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A COMPARATIVE STUDY OF INVASIVE *Helianthus annuus* POPULATIONS IN THEIR NATURAL HABITATS OF ARGENTINA AND SPAIN

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SUMMARY

Wild *Helianthus annuus* is native to North America but it naturalized in other parts of the world as well. Although the origin of exotic populations is uncertain, they have probably evolved very differently in different countries. To unravel the origin of invasive populations from Argentina and Spain, morphological and agro-ecological data of nine populations from central Argentina, six from Andalusia and one from Gerona were collected in their natural habitats during three exploration trips in 2007 and 2008. In Argentina wild *H. annuus* was found mainly in disturbed areas between roads and fences. In a few cases the populations were located on the margins of cultivated fields. The Argentinean populations are spread across more than 50,000 m^2 at a density of about 25 plants m^{-2}. In Spain, the populations were found mainly in croplands. The largest population covered about 1,500 m^2 and comprised no more than 200 plants. The Argentinean populations had taller plants with a higher number of heads of small size, while the Spanish populations were characterized by bigger heads with wider ligules and bracts. Plants were shorter and leaf size was larger in Gerona than in Andalusia. Multivariate analysis differentiated populations from Argentina and Spain by many traits. Wild-crop gene flow is likely the source of genetic variation among them. In Argentina, the populations keep the appearance of early wild introductions, while the Spanish populations are weedier and probably originated from pollen contamination of commercial seed with wild plants or crop-wild hybrids.

Key words: **weedy sunflower, gene flow, diversity, morphology, naturalized**

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INTRODUCTION

Wild *Helianthus annuus* is native to North America but is also found in other parts of the world. In Europe it is present in several countries, such as France (Faure *et al*., 2002), the Czech Republic (Holec *et al*., 2005), Spain (Muller *et al*., 2006), and Italy (Vischi *et al*., 2006), and has been reported ephemerally in other countries as well (Holec *et al*., 2005). This species and other wild *Helianthus* species are also present in Australia (Dry and Burdon, 1986; Seiler *et al*., 2008), Argentina (Poverene *et al*., 2002), and South Africa (Vischi *et al*., 2004), and are now widespread over all the continents. The origin of exotic populations is uncertain. The authors above cite intentional and inadvertent introductions, mostly as contaminants of forage seed or litter for animals or escapes from gardens.

Wild *H. annuus* is established in central Argentina (Poverene *et al*., 2008), Australia (Seiler *et al*., 2008), France and Spain (Muller *et al*., 2009), where it is found in crop fields and in uncultivated places. Although it is a recognized germplasm source for several valuable traits that can be transferred to cultivated sunflower (Jan and Seiler, 2007), wild sunflower is also an invasive species for summer crops and pastures (Geier *et al*., 1996; Marshall *et al*., 2001; Deines *et al*., 2004). In particular, it can become troublesome for sunflower crops, given their genetic similarity that allows gene flow in both directions, wild-to-crop and crop-to wild (Reagon and Snow, 2006; Ureta *et al*., 2008a). Naturalized strains probably have evolved very differently in different countries and it would be of interest to know if there are any adapted ecotypes that could provide novel traits for sunflower breeding, *i.e*. resistance to biotic or abiotic constraints. In Argentina wild *H. annuus* grows in a wide range of agro-ecological environments (Cantamutto *et al*., 2008). Phenotypic characterization under common garden conditions revealed a high variability between Argentinean accessions and enough differentiation from the native populations to qualify them as a novel genetic resource (Presotto *et al*., 2009a; Cantamutto *et al*., 2010a). The goal of the present work was to examine and compare invasive populations from Argentina and Spain in an attempt to unravel their origin.

MATERIALS AND METHODS

Study materials from both countries were collected in their natural habitats during three exploration trips in 2007 and 2008. Wild strains from Argentina included nine representative *Helianthus annuus* populations from different geographic regions in the central part of the country (Table 1). Of the seven populations from Spain, six were collected in Andalusia and one in Gerona (Table 2).

