

# Migration pattern suggested by terrestrial proximity as possible origin of wild annual *Helianthus* populations in central Argentina

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**Abstract** There is a high interest to understand and recreate the invasive process of successful non-native plant invaders. The genetic tools provide scanty information when the invasion is recent and there is gene flow among the invader and its crop relative. The concern about the government and private companies' responsibilities in the diffusion process and the risk of occupancy of new areas motivated the interest in two wild annual *Helianthus* species naturalized in the central agricultural lands of Argentina. We used multivariate techniques and random tests to estimate the successive steps accomplished by the plant invaders across transportation routes, following an environmental and ecological gradient. A minimum connection tree through road distances was created considering dispersal from a unique dispersal point for each species. The proposed tree minimized, at the same time, the environmental and the ecological distances calculated by Euclidean and Gower indexes with abiotic and biotic habitat

variables, being significantly different from random ( $P \leq 0.05$ ). Our methodology allowed the development of an approach for the best estimation of the invasion route. This could be used to clarify the role of different agents involved in the diffusion process and to develop management strategies to prevent the plant invasion. The migration pattern suggests that after their historical introduction, both wild species moved in successive steps across a biotic and abiotic gradient, aided by anthropogenic activity along the road connection infrastructure. There were no evidences of escapes from sunflower breeding stations.

**Keywords** Plant invasion · Fertility · Sunflower · Weed community · Random tests

## Introduction

Only a small proportion of exotic plant species introduced into a new region would show invasiveness and widespread as a non-native invader. After introduction and naturalization, a successful plant invasion will happen if an adequate propagule pressure occurs into a vulnerable habitat (Huston 2004; Martínez-Ghersa and Ghersa 2006). Usually, as the propagule transportation is promoted by human activity, the plant invader migration patterns follow the transportation routes (Boot et al. 2003). At an environmental level, soil, climate (Mann et al. 1999;

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de Blois et al. 2002; Shea and Chesson 2002; Sugiyama 2003; Retuerto and Carballeira 2004; Härdtle et al. 2005; Milberg et al. 2006) and the plant community structure (Inderjit et al. 2005) modulate the geographical distribution of a non-native invader. Environmental characteristics can be used to quantify the probability of establishment of an invader (Stephenson et al. 2006).

The Argentina croplands were developed on a grassland plateau in the central part of the country, devoted to agriculture after 1890 (Arriaga 1999). Since then, the farming activity has promoted the naturalization of several crop-associated non-native invaders, mainly cosmopolitan weeds unintentionally introduced by immigrants coming from Europe (Taylor 1997). This is the case of two annual sunflowers native to North America, *Helianthus annuus* L. and *H. petiolaris* Nutt. (Asteraceae) established across drylands and irrigated valleys of central Argentina (Poverene et al. 2002).

The origin and distribution of the wild *Helianthus* in central Argentina are unknown. Earliest reports of their presence in open spaces indicate that wild *H. annuus* was intentionally introduced before 1948 in Rio Cuarto, Cordoba province, with feeding purposes (Bauer 1991). During the following decade, Manfredi experimental station included this wild resource among crossing materials in the sunflower breeding program (Giordano and Senin Garcia 1967). *Helianthus petiolaris* was for the first time found growing as a ruderal species in Catrilo, La Pampa province in 1954 (Covas 1984), probably introduced as a contaminant of forage seeds imported from Texas (Dr. A. Luciano, pers. comm.).

After 1960, importation of wild *Helianthus* species from the USA as germplasm sources was frequent (Kinman 1964; Luciano 1964; Seiler and Rieseberg 1997), so wild strains could have escaped from experimental fields. Farmers suppose that wild populations came from volunteers grown along roadsides. This could be addressed to the existence of wild ancestors in several well adopted sunflower varieties (Bertero de Romano and Vazquez 2003). This origin is also difficult to discard due to the intense gene flow from the crop to both annual wild *Helianthus* (Poverene et al. 2004; Ureta et al. 2008), that made possible the development of exo-ferality (Gressel 2005).

