of these patches is crucial. When applying the multiple regression equation (Table 2) for the different patch sizes, interpatch separations and the TCA obtained from the simulated patch distribution models (Figs. 3 and 5), we observed that, as separation distances increase, patch size has less effect on dispersive *D.* kuscheli abundance in an area. Nevertheless, TCA affects not only the maximum amount of individuals but also the lower threshold of the dispersive insects in an area (Fig. 6).

4. Discussion

This study was performed in a region known as the "Argentine Maize Central Area" (Teyssandier et al., 1983) where farmers produce 80% of the maize in the country (Indec, 1995) (Fig. 2). Since *D. kuscheli* does not breed in maize but migrates to it from other sources (Ornaghi et al., 1993), the study of the response of the insect to different landscape patterns is crucial to understanding its ecology. We know that *D. kuscheli* is strongly affected by the condition and distribution of vegetation (Grilli and Gorla, 1997). Its abundance is related to the distribution and abundance of host plants at a regional level (Grilli and Gorla, 1999).

In natural systems, the distribution of plants tends to form discrete patches because of their spatial aggregation. This situation is more evident in agricultural landscapes, where 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, their 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 disturbances through farming operation and with an increased environmental stochasticity caused by the disappearance of patches whenever a host crop is changed for a different crop type (Hanski and Gilpin, 1997; Fahrig and Jonsen, 1998).

Many authors have emphasised the role of landscape context in terms of patch area and isolation on immigration rates, in particular for specialist species (Krauss et al., 2003, 2005; Thies et al., 2003).

The analysis of Landsat 5 TM showed local differences in the use of the land based on the proportion of areas with host and non-host crops during winter and the beginning of spring (Fig. 3). This indicates that farmers modify the landscape very rapidly, which creates an unstable habitat for *D*. *kuscheli* (Ornaghi et al., 1993; Grilli and Gorla, 2002).

Host area and configuration were very variable during the study period (Table 1). We were able to describe the effect of

landscape pattern on the abundance of dispersive individuals of *D. kuscheli*. It is important to note that we sampled only the individuals that were in active process of dispersing, as these individuals are the ones which would finally colonize other crops and eventually transmit the disease (Remes Lenicov et al., 1999). Area and connectivity of host patches have a direct effect on *D. kuscheli* population. The abundance of dispersing *D. kuscheli* individuals is affected not only by the total host area immediately surrounding the sampling traps but also by the proximity of these patches (Table 2).

There are many conceptual explanations for the relationship between insect species abundance and the area and configuration of its hosts. The area requirements of planthopper populations are variable and depend on the species (Biedermann, 2002); this variability may be attributed to parameters of population dynamics or life traits, among many other causes. Species which are able to build up high densities in their patches may reach sufficient population sizes to reduce the extinction risk from environmental stochasticity (Lande, 1993). Populations in larger patches may persist at higher mean densities than populations in small patches due to a higher probability of finding mates or higher winter survival among other factors (Raupp and Denno, 1979; Denno et al., 1981; Møller, 1991, 1995). This positive correlation between population density and patch area can be caused by a number of mechanistic explanations (Connor et al., 2000) acting individually or collectively, like the resource concentration hypothesis (Risch, 1981; Kareiva, 1983). This hypothesis predicts that specialist herbivores should have higher densities in large patches of their host plants based on the conjecture that these higher densities are solely a consequence of the movement of individuals from small to big habitat patches (Root, 1973).

Multiple regression was employed only to define the equation that relates the landscape metrics with the abundance of the dispersing individuals collected in the traps, so as to be able to simulate the different possible configurations of the landscape.

As shown by the simulation models developed (Fig. 6), interpatch separation and mean patch area are the key factors affecting *D. kuscheli* mean abundance: the bigger the interpatch separation, the lower the dispersive *D. kuscheli* mean abundance in an area, until the insect abundance reaches the minimum established by TCA, with the slope regulated by the mean patch size of that area.

In fragmented habitats, 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). For *D. kuscheli*, host patch proximity has a direct effect on the abundance of dispersive individuals. A possible explanation for this is that an increase in interpatch separation will cause an increase of the dispersers' mortality rate due to a lower probability of finding a suitable patch. Mortality during dispersal is often ignored in spatial population studies, but this source of mortality may in certain cases be very significant, in particular in specialist species (Matter et al., 2004; Hanski et al., 2000). *D. kuscheli* can be considered a specialist species as it has a very limited range of hosts (Remes Lenicov and Virla, 1999). In a recent survey, Debinski and Holt (2000) showed that in at least half of the cases anal-

ysed the abundance of different insect populations decreased with habitat fragmentation and this effect was more evident if specialist species were considered (Vandewoestijne et al., 2005). In specialist insect species, even small-scale habitat fragmentation causes a significant decrease in population abundance, because they depend on conditions that are less likely to occur on small patches (Zabel and Tscharntke, 1998).

Habitats may differ in their permeability to dispersing individuals. Thus the effective isolation of populations may depend on both the type and the amount of habitat through which organisms move (Kuussaari et al., 2000).

Success in terms of abundance of *D. kuscheli* in an area is basically related to the presence and configuration of its host patches. The migratory behaviour of *D. kuscheli* is triggered by the condition of the host (Ornaghi et al., 1993). Insects with little control over their ultimate destination when dispersing would be deposited into habitat patches in direct proportion to patch area, and if the matrix is a hostile habitat, those falling into the matrix will die (Bowman et al., 2002).

In early 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, in the study, the individuals trapped in the sticky traps that were in an actively dispersing process were those that were leaving the patches. The amount of dispersing individuals will vary then according to the abundance of the populations in the patches that surround each sticky trap minus the ones that "don't make it" and die during dispersal because suitable habitat patches are too separated from each other.

The proportion of viruliferous *D. kuscheli* individuals is very low in the field, only between 7.9 and 10.5% of the captured individuals (Remes Lenicov et al., 1999). Nevertheless, Mal de 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). The mechanisms by which *D. kuscheli* populations increase to unusual values in a certain region were not completely clear until now. Previous studies indicate that the agroecosystem management and the amount of green vegetation in a region can have some effect on *D. kuscheli* populations present in that region (Grilli and Gorla, 1997, 1998).

We found that the distribution and abundance of dispersing *D. kuscheli* in a region depends on factors related to the presence and configuration of host patches. Until now, only the change of sowing dates was employed to avoid maximum *D. kuscheli* abundances to minimize Mal de Río Cuarto Disease risk (Lenardón, 1987; Remes Lenicov et al., 1999). These results show that a rational area-wide management of host patches can keep populations of the vector at a very low level, diminishing the risk of a regional outbreaks like the one that occurred in 1997 (Lenardón et al., 1998).

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