Agro-ecological and morphological data were scored as follows:

Habitat data: On the basis of latitude and longitude of each population, climatic data from the nearest locality were scored: latitude (°), altitude (mosl), day-

light of the longest day (min), rainfall (mm), mean temperature of the hottest month and mean temperature of the coldest month (°). The climate data for Spain were taken from Agencia Estatal de Meterología (AEMET) of the Spanish government. The climatic data for Argentinean locations were estimated according to Cantamutto *et al*. (2008). Data for two of the Argentinean populations, located in the irrigated zones of San Juan and Mendoza provinces, were adjusted by adding 500 mm to the annual rainfall. Additional data on the location of the population were roadside (yes/no), waterside (yes/no), close distance to crops: sunflower, corn, wheat (yes/no), inside sunflower crop (yes/no), presence of sunflower volunteers (yes/no).

Table 1: *Helianthus annuus* populations from Argentina evaluated in their natural habitats

Population	UNS code	Nearest town and Province	Site description
DIA	1007	Diamante, Entre Rios	Crags along Parana river
JCE	1107	La Carlota, Córdoba	Roadsides of Hwy 4
RCU	1207	Rio Cuarto, Cordoba	Roadside, dirt road
MAG	1407	Media Agua, San Juan	Field margins close to a vineyard
LMA	1507	San Rafael, Mendoza	Field margin and dirt road
RAN	2007	Rancul, La Pampa	Roadside of Hwy. 188
BAR	2307	Colonia Barón, La Pampa	Roadside of Hwy 10
AAL	2807	Puan, Buenos Aires	Along a ditch near a malting factory
CHU	2907	Carhué, Buenos Aires	Along a ditch

Table 2: *Helianthus annuus* populations from Spain evaluated in their natural habitats

Population	UNS code	Nearest town and Province	Site description
COR	0108E	Cordoba, Cordoba, Andalusia	Fallow land close to sunflower crop
BUJ	0308E	Bujalance, Cordoba, Andalusia	Narrow land between a reed bed and a sunflower crop
FNU	0408E	Fernan Nunez, Cordoba, Andalusia	Roadside close to a sunflower crop
MON	0508E	Montilla, Cordoba, Andalusia	Roadside
MBA	0608E	Posadas (Molino Bajo), Cordoba, Andalusia	Within sunflower crop
PAL	0708E	Palma del Rio, Cordoba, Andalusia	Roadside
GER	0908E	St. Pere Pescador, Gerona	Borders of wheat crop

Plant traits: Branching type (no, basal, apical, full branching); presence of main head (yes/no); plant height (cm); stem diameter at mid-height (cm).

Leaf traits: Leaf length and width (cm); petiole length (cm); leaf base (cuneate, cordate); leaf shape (oblate, triangular, cordate, lance or round-shaped); leaf surface (flat, waxy, curled); leaf margin (smooth, serrate, deeply serrate); anthocyanin in stem and petioles (yes/no).

Inflorescence traits: Head position (°); dorsal leaflet (yes/no); number of heads (n); number of ray flowers (n); ray length and width (cm); bract (phyllary) number

(n); bract pubescence (range from 0, 25, 50, 75 y 100%); bract length and width (cm); head diameter (cm); disk flower color (yellow, red).

Separate Kruskal-Wallis tests (a non parametric ANOVA test) were performed for all traits showing variation among and/or within populations. The origins were compared considering all the populations nested in the countries as replicates.

Multivariate analysis comprised Discriminant, Principal Component (PCA) and Cluster analyses on individual measures and mean (metrics) or frequency (categorical) values per population. Classification employed the hierarchical agglomerative clustering method with Gower distance as the similarity measure (Gower, 1971).