Wild, weedy and feral sunflower populations are of concern in several regions of the world because of

their invasive capacity and crop interference (Bervillé et al. 2005; Vischi et al. 2006; Müller et al. 2006; Stanković-Kalezić et al. 2007). The invasive capacity of *H. petiolaris* is unknown, since Argentina is the only reported case of this species' invasion in the world. Wild or common sunflower, *H. annuus* is a ruderal species of which mechanical transportation seems to be the main distribution way. It has been suggested that bison (*Bison bison* Skinner and Kaiser) disseminated wild sunflowers within the natural distribution area in prehistoric times, whereas road traffic appears to be the modern way for wild sunflower diffusion (Heiser 2008). In central Argentina the wild populations of both annual species grow in patches on human-disturbed habitats as firelines, roadsides, water channels, but sometimes invade crops (Cantamutto et al. 2008). The risk of gene exchange with the crop is high because sunflowers are open pollinating species. The presence of those taxa in a given area constitutes a serious constrain to the possible release of transgenic sunflower (Cantamutto and Poverene 2007). In spite of this, no work has been done to understand the forces conditioning the invasive process of both wild species.

There is a general interest to understand, recreate and predict the migration pattern of non-native plant invaders, but few numerical tools have been developed. The interest is greater when human activities disrupt patterns of diffusion (Shea and Chesson 2002). In the case of the two wild annual *Helianthus* invaders of central Argentina, the invasive populations were likely originated in escapes from experimental fields, repetitive non-intentional introductions or uncontrolled outcrossings in the seed production plots. This is of concern for sunflower breeding companies and organisms of government control, because it may indicate an imprudent management or inadequate control of the seed production and importation processes. Additionally, the detection of the anthropogenic and/or natural forces that have driven the invasion could be useful to detect other potential vulnerable habitats and develop strategies to prevent their colonization.

A critical issue relevant to both invasion biology and biological control concerns the difficulty of characterizing the spatial progress of a spreading population (Fagan et al. 2002). Here we explore the existence of migration patterns starting in a unique diffusion point for each of the two annual wild

*Helianthus* invaders in central Argentina, using multivariate analysis of environmental and ecological variables of stable populations. If the habitat connection by ecological and environmental similarities were different from the minimum road connection, the hypothesis of mechanical dispersion from a unique point would be rejected. If the stable wild populations were located near the breeding stations where wild resources were used, the second hypothesis of no escapes would also be rejected. The objectives of this work were: (1) To test if the minimum habitat connection tree by road minimizes at the same time the changes occurred during the diffusion process in terms of environmental and ecological variables; (2) To test if the road connection from wild populations to sunflower breeding stations was shorter than from other wild populations.

## Methods

The migration pattern of two non-native species in Argentina, *Helianthus annuus* and *H. petiolaris*, was estimated based on the habitat of nine and 13 populations respectively, which are the largest stable populations as well as representative of the diverse agro-ecological distribution in central Argentina (Table 1). These are considered the origin of a number of smaller populations and patches (Poverene et al. 2002) developing along roads connecting the habitats. Plants sometimes invade crop fields but always as a continuum of the roadside populations. The study comprises only populations found five or more years in the same place during 2000–2007. Isolated plants or small populations were not considered.

The latitude and longitude of each location were determined with a GPS system (Trimble, horizontal accuracy 1–3 m differentially corrected, error HDOP  $\leq 3$ ). Geo-referenced populations were then overlaid on maps of estimated environmental (abiotic) habitat variables. These included altitude, average annual rainfall, and mean temperature of the hottest and coolest month (De Fina 1992). Soil sub-order percent into each soil cartographic unit, average organic matter content, and soil use capacity at every population site were obtained (INTA 1990).

Laboratory standard analyses of a composite surface soil sample (0–15 cm) collected at each

**Table 1** Nearest locality and size of representative stable populations used to estimate the diffusion pattern of two annual wild *Helianthus* in Argentina

Locality	Province	Eco-region <sup>a</sup>	Size <sup>b</sup>	Acronym
<i>Helianthus annuus</i> (ANN)				
Río Cuarto	Córdoba	Espinal	***	RCU
Adolfo Alsina	Buenos Aires	Espinal	***	AAL
Colonia Barón	La Pampa	Pampa	***	BAR
Carhué	Buenos Aires	Pampa	**	CHU
Diamante	Entre Ríos	Espinal	**	DIA
Juarez Celman	Córdoba	Pampa	****	JCE
Las Malvinas	Mendoza	Monte	***	LMA
Media Agua	San Juan	Monte	***	MAG
Rancul	La Pampa	Espinal	*	RAN
<i>Helianthus petiolaris</i> (PET)				
Catriló	La Pampa	Pampa	***	CAT
Colonia Barón	La Pampa	Pampa	***	BAR
Carhué	Buenos Aires	Pampa	***	CHU
Hilario Lagos	La Pampa	Pampa	*	HLA
Villa Mercedes	San Luis	Espinal	***	MER
Nueva Galia	San Luis	Espinal	***	NGA
Pellegrini	Buenos Aires	Pampa	***	PEL
Salliqueló	Buenos Aires	Pampa	***	SAL
Santa Rosa	La Pampa	Espinal	**	SRO
Trenque Lauquen	Buenos Aires	Pampa	***	TRE
Unión	San Luis	Espinal	*	UNI
Uriburu	La Pampa	Espinal	***	URI
Winifreda	La Pampa	Pampa	*	WIN

<sup>a</sup> Burkart et al. (1999)

<sup>b</sup> Population size: \* 30–300; \*\* 301–3,000; \*\*\* 3,001–30,000; \*\*\*\* > 30,001

localization was used to estimate micro-environmental habitat variables, as described in Cantamutto et al. (2008).

