

Spatial synchrony of planthopper species with contrasting outbreak behaviour

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- Abstract**
- 1 We studied the synchrony of two sympatric delphacids species with different outbreak behaviours over a range of 250 km in Argentina.
 - 2 The spatial synchrony in the dynamics of *Delphacodes kuscheli* and *Toya propinqua* was quantified by collecting individuals of both species simultaneously at three sampling heights: ground, 1.5 m and 6 m above the ground. Synchrony between paired sampling sites separated by increasing distances was estimated using a nonparametric covariance function.
 - 3 A significant difference was found between the spatial synchrony of the species studied. *Delphacodes kuscheli* individuals collected at 6 m above the ground showed consistent spatial synchrony over long distances with correlation values declining by 40%. Population dynamics showed declining synchrony as site separation increased. *Toya propinqua* populations did not show this pattern. This species had a lower mean regional synchrony at 6 m above the ground, but their ground height synchrony was greater than that observed for *D. kuscheli*.
 - 4 One possible synchronizing mechanism is seasonality and the dispersal strategies of each species. The main host plants of *D. kuscheli* are winter cereals sown as pasture for cattle grazing and the synchrony of the crop may affect the general pattern of dispersing individuals of this species. The lack of synchrony observed in *T. propinqua* populations was probably due to the wider host range of this species.

Keywords *Delphacodes kuscheli*, planthopper, spatial dynamics, synchrony, *Toya propinqua*.

Introduction

The synchronous fluctuation of population dynamics over large geographic areas (spatial synchrony) is a common feature among a variety of species, including insect populations (Liebhold & Kamata, 2000; Peltonen *et al.*, 2002). The mechanisms explaining spatial synchrony vary among species (Liebhold *et al.*, 2004) and its determination within the dynamics of conspecific populations can be crucial to the understanding of metapopulation dynamics and conservation biology (Hanski & Woiwod, 1993). The comparison of spatio-temporal synchrony in different but related species may be useful for generating and testing hypotheses about causality (Peltonen *et al.*, 2002; Liebhold *et al.*, 2004).

Three mechanisms may cause synchrony in population dynamics: dispersal among populations; synchronous stochastic

effects (known as the ‘Moran effect’); and trophic interactions with other species that are either synchronized or mobile (Liebhold, *et al.*, 2004). Identifying the synchronizing process present in a specific population is difficult because all three may produce almost identical signatures of synchrony (Liebhold *et al.*, 2004).

Spatial synchrony can be defined as the process by which populations in spatially separated locations fluctuate in a similar manner. Qualitative observations of this phenomenon have been made for many years (Shepherd *et al.*, 1988; Myers, 1998), but only recently have quantitative methods been employed (Ranta *et al.*, 1995b; Bjørnstad *et al.*, 1999; Williams & Liebhold, 2000). The greatest challenge to ecologists studying spatial synchrony is to differentiate the effect of regional stochasticity from the effect of dispersal or other synchronizing factors. There are some particular systems in which dispersal (Williams & Liebhold, 1995; Grenfell *et al.*, 1998) or regional stochasticity (Holyoak & Lawler, 1996) can be ruled out and the source of synchrony identified.

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In general, however, these are simultaneous processes and the interaction between dispersal and regional stochasticity as a cause of synchrony may not be simple: overall synchrony may be lower than that expected by simply adding the synchrony from dispersal to that from regional stochasticity (Kendall *et al.*, 2000).