RESULTS AND DISCUSSION

Habitat

The Argentinean *H. annuus* populations were found at a lower latitude than in the centre of origin (Cantamutto *et al.*, 2010a). The Spanish populations were located at a higher latitude than Argentinean ones and as a consequence grew under longer-day, dryer and hotter conditions than the populations in Argentina (Table 3).

Table 3: Environmental and ecological variables of wild sunflower habitats in Argentina and Spain. Difference significance by the Kruskal-Wallis non parametric test

Environmental variables[1]	Argent.	Spain	Sign.
Latitude (°)	34.64	38.29	***
Altitude (m.o.s.l.)	276.8	193.9	ns
Daylight (h:min)	14.20	14.40	***
Rainfall (mm)	702	549	**
Mean Temperature (°C)			
Hottest month	24.2	26.7	*
Coldest month	8.12	8.84	*

Ecological variables[2]	Argent.	Spain	Sign.
Roadside	0.67	0.43	ns
Waterside	0.44	0.00	ns
Sunflower crop	0.33	0.57	ns
Maize crop	0.22	0.14	ns
Wheat crop	0.00	0.29	ns
Volunteers	0.22	0.14	ns
Inside crop	0.00	0.86	***

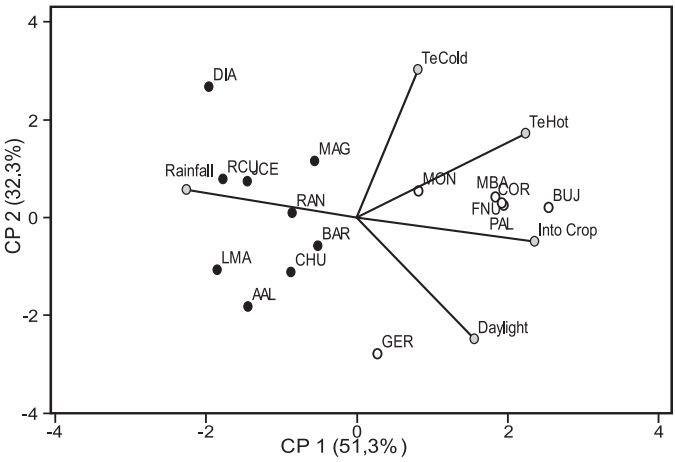
[1]mean values; [2]frequencies

Wild *H. annuus* was introduced to Argentina for agronomic purposes and probably escaped from cultivation and spread (Bauer, 1991) over extended areas in the central part of the country covering a wide range of agro-ecological conditions (Poverene *et al.*, 2002; Cantamutto *et al.*, 2008). At present, the wild sunflower grows mainly in disturbed areas between roads and fences (Poverene *et al.*, 2008). In a few cases the populations have invaded croplands, although they are usually located on the margins of cultivated fields (Table 4). In Spain, by contrast, the wild sunflower is frequently present within the crops, so six out of the seven populations from our study were found in that type of environment. Only one small population was located in a non-tilled area, near an olive plantation. The Argentinean populations cover more than 50,000 m^2 and have a density of about 25 plants m^{-2}. In Spain, the largest population covers an area of about 1,500 m^2 and comprises no more than 200 plants (Table 4).