The agro-ecological characteristics were estimated considering other native and non-native plant community species and the spatially co-occurring crops at wild sunflower habitat. In a survey conducted in February 2007, plant composition and richness were estimated at the location of each wild sunflower population following the method used by Clay and

Johnson (2002). At each site, a 100 m by 25 m grid was established. At 10 grid nodes a 2 m<sup>2</sup> circle sample was taken and the relative dominance of each plant species was estimated with an ordinal scale (0 = absent, 5 = dominant). The same scale was used to estimate the dominant landscape representation of crops (wheat, corn, sorghum, soybean, peanut, fruit trees, pasture and sunflower) in each agroecosystem (neighbouring 10 km of road) associated with the populations sampled.

### Procedure and statistical analysis

(1) Model assumption for each species: If the diffusion occurred through seed transportation starting in unique point following terrestrial connection that links similar habitats in successive short steps, it would be possible to estimate a migration pattern accomplishing simultaneously three conditions: (a) To minimize the total distance covered by road for terrestrial transport; (b) To minimize the sum of environmental changes during the migration process; (c) To minimize the sum of plant community changes during the migration process.

(2) Distance estimation for each one of the three analysis dimensions: Environment and plant community analyses estimated habitat similarities under different dimensions calculated with geographic, environmental and ecological aspects of site variables (Table 2) grouped in layers of descriptive information. In each dimension, one habitat was more proximate to the other as the distance between both was shorter. Triangle matrices containing distance information between all pairs of habitats were calculated in the following dimensions: (a) Terrestrial transport, estimated through road distances obtained from road maps and dirty roads in Argentina; (b) Environmental dissimilarity, calculated through the Euclidean distance (Quinn and Keough 2005) with abiotic variables (Table 2) range-transformed and standardized, to avoid scale differences; (c) Plant agro-ecosystem dissimilarities, calculated through the complement of Gower index (Gower 1971; Quinn and Keough 2005) considering the complete floristic composition in each habitat. The average dominance or importance of 27 co-occurring species and eight crop or agriculture land uses determined in each site were previously range-transformed and standardized.

**Table 2** Selected variables used to estimate the diffusion process of two annual *Helianthus* species in Argentina by multivariate analysis (means  $\pm$  SD)