Among the Fulgoroidea superfamily, delphacid planthoppers are the most important in economic terms because of their capability of transmitting plant pathogens (Nault & Ammar, 1989; Remes Lenicov *et al.*, 1997). Several of the 16 delphacid species in the central region of Argentina have proved to be vectors of plant viruses (Rodríguez Pardina *et al.*, 1998; Remes Lenicov *et al.*, 1999; Laguna *et al.*, 2002) and *Delphacodes kuscheli* and *Toya propinqua* are among the most abundant in this area (Remes Lenicov *et al.*, 1987; Boito *et al.*, 1993; Ornaghi *et al.*, 1993; Remes Lenicov & Virla, 1993; Virla & Maragliano, 1993; Grilli & Gorla, 1997, 1998; Presello *et al.*, 1997). Both of these planthoppers produce two wing forms: long-winged macropters, which can fly (dispersive generation), and short-winged brachypters, which are flightless (Ornaghi *et al.*, 1993; Remes Lenicov & Virla, 1999). In planthoppers, wing morph is determined by a developmental switch that responds to environmental cues (Kisimoto, 1981; Cook & Perfect, 1985). Macropter individuals can migrate long distances (1000 km) when transported by wind (Kisimoto, 1976), but most dispersal occurs over short distances in the range 1–3 km (Riley *et al.*, 1987). There are no studies with respect to how many generations per year these species have but, according to their development time, they could have more than four (Virla & Remes Lenicov, 1991; Remes Lenicov *et al.*, 1997).

Delphacodes kuscheli has a limited range of hosts in the study area during winter because the insect can breed only on winter cereals such as rye (*Secale cereale* L.), barley (*Hordeum vulgare* L.) or wheat (*Triticum aestivum* L.), and winter pastures such as oats (*Avena sativa* L.), which are the only gramineous species found at this time. Oats comprise the most important overwintering host because it is sown by the end of the summer and lasts until spring, and thus becomes the main source from which *D. kuscheli* migrates to maize fields during spring and summer (Tesón *et al.*, 1986; Virla & Remes Lenicov, 1991; Ornaghi *et al.*, 1993; Garat *et al.*, 1999; Remes Lenicov *et al.*, 1999).

Toya propinqua is associated with natural grasses in general and with *Cynodon dactylon* in particular (Remes Lenicov & Virla, 1993). Nevertheless, as this host dries up during winter, individuals can use alternative hosts such as oats (*Avena sativa* L.), wheat (*Triticum aestivum* L.) or millet (*Panicum miliaceum*) (Harpaz, 1972; Remes Lenicov & Virla, 1993; Remes Lenicov & Virla, 1999).

Although these two delphacid species share host plants, and can be considered as pests because their capability of transmitting viruses, only *D. kuscheli* is reported as having regional outbreak behaviour, and the main management recommendation by experts is to avoid these outbreaks by sowing maize as early as possible in the season (Ornaghi *et al.*, 1993; Lenardón *et al.*, 1998; Remes Lenicov & Virla, 1999; Grilli & Gorla, 2002). For this reason, in the present study,

we compared the spatial synchrony in the population dynamics of the two species.

Materials and methods

The study was conducted in the central and south-western region of Córdoba province in central Argentina. This area is mainly flat agricultural land (Fig. 1). Land use varies along the study transect; in the northern part, land parcels are small and intensively used throughout the year for the cultivation of grain crops. The southern region, however, consists of large land parcels that are used especially for cattle production (Indec, 1995).

Insect data

Insects were collected along an approximately 250-km transect, running from site A, close to the town of Manfredi in the northeast, to site H, near the town of Mercedes in the southwest, over a 2-year period (Fig. 1), with eight sampling sites, each located 20–50 km apart.

At each site, samples were collected at three heights: at ground level (natural grasses, mainly *Cynodon dactylon*); from five sticky traps at a height of 1.5 m; and from one trap at a height of 6 m.

Ground samples were collected using a vacuum sampling device (Sears Craftsman 32cc) for ten units at each of the eight sites. For each sampling unit, the vacuum sampling device was applied to the ground for 5 s (almost 1 m²). The sampling units were 2 m apart.

The sticky trap located at 6 m consisted of a metal cylinder 50 cm high and 16 cm in diameter, whereas the traps placed at 1.5 m consisted of a metal cylinder 20 cm high and 8 cm in diameter. Although the total sampling area of sticky traps at both heights was 2513.27 cm², at 1.5 m, we distributed this area over five traps to facilitate management. An adhesive-coated plastic film was placed around the cylinders. The films were replaced with clean film every 7–15 days during spring/summer and monthly during the remainder of the year. Ground samples were also taken every time that the plastic film was replaced.