Table 4: Ecological conditions of sampled *Helianthus annuus* populations

Population	Habitat	Demography	Other data
		Argentina	
DIA	Crags and riverside, 100 m wide. Clay and calcareous soils	>1000 plants in patches along 2 km	Big plants, long life cycle
JCE	Roadside with no volunteers or intermediate plants	>100,000 plants along 10 km	Dense population, very tall plants
RCU	Dirt road near the city, 15 m wide both roadsides	ca. 20,000 plants along 2 km	Dense population, big plants
MAG	Fallow land near a vineyard, irrigated	>8000 plants on 24,000 m^2	Dense population, shorter plants
LMA	Dirt road near town, along corn crop margins	ca. 5000 plants on 1700 m^2	Possible introgression of cultivated sunflower
RAN	Roadside close to rangeland and xerophytic shrubs	32 plants on 1300 m^2	Loose population, variable morphology
BAR	Roadside close to soybean, corn and alfalfa crops, volunteers and *H. petiolaris* present	ca. 12,000 plants on 62,000 m^2	Big plants, not dense but numerous
AAL	Along a ditch of 1200 m, close to sunflower crop and volunteers	Two patches of 6600 and 1800 plants each	Dense population, shorter plants
CHU	Dirt road, *H. petiolaris* volunteers or intermediate plants present	ca.2600 plants on 8,400 m^2	Possible introgression with cultivated sunflower
		Spain	
COR	Fallow land between sunflower and wheat crops. Some plants among sunflower crops	80-100 plants on a patch of 10 m diameter	Red discs and male-sterility among plants
BUJ	Feral plants on the border of a sunflower crop	Less than 100 on a patch of 1440 m^2	Many crop traits among plants
FNU	Roadside and border of sunflower crop	150-200 plants on a patch of 1200 m^2	Crop-wild traits and male sterility
MON	Roadside close to olive plantation	150-200 plants on 140 m^2	Wild appearance, dense pubescence
MBA	Wild-type plants in a sunflower crop	5-7 plants per 100 m^2	Red discs, male sterility long cycle
PAL	Roadside and border of a corn crop	Less than 50 plants	Wild and wild-crop appearance
GER	Dirt road and inside wheat crop	100-150 plants in 1200 m^2	Seem volunteers with anthocyanin pigmentation

Taken as a group, the habitats of the wild sunflower populations in Argentina were different and allowed to explain the invasive process (Cantamutto *et al.*, 2010b). When compared to the Spanish populations, five of the agro-ecological variables differentiated the habitat from both countries by means of PCA (Figure 1). Among the Spanish populations, Gerona seems to have special features, different from those of Argentina and the remainder of the Spanish habitats. The most outstanding feature in populations from Andalusia was their presence within sunflower crops.



(TeCold=Mean temperature of coolest month, TeHot=Mean temperature of hottest month; Day light=sunshine of the longest day; Into Crop=wild sunflower intrusion into cultivated sunflower).

Figure 1: Ecological diversity of Argentinean and Spanish wild sunflowers habitats explained by a PCA biplot of the five most explicative variables. See population acronym in Tables 1 and 2.

Plant morphology

Plants were screened for 24 morphological traits, which allowed a fairly good classification of the 16 populations. Kruskal-Wallis nonparametric analyses showed that most metric traits were highly significantly different between the countries, whereas categorical traits did not differ to a comparable extent (Table 5). However, some of the latter showed significant differences in traits that are characteristic of wild or cultivated sunflower - anthocyanin presence and red disc flowers in the Argentinean populations, no branching and main head presence in the Spanish populations.

Table 5: Mean value (metric traits) and frequency (categorical traits) in Argentina and Spain and significance of differences by the Kruskal-Wallis non parametric test

Metric traits	Arg.	Spain	Sign.
Plant height (cm)	206	176	*
Stem diameter (cm)	1,8	1.8	ns
Head angle (°)	76.8	86.5	***
Leaf width (cm)	15.6	26.0	***
Leaf length (cm)	18.8	32.3	***
Petiole length (cm)	12.4	19.9	***
N ligules (n)	25.6	34.3	***
Ligule width (cm)	1.4	1.7	***
Ligule length (cm)	4.0	5.8	***
N bracts (n)	36.9	39.7	**
Bract width (cm)	1.2	1.7	***
Bract length (cm)	1.7	3.1	***
Disc diameter (cm)	3.9	6.1	***