	Wild <i>H. annuus</i>	<i>H. petiolaris</i>
<b>Localization</b>		
Latitude (°S)	34.6 $\pm$ 2.1	35.9 $\pm$ 0.9
Longitude (°W)	66.3 $\pm$ 2.5	64.0 $\pm$ 1.0
<b>Environment</b>		
Altitude (m.a.s.l.)	267 $\pm$ 202	199 $\pm$ 123
Hottest month temperature (°C)	24.2 $\pm$ 1.1	24.3 $\pm$ 0.4
Coollest month temperature (°C)	8.1 $\pm$ 1.5	7.7 $\pm$ 0.4
Rain (mm year <sup>-1</sup> )	591 $\pm$ 259	601 $\pm$ 78
Irrigation (mm year <sup>-1</sup> )	67 $\pm$ 123	0.0 $\pm$ 0.0
Soil unit organic matter (%)	2.2 $\pm$ 1.1	1.2 $\pm$ 1.1
Soil unit use capacity (1–7 scale)	4.1 $\pm$ 1.2	4.8 $\pm$ 1.2
Haplustolls	13.3 $\pm$ 33.2	52.3 $\pm$ 40.0
Argiustolls	20.3 $\pm$ 27.6	3.1 $\pm$ 11.1
Hapludolls	7.1 $\pm$ 16.0	6.2 $\pm$ 22.2
Ustipsaments	0.0 $\pm$ 0.0	16.9 $\pm$ 20.6
Torripsnments	22.2 $\pm$ 44.1	7.7 $\pm$ 27.7
Natraqualfs	2.8 $\pm$ 5.5	6.15 $\pm$ 17.1
<b>Microenvironment</b>		
Available P (ppm)	30.4 $\pm$ 15.8	25.4 $\pm$ 13.0
Organic matter (%)	3.6 $\pm$ 1.0	1.6 $\pm$ 1.1
Clay (%)	13 $\pm$ 8	6 $\pm$ 3
Loam (%)	30 $\pm$ 13	14 $\pm$ 12
Sand (%)	57 $\pm$ 20	80 $\pm$ 15
<b>Plant community</b>		
Co-occurring plants (abundance 0–5 scale)		
<i>Cynodon dactylon</i>	0.89 $\pm$ 0.33	0.77 $\pm$ 0.44
<i>Chenopodium album</i>	0.78 $\pm$ 0.67	0.92 $\pm$ 0.86
<i>Sorghum halepensis</i>	0.78 $\pm$ 0.67	0.92 $\pm$ 0.49
<i>Melilotus albus</i>	0.89 $\pm$ 0.60	0.23 $\pm$ 0.60
<i>Centaurea solstitialis</i>	0.67 $\pm$ 1.12	0.46 $\pm$ 0.97
<i>Salsola kali</i>	0.56 $\pm$ 0.73	0.92 $\pm$ 0.76
<i>Eragrostis curvula</i>	0.56 $\pm$ 0.53	0.69 $\pm$ 0.63
Associated crops (importance 0–5 scale)		
Sunflower	2.67 $\pm$ 1.41	1.23 $\pm$ 0.83
Wheat	2.11 $\pm$ 1.45	0.85 $\pm$ 0.80
Sorghum	1.56 $\pm$ 1.01	1.60 $\pm$ 1.60
Soybean	1.67 $\pm$ 1.32	1.23 $\pm$ 1.01

(3) Connection trees: The minimum connection trees by road distance were calculated using the IML procedure of SAS Institute Inc (2006). Likewise, the

total distance covered to connect all populations under the three analysis dimensions was calculated and the probability to obtain this value under random was estimated by the procedure described in (4).

(4) Connection tree validation: A permutation test was performed in order to verify if the obtained tree was different from random. Fifty thousand paths were simulated through a specially designed macro to connect every habitat with the entry point, without limitation in the number of branches. Each simulation first began with a sorting on the connection order of each habitat with the growing tree. The first population linked to the entry point, while each of the remainder was sorted to link with any of the populations already connected to the tree. For each simulated pathway the total distance was calculated using the three independent distance matrices. The Gaussian-shaped histograms of distance distribution frequencies were used to test the distance covered by each tree as different from random. In each histogram of path length distribution frequency, the critical values for  $P \geq 0.01$  and  $P \geq 0.05$  were determined for the least path length.

(5) Analysis of the likely escape from experimental fields: The null hypothesis stated that if any population came from wild germplasm escapes in breeding stations, the road distance from the nearest experimental field (which could have used the wild germplasm) would be shorter than the distance to any other wild population. A new triangle matrix was constructed based on the road distance between wild *Helianthus* populations and the breeding stations.

Breeding stations which likely used wild germplasm were located in Alberti, Arrecifes, Baigorrita, Balcarce, Barrow, Castelar, Charata, Manfredi, Paraná, Pergamino, Pirovano, Salto, and Venado Tuerto. Clustering was based on single linkage.

The procedures CORRCAN, DISTANCE, IML, CLUSTER, UNIVARIATE and TREE of SAS Institute Inc (2006) were used to perform the statistical tests.

## Results

For both species the minimum connection tree joining all populations by road distances was highly different from random at the environmental level (Table 3). At the agro-ecological level the connection trees for *H. annuus* and for *H. petiolaris* were different from random at  $P \leq 0.05$  and  $P \leq 0.01$  respectively. Connection trees for *H. annuus* and for *H. petiolaris* are shown in Figs. 1 and 2 respectively.

Figure 3a represents the road distances from a unique dispersion point to the wild *H. annuus* populations, being the total distance of 2,355 km. In the same way, Fig. 3b represents the distances in environmental (abiotic) and agro-ecological conditions, expressed as a fraction or percentage of the total dissimilarity compared with the conditions of the same dispersion point. Similarly, Figs. 4a, b represent distances from a unique dispersion point to eight main *H. petiolaris* populations, being the total road distance of 1,329 km.