The exposed films and ground samples taken were processed in the laboratory under a stereomicroscope, identifying species according to the protocol of Remes Lenicov and Virla (1999). Insects were collected from October 1992 to November 1994 and kept in the laboratory in 70% alcohol until analysis.

Insect density was estimated in different ways depending on the sampling method employed to capture the individuals. Density at ground level was estimated as the log of the mean number of individuals collected at each sampling site during each sampling date, whereas, at the 6 m and 1.5 m heights, density was calculated as the log number of individuals collected per cm² of trap surface divided by the number of days that the plastic film was exposed to field conditions.

A comparison of the number of individuals observed on each sampling date was made using linear correlation analysis.

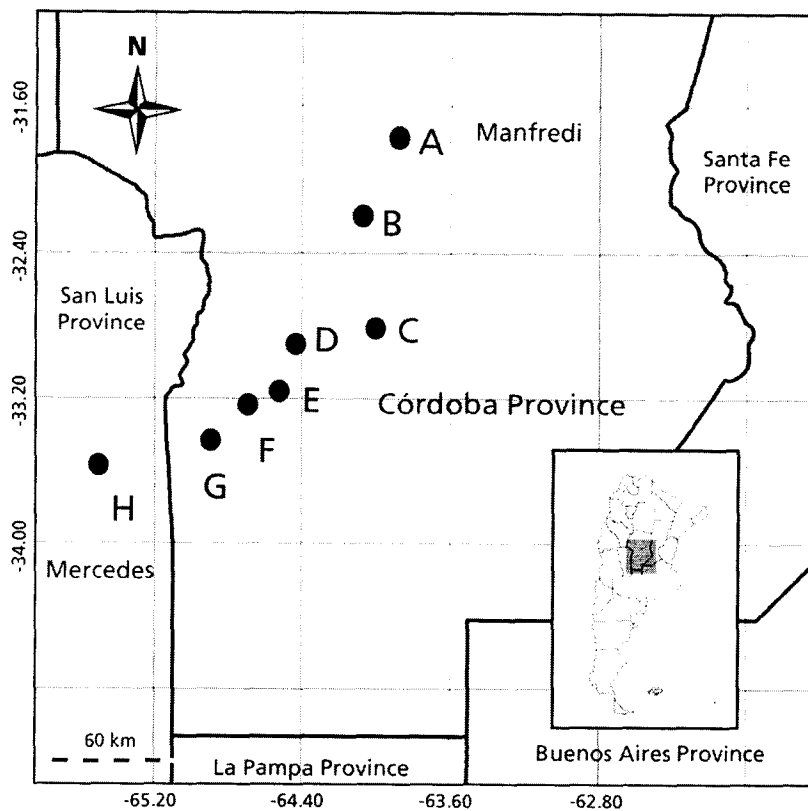


Figure 1 Study area. Sampling sites A, B, C, D, E, F, G, are in Córdoba province; site H is in San Luis province (central Argentina).

The analysis was carried out for each species and between each sampling method employed in the study.

Measuring the synchrony of the species

Spatial synchrony can be described as a coincident change in abundance during a certain time period in geographically separated populations (Buonaccorsi *et al.*, 2001; Liebhold *et al.*, 2004). In general, previous studies of spatial synchrony indicate that synchrony is not homogeneous; populations located nearby tend to be more synchronous than those located farther apart (Ranta *et al.*, 1995a; Bjørnstad *et al.*, 1999; Koenig, 1999). One method of quantifying spatial synchrony is by plotting the pairwise correlation coefficients between time series of spatially separated populations against the Euclidean distance separating each pair (Buonaccorsi *et al.*, 2001).