Categorical traits	Arg.	Spain	Sign.
Anthocyanin presence	0.92	0.74	***
No branching	0.00	0.35	**
Total branching	0.11	0.14	ns
Main head presence	0.00	0.28	**
N heads <10	0.03	0.16	ns
(ranges) 11-25	0.28	0.13	ns
N heads >25	0.69	0.63	ns
Leaf base (cordate)	0.68	0.93	*
Leaf shape (cordate)	0.77	0.89	ns
Leaf surface	0.10	0.29	*
Leaf margin	0.33	0.12	ns
Dorsal leaflet	0.54	0.35	ns
Dense bract pubescence	0.00	0.25	*
Flower disc color (red)	0.93	0.71	*

On the whole, the Argentinean populations had taller plants with a higher number of heads of small size, while the Spanish ones were characterized by larger leaves and bigger heads with larger ligules and bracts. The plants were shorter and leaf size was larger in Gerona than in Andalusia.

Principal Component Analysis based on metric traits showed that the Argentinean and Andalusian populations spread along the first PC, the former showing a better clustering of individuals from each population. The population from Gerona was close to the Spanish group, but separated by the second PC. It also showed a loose clustering of individuals (Figure 2), indicating a high variability within this locality. However, these variables only explained 53% of the total variability.

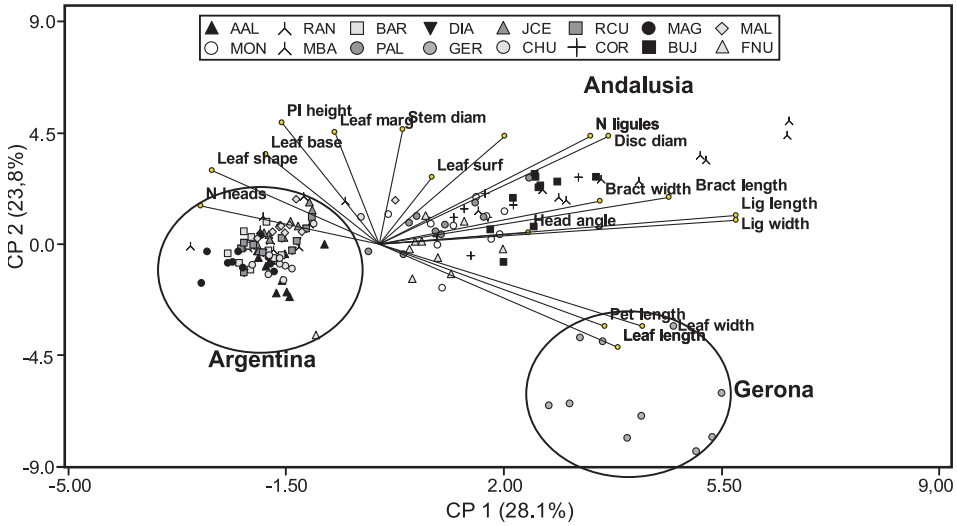


Figure 2: Morphological differentiation among wild sunflowers from Argentina and Spain in a PCA biplot based on standardized values for 17 traits. Plants are represented by points and traits by vectors from the origin. See Tables 1 and 2 for population acronyms and Table 5 for traits.

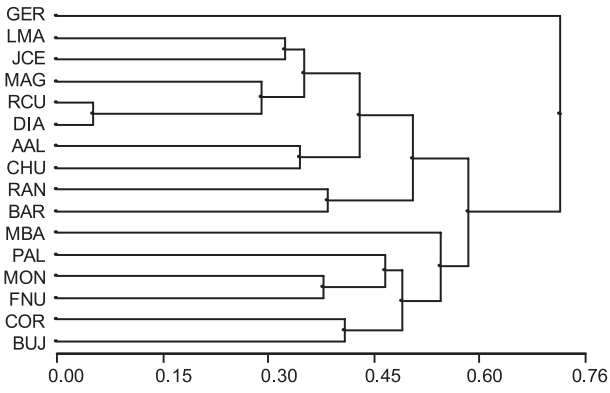


Figure 3: Overall similitude among 16 wild sunflower populations based on 24 morphological traits. UPGMA clustering was performed using Gower's distance matrix (Cophenetic correlation 0.95). See Tables 1 and 2 for population nomenclature.