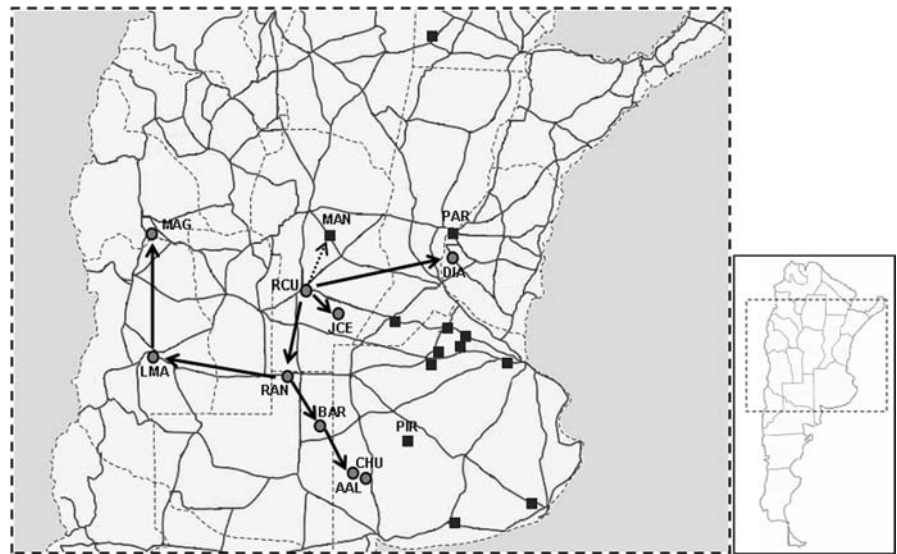
**Table 3** Differences from random distribution on the connections between habitats of two wild annual *Helianthus* showed in Figs. 1 and 2, with road (km), environment (Euclidean) and plant community (Gower) distances

		Distance dimension		
		Road	Environment	Community
<i>Wild Helianthus annuus</i>				
Total connection		2,021	31.2	2.17
Significance		**	**	*
Upper limit at random	$P \leq 0.05$	3,195	37.5	2.20
	$P \leq 0.01$	2,874	35.1	2.07
<i>Helianthus petiolaris</i>				
Total connection		870	31.3	2.85
Significance		**	**	**
Upper limit at random	$P \leq 0.05$	1,775	45.4	3.03
	$P \leq 0.01$	1,609	42.6	2.86

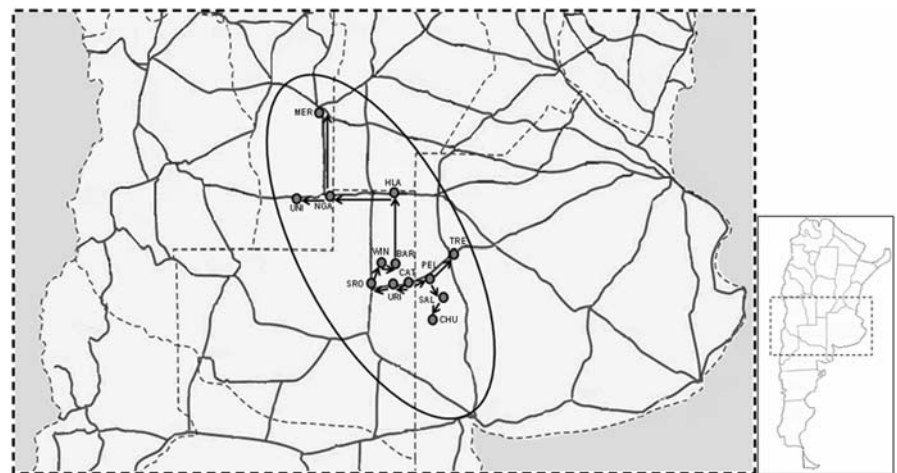
\* $P \leq 0.05$ , \*\* $P \leq 0.01$



**Fig. 1** Migration pattern suggested by road connection, environmental, and plant community proximities between wild *Helianthus annuus* stable populations (circles). Population names as in Table 1. Breeding stations (squares) closest to wild populations are Manfredi (MAN), Paraná (PAR), and Pirovano (PIR). MAN station used wild sunflower from RCU (dotted arrow)



**Fig. 2** Migration pattern suggested by road connectivity, environmental, and plant community proximities between habitats of *Helianthus petiolaris* stable populations. Population names as in Table 1. The ellipse shows the area where isolated plants were found in 2000–2007 surveys