In the present analyses, we used the nonparametric covariance function (NCF) to explore how synchrony decreases with increasing distance (Bjørnstad *et al.*, 1999; Bjørnstad & Falck, 2001). The NCF is a smoothing spline function fit to the pairwise cross-correlations as a function of lag distance, producing a direct continuous estimate of spatial covariances. Confidence intervals for the estimated functions were calculated using bootstrap resampling with 500 iterations (Bjørnstad *et al.*, 1999; Bjørnstad & Falck, 2001; Økland *et al.*, 2005). The analysis was performed using the spatial nonparametric cross-correlation function module within

the R statistical package (Hornik, 2006). Spatial correlograms, which quantify spatial autocorrelation as a function of lag distance, were calculated for each species and each sampling height.

Results

The correlation between the abundance of *D. kuscheli* captured at 6 m and that of those captured at 1.5 m was significantly positive (linear model: $r = 0.74$, $P < 0.01$; exponential model: $r = 0.76$, $P < 0.01$) (Fig. 2A). The ratio between *D. kuscheli* captured at 6 m and those from the ground fitted to a linear model ($r = 0.68$, $P < 0.01$) (Fig. 2B) and the same comparison, but using the abundance of individuals collected at 1.5 m as the independent variable, showed a correlation coefficient of 0.61 ($P < 0.01$) (Fig. 2C).

Additionally for *T. propinqua* populations, we found that the ratio between dispersing individuals at 6 m and at 1.5 m was also significant ($r = 0.66$, $P < 0.01$) (Fig. 2D). When comparing the abundance of dispersing individuals of this species captured at 6 m and those collected from the ground, a positive and significant correlation was also observed ($r = 0.59$, $P < 0.01$) (Fig. 2E). Finally, a comparison between dispersing individuals collected at 1.5 m and those at ground level also showed a significant correlation (linear model: $r = 0.74$, $P < 0.01$; logarithmic model: $r = 0.78$, $P < 0.01$) (Fig. 2F).