Cluster analysis based on mean values of all the traits displayed two main clusters corresponding to both countries, while the Gerona population remained as a

third group (Figure 3). Considering these three groups, discriminant analysis differentiated populations from Argentina and Spain mainly by leaf shape, branching, plant height, and head size and color. The Spanish populations clearly split in those from Andalusia and the one from Gerona. There was better differentiation among the Argentinean populations with a marked clumping of individuals, also showing a separation between Rancul (RAN) and Baron (BAR) and the remaining populations (Figure 4).

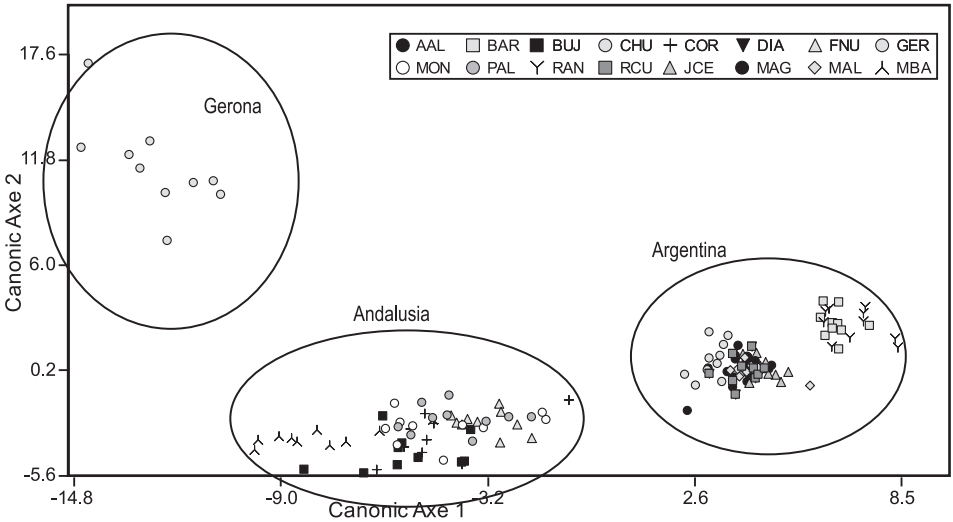


Figure 4: Discriminant analysis of 160 plants sampled in the field in Argentina and Spain based on 24 morphological traits. Each point represents the score for an individual. There is a noticeable grouping by populations.

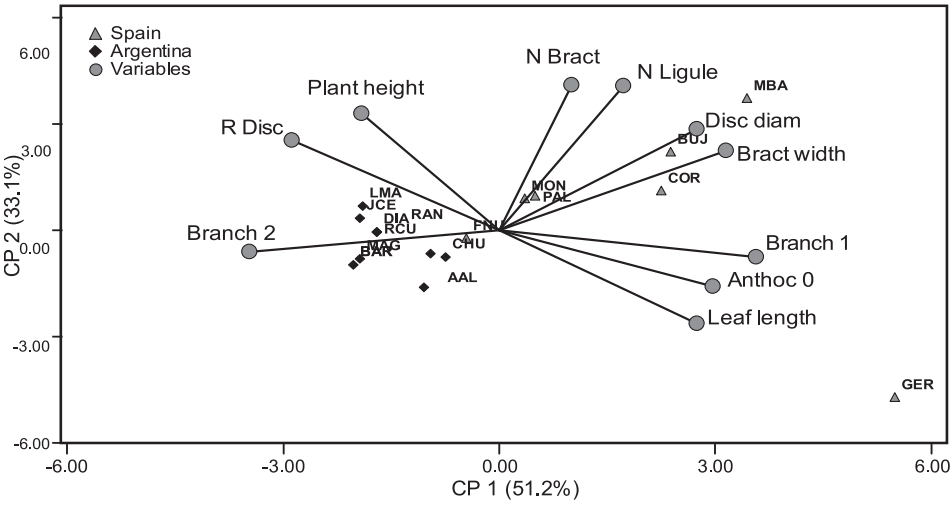


Figure 5: Biplot of the 10 variables that better explain the diversity among Argentinean and Spanish wild sunflower populations. See Tables 1 and 2 for population acronyms and Table 5 for traits.