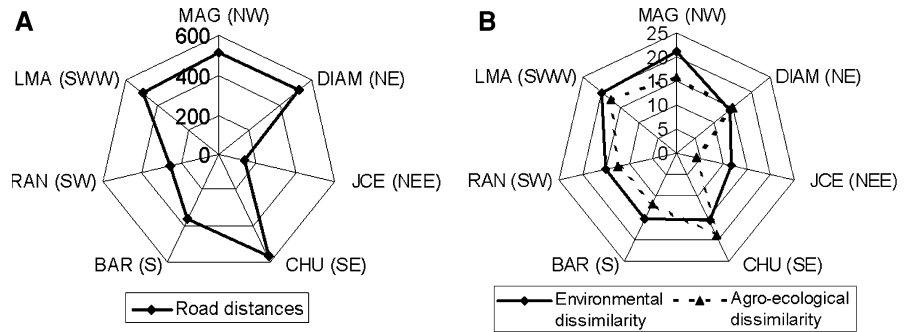


The pattern indicated that *H. annuus* migrated from the entry point ca. 500 km towards three main extreme habitats at NE, NNW and SWW direction (Fig. 3a). Among these, Diamante represented the smallest dissimilitude accounted in terms of plant community and environmental level. The habitats situated in the western irrigated area, entailed wider changes in terms of biotic parameters because populations co-occurred with different crops such as fruit trees (Fig. 3b). The fourth extreme destination reached by *H. annuus*, at the SE direction, implied 600 km of migration, being the community composition change more intense than the former three extreme points (Figs. 3a, b).

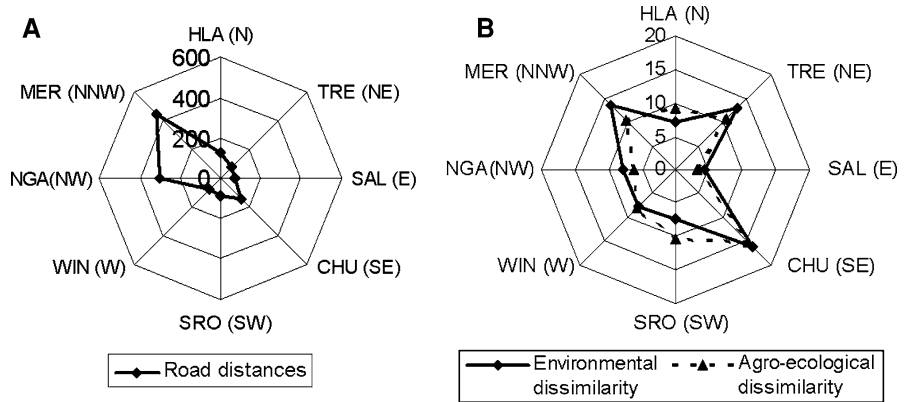
Stable populations of *H. petiolaris* have undergone the most intense environment and plant community changes towards the migration to SE and NE directions, in spite of the short geographical distance traveled (Fig. 4b). The migration to NW and NNW direction implies more distance, ca. 400 km, and was accompanied by strong environmental changes. Also, an extended area comprising very small patches or isolated plants without forming permanent populations was found (ellipse in Fig. 2).

Edaphic variables did not completely distinguish the micro-environment of both wild annual *Helianthus* species. Cluster analysis formed three main groups,

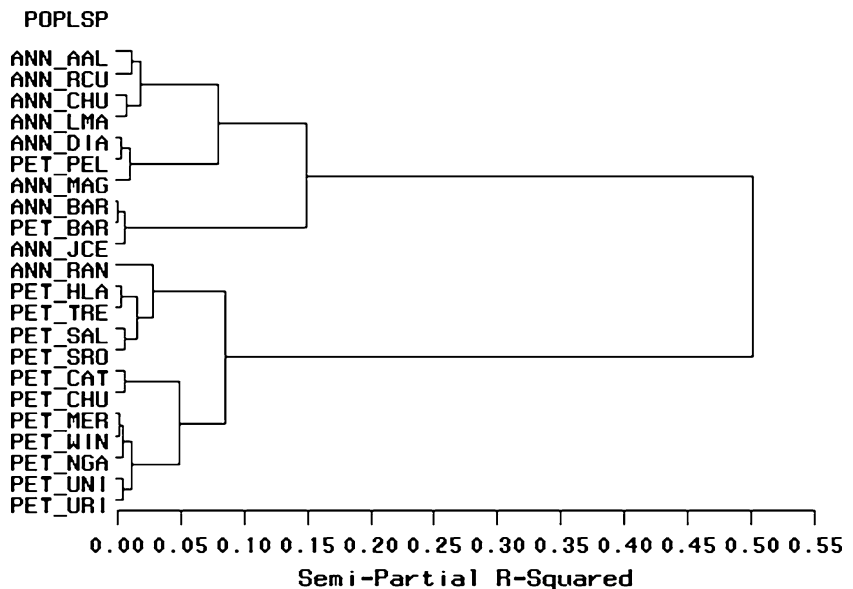
**Fig. 3** Distances from the entry point of wild *Helianthus annuus* (Rio Cuarto, Cordoba province) to the main populations in Argentina. **a** Road distance, **b** Environmental and ecological distances expressed as percent of the total distance to connect all populations