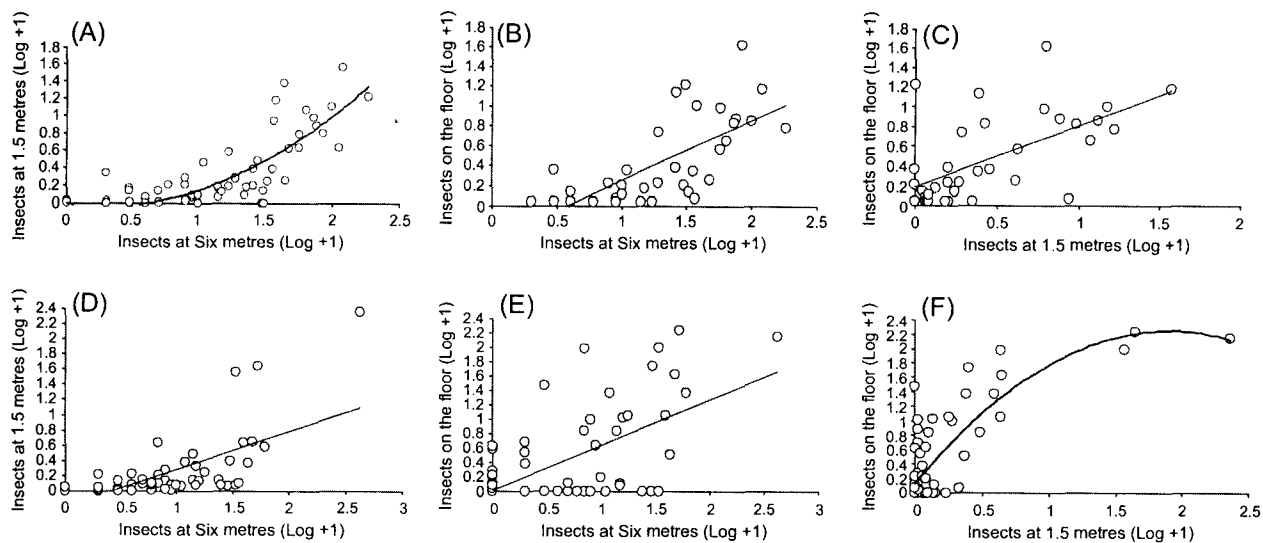


Figure 2 Comparison of the abundance of individuals sampled by different sampling methods: (A) *Delphacodes kuscheli* collected at 6 m versus *D. kuscheli* captured at 1.5 m, $r=0.74$, $P < 0.01$; (B) *D. kuscheli* collected at 6 m versus *D. kuscheli* captured at ground height, $r=0.68$, $P < 0.01$; (C) *D. kuscheli* collected at 1.5 m versus *D. kuscheli* captured at ground height, $r=0.61$, $P < 0.01$; (D) *Toya propinqua* collected at 6 m versus *T. propinqua* captured at 1.5 m, $r=0.66$, $P < 0.01$; (E) *T. propinqua* collected at 6 m versus *T. propinqua* captured at ground height, $r=0.59$, $P < 0.01$; (F) *T. propinqua* collected at 1.5 m versus *T. propinqua* captured at ground height, $r=0.74$, $P < 0.01$.

Synchrony analysis

Spatial synchrony decreased with increasing sampling distance (Fig. 3, Table 1). For both species and for the three sampling heights, synchrony was greatest between nearby populations (local synchrony), and spatial correlation declined with increasing distances (Fig. 3). There were contrasting differences, however, in the synchrony between the two planthopper species. These differences were evident in the populations collected at ground height and in the populations that were actively dispersing (sampled at 6 and 1.5 m above the ground height).

Considerable differences were found in the spatial covariance function between species and between sampling heights. On the one hand, *T. propinqua* at ground height showed a rapid decline in synchrony with distance. Population dynamics were more similar in those sites that were close to each other, showing a constant decline in synchrony as the distance between sample sites increased, with a local synchrony of in the range 0.80–0.10 for the maximum lag (250 km) (Fig. 3, Table 1).

On the other hand, *D. kuscheli* collected at ground height showed a more dramatic decline, with almost no synchrony between places separated by 100 km (Fig. 3, Table 1). When comparing the synchrony of individuals in an active dispersal process (i.e. those flying macropters captured in the sticky traps placed at 1.5 and 6 m above the ground height), *D. kuscheli* showed positive values of regional synchrony, even in places separated by more than 100 km. The mean regional synchrony of *D. kuscheli* captured at 6 m above the ground height was significantly greater than for the same species captured at 1.5 m or at ground height, and for any of the sampling heights of *T. propinqua* (Fig. 3).

The greatest local synchrony (synchrony at lag 0) was that for *D. kuscheli* captured at 6 m (0.87). In general terms, these individuals also showed greater spatial synchrony values for longer distances than those collected at 1.5 m or on the ground (Fig. 3, Table 1). *Toya propinqua* captured at 6 and 1.5 m showed very close values of synchrony, even in those places separated by more than 100 km. At 6 m above the ground, synchrony values were in the range 0.41–0.33 and, at 1.5 m, synchrony values were in the range 0.41–0.26 (Fig. 3, Table 1).

Discussion

A remarkable contrast in spatial synchrony of the studied delphacid species was observed. Although these samples were collected at the same time and in the same place, differences in their spatial pattern were evident.

There are two explanations for the pattern of decreasing synchrony with increasing distance: spatially autocorrelated environmental variability and distance-dependent dispersal (Ranta *et al.*, 1997; Grenfell *et al.*, 1998; Swanson & Johnson, 1999; Williams & Liebhold, 2000). If populations fluctuate as the result of some endogenous processes, spatially separated populations will come into synchrony either as the result of a small amount of dispersal among populations or as the result of regional stochasticity, frequently caused by synchronous weather variability (Moran, 1953; Ranta *et al.*, 1995b, 1999; Kendall *et al.*, 2000).