**Fig. 4** Distances from the entry point of *Helianthus petiolaris* (Catriló, La Pampa province) to main populations in Argentina. Environmental and ecological distances expressed as percent of the total distance to connect all populations



**Fig. 5** Clustering of wild *Helianthus annuus* (ANN) and *H. petiolaris* (PET) populations (POPLSP) in Argentina landscape by micro-environment habitat. The sites (same nomenclature as Table 1) were clustered by Ward minimum variance criteria of Euclidean distance of soil test variables range transformed and standardized. Pseudo T-Squared Statistics indicated the existence of three main clusters



with clear predominance of one species in two of them, but mixed in the remainder (Fig. 5).

The mean distance between each breeding station and the nearest wild *H. annuus* populations was  $299 \pm 154$  km, while the mean distance between

each one of the five populations and the nearest one reached  $170 \pm 212$  km. Clustering wild *H. annuus* populations and breeding stations by road distance confirmed Rio Cuarto as the original dispersion point (Fig. 6). The central and southern populations

connected with Pirovano rather than Rio Cuarto, but this historic breeding program never used wild sunflower as germplasm source.

## Discussion

A better understanding of the factors that affect biological invasions requires knowledge about the physical environment and the characteristics of invaded communities (Shea and Chesson 2002). Efforts to identify general attributes of future invaders have often been inconclusive, and predicting susceptible locales for future invasions seems even more problematic (Mack et al. 2000). However, to recreate the diffusion pattern would be still more difficult, being the register of herbaria specimens the only tool to trace back an invasion process.

Demographic and environmental stochasticity should be expected to play a major role in invasion dynamics, both in their initiation and over the long term dispersion (Fagan et al. 2002). According to them, this process typically produces ‘patchy’ spread, which was the observed pattern in wild *Helianthus*.

An essential stage of invasions is the transportation of the organism to a new location (Shea and Chesson 2002). Distance from the closest seed source and substrate conditions were important predictors of an invader seedling establishment (Stephenson et al. 2006). Long jumps in distance dispersal are much more influential than the small steps in determining the geographical distribution of invasive plant species (Nathan 2006). Long distance dispersal is likely of even greater consequence in agricultural landscapes or situations in which human-aided transport is possible (Fagan et al. 2002).

Seed dispersal of feral plants following communicational infrastructure is a common process for several crop related species. The traffic direction and anthropogenic vectors in the agro-ecosystem modulate and determine the widespread of feral plants along roadsides (Garnier et al. 2008). Achenes of both wild annual *Helianthus* invaders possess papus that could facilitate the attachment to transports, to be successful in long distance movement, carried by cars, tracks and grain transportation trailers. The widespread of both invaders might have also been facilitated by the machinery used for agriculture activity, which is usually accomplished by

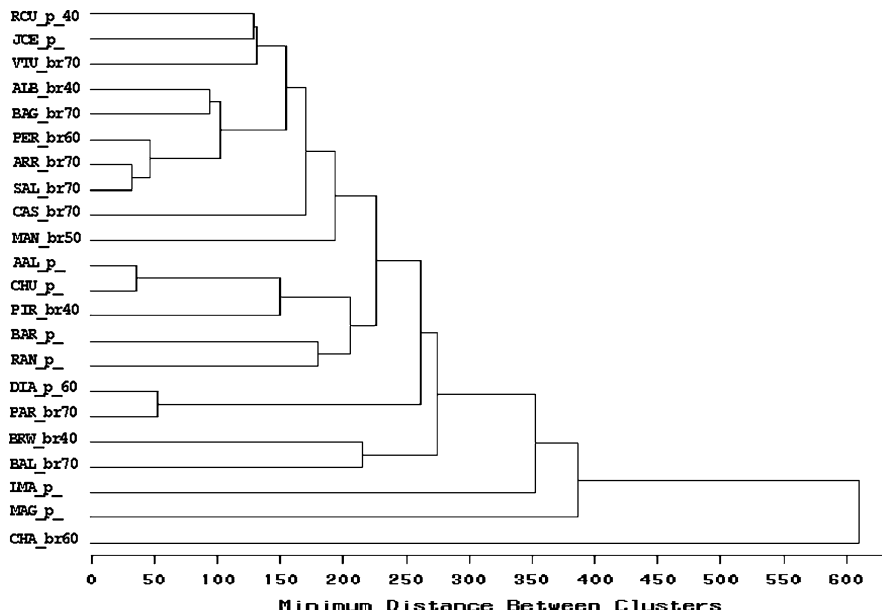
big equipment moving into the cultivated area of central Argentina. Road activity not only facilitates the propagule dispersion by its traffic, but also its construction and maintenance create the appropriate disturbance to favor the establishment of new populations.

The estimation of the diffusion process by means of the genetic relationship between the wild annual *Helianthus* populations could face two main constraints. First, wild populations are highly outcrossing and self-incompatible, showing high gene flow with the sunflower crop; this turns extremely difficult to use molecular markers associated to their geographic localization (Ureta et al. 2008). Second, the invasive process is relatively new, less than 60 years old, and possibly still not stabilized. The environmental and ecological approach overcomes those restrictions because it ignores the present and past gene exchange with the sunflower crop, and the absence of complete adaptation to the invaded habitat. Both genetic and ecological approaches are based on similarity of relative frequencies. Gene frequencies are used in the classical genetic approach whereas in our ecological approach we propose the use of abiotic and biotic features.

The coexistence of both wild annual *Helianthus* species in several habitats in central Argentina could explain the absence of differences between their respective micro-environments (Cantamutto et al. 2007). Also, in a previous study we found that soil properties of the microhabitat did not always match the average properties of the cartographic soil units due to the disturbance of the microhabitat (Cantamutto et al. 2008). Microhabitat edaphic factors seem to have minor influence over plant community distribution (Cousens et al. 2006). In our study they did not clearly reflect the environmental determinants of the soil unit (Fig. 5) thus they were not useful to estimate migration patterns.

The proposed migration pattern of wild *H. annuus* agrees with a previous phenotypic study in an experimental field (Presotto 2007). Movement to Diamante is the most difficult explanation because this species was present before the land connection of 1969, when a tunnel was opened below river Paraná bed and before the inclusion of wild resources in the breeding station developed in this locality (Cabrera 1974; <http://www.darwin.edu.ar>). Diamante population differs from the remaining wild resources of





**Fig. 6** Cluster ordination of road distances by hierarchical agglomerative single linkage between Argentine wild *Helianthus annuus* populations (P) and sunflower breeding stations (br), Alberti (ALB), Arrecifes (ARR), Baigorrita (BAI), Balcarce (BAL), Barrow (BRW), Castelar (CAS), Charata

(CHA), Manfredi (MAN), Paraná (PAR), Pergamino (PER), Pirovano (PIR), Salto (SAL), and Venado Tuerto (VTU). The two digit numbers indicate the decade of the first register of wild populations (before Poverene et al. 2002.) or the possible beginning of wild sunflower cultivation in experimental field

Argentina because of its long life cycle and yellow disc flowers frequency (Presotto 2007).

Although five wild *H. annuus* stable populations were found near sunflower breeding stations, their origin as escapes can be ruled out because of the close vicinity of another wild population as a possible seed source. Regarding *H. petiolaris*, there are evidences of its usage as disease resistance source in breeding stations of eastern and northern Argentina in the decade of 1960 (Luciano 1964; Bertero de Romano and Vazquez 2003) but escapes from there seem unlikely. A specimen at the Multidisciplinary Institute of Vegetal Biology Herbarium (<http://imbiv.unc.edu.ar/cpi/imbiv.htm>) constitutes evidence that *H. petiolaris* occurred in San Luis province before 1963. The road distance from those breeding stations to the nearest populations is of  $412 \pm 57$  km, whereas the populations are placed  $94 \pm 76$  km apart from each other.

It was possible to estimate a migration pattern for the two wild annual sunflowers through multivariate analysis and random test of road, environment and plant community proximity between stable populations of central Argentina. As the habitat connection by

ecological and environmental similarities was not different from the minimum road connection, the hypothesis of mechanical dispersion from a unique dispersion point could not be rejected. Also, as the stable wild populations were located far from breeding stations, the second hypothesis of no escapes could not be rejected. According to these results the alternative hypothesis of mechanical dispersion from a unique point appears as the most acceptable origin of the wild sunflower stable populations in central Argentina.

While the mathematical theory of biological invasions is still dominated by deterministic models, research on stochastic models is an area of increasing interest (Fagan et al. 2002). Our approach can be useful to estimate the diffusion process of successful non native plant invaders, when there are not enough historical registers and vouchers specimens available.

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