The periodicity of population dynamics greatly contributes to the appearance of spatial synchrony (Bjørnstad, 2000). This could be the case for both species. For *D. kuscheli*,

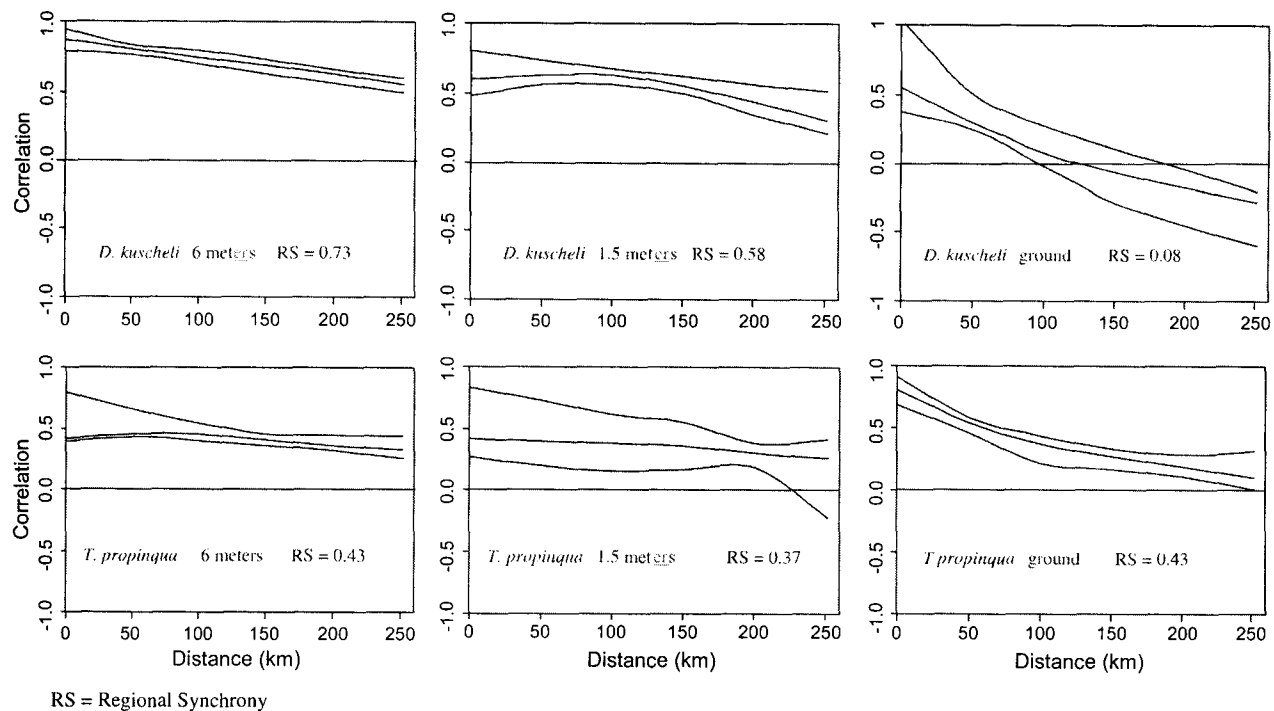


Figure 3 The spatial covariance functions estimated from the abundance of the two planthopper species during the study period. The upper and lower lines represent the 95% bootstrap confidence intervals. RS, regional synchrony.

general synchrony patterns appear to be governed by dispersal. Individuals collected at 6 m showed not only the greatest value of mean regional synchrony, but also a general pattern with a very smooth slope within the 250 km of the transect (Fig. 3). Furthermore, there was a close relationship between the temporal patterns in the abundance of individuals collected at 6 m and those collected at 1.5 m above ground level (Fig. 2). The results obtained in our previous studies indicate that the species is strongly affected by the area and configuration of winter pastures (Grilli, 2006; Grilli & Bruno, 2007). At a regional level, its abundance is affected not only by the host area in a region, but also by the phenology and succession of the different host species (Grilli, 2006).

The patches on which ground samples were collected were not winter pastures but comprised natural grasses that are still good hosts for this species, at least during spring and summer. Winter cereals sown as pastures for cattle grazing affect the general pattern of dispersing individuals, synchronizing the dispersing populations as a result of the inevitable synchrony of the crop. Because these host plants are responsible for most of the circulating individuals, these flying populations are then responsible for the synchronization of ground populations of other patches.

Between May and September (winter in the southern hemisphere), *D. kuscheli* does not disperse, thus showing clear spring–summer–early fall seasonality (Grilli & Gorla, 1997, 1998). This seasonal variability may explain the synchronization of the overall populations in a region, and can also explain the role of winter pastures, winter cereals and natural

perennial pastures in *D. kuscheli* dynamics. Winter pastures (mainly oats) are sown by the end of February and are kept by farmers until the beginning of October. At the time winter pastures begin to grow (end of March), the activity of *D. kuscheli* declines and the insect finds winter refuge in these crops. The opposite occurs at the end of September (spring in the southern hemisphere) when winter pastures decline and *D. kuscheli* begins its activity and escapes from this declining resource. By this time, the only available hosts are the winter cereals that were sown in June and the natural pastures that are beginning to regrow, and *D. kuscheli* starts to colonize the latter (Grilli & Gorla, 1997; Grilli, 2006).

The low synchrony values of *T. propinqua* populations, however, may be caused by their wider host range and, in particular, by their preference for *C. dactylon* as their main host (Harpaz, 1972; Remes Lenicov & Virla, 1999). It is very important to consider that, in an agricultural system, natural *C. dactylon* patches will be small and marginal, and located in areas where there are no cultivated crops. These patches will not show the same synchrony as cultivated patches. Therefore, *T. propinqua* populations in each of these patches will have their own dynamic and will disperse when triggered by density-dependent mechanisms and not by the senescence of the patch.

Clearly, dispersal is a key factor acting to synchronize populations with different regulative mechanisms but, if their density-dependent parameters are very different, synchronization may be difficult (Barbour, 1990; Ranta *et al.*, 1998; Swanson & Johnson, 1999). The occurrence and density of

Table 1 Spatial synchrony of two planthopper species at three sampling heights

Species and sampling height	Distance (km)					
	0	50	100	150	200	250
<i>Delphacodes kuscheli</i> 6 m	0.87 (0.78–0.95)	0.80 (0.76–0.83)	0.74 (0.70–0.80)	0.69 (0.63–0.57)	0.63 (0.57–0.67)	0.55 (0.50–0.60)
<i>Delphacodes kuscheli</i> 1.5 m	0.60 (0.48–0.80)	0.64 (0.57–0.74)	0.63 (0.57–0.67)	0.56 (0.50–0.63)	0.43 (0.34–0.57)	0.30 (0.21–0.52)
<i>Delphacodes kuscheli</i> ground	0.56 (0.37–1.00)	0.29 (0.24–0.50)	0.08 (–0.01 to 0.2)	–0.05 (–0.29 to 0.1)	–0.17 (–0.4 to –0.03)	–0.28 (–0.16 to –0.2)
<i>Toya propinqua</i> 6 m	0.41 (0.39–0.79)	0.45 (0.43–0.65)	0.46 (0.40–0.54)	0.41 (0.36–0.45)	0.36 (0.32–0.45)	0.33 (0.25–0.43)
<i>Toya propinqua</i> 1.5 m	0.41 (0.27–0.83)	0.39 (0.20–0.73)	0.38 (0.14–0.62)	0.35 (0.16–0.54)	0.30 (0.18–0.38)	0.26 (–0.22 to 0.41)
<i>Toya propinqua</i> ground	0.80 (0.68–0.91)	0.56 (0.46–0.57)	0.37 (0.21–0.43)	0.27 (0.16–0.33)	0.18 (0.11–0.28)	0.10 (0.005–0.31)

Values represent correlation coefficients. Numbers in parenthesis represent 95% confidence intervals.

planthoppers in a particular habitat patch may depend on the area, isolation, quality and surrounding landscape structure of the patch (Biedermann, 2002; Grilli, 2006; Grilli & Bruno, 2007). In many cases, dispersal from habitat patches will be affected by patch size and distribution (Connor *et al.*, 2000; Cronin, 2003; Grilli, 2006; Grilli & Bruno, 2007).

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