Taking into account categorical variables in PCA as well, there were 10 that retained more than 84% of the original information (Figure 5). Higher frequencies of no branching, absence of anthocyanin, large leaves, shorter plants and lower frequency of red discs were found in the Gerona population. On the other hand, profuse branching, tall plants and red disc flowers characterized the Argentinean populations, while the Andalusian ones had bigger heads with a higher number of ligules and bracts and wider bracts. Strong branching, reduced size of heads, and anthocyanin presence are typical wild traits (Burke *et al*., 2002). Muller *et al*. (2009) described some Andalusian populations as weedy plants growing between the rows of sunflower crop showing anthocyanin pigmentation, small discs, strong branching, and reduced apical dominance. Self incompatibility and seed dormancy were found among those plants. They also recorded similar plants outside sunflower fields and called them escaped weedy populations. Their finding of a combination of wild and domesticated traits was confirmed in this study.

Gene flow from wild and domestic sunflowers to weedy populations is likely the source of genetic variation among them. Hybridization among wild and cultivated *H. annuus* is fairly common under Argentinean conditions (Ureta *et al*., 2008a,b). Crop traits can be recognized in wild plants of some populations, for example AAL, MAG and LMA (Presotto *et al*., 2009). Another naturalized annual species in Argentina, *H. petiolaris*, can also hybridize with *H. annuus* and thus constitutes another source of variation (Gutierrez *et al*., 2009). However, morphological traits confirmed that naturalized Argentine populations correspond to the wild form of the species in comparison with North American populations (Cantamutto *et al*., 2010a).

CONCLUSIONS

Wild sunflower populations are established in non-tilled areas within the agricultural regions of central Argentina, between 32° and 38° S latitude. In Spain, invasive sunflowers are found mainly in croplands between 36° and 42° N latitude. In spite of the intensive gene flow between them and the cultivated sunflower, Argentinean populations seem to have retained a much wilder appearance than Spanish populations. Our morphological data seem to confirm the hypothesis on the origin of seed contamination with wild sunflower for Andalusian populations, while the population in Gerona was probably derived from volunteer plants.

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POBLACIONES INVASORAS DE *Helianthus annuus* EN ARGENTINA Y ESPAÑA

RESUMEN

Helianthus annuus silvestre es originario de América del Norte pero se encuentra también en otras partes del mundo. El origen de las poblaciones exóticas es incierto y probablemente han evolucionado muy diversamente en los distintos países. Para develar el origen de las poblaciones invasoras en Argentina y España, se colectaron datos morfológicos y agro-ecológicos de nueve poblaciones de la región central de Argentina, seis poblaciones de Andalucía y una de Girona, en su hábitat natural, durante tres viajes de exploración en 2007 y 2008. En Argentina, *H. annuus* silvestre fue hallado principalmente en áreas disturbadas entre caminos y alambradas. En unos pocos casos las poblaciones es encontraban localizadas en los márgenes de campos cultivados. Las poblaciones argentinas alcanzaron más de 50.000 m^2 y una densidad de alrededor de 25 plantas/m^2. En España, las poblaciones se encontraron principalmente en tierras cultivadas. La de mayor tamaño cubría alrededor de 1500 m^2 y contenía no más de 200 plantas. Las poblaciones argentinas mostraron plantas más altas con mayor número de capítulos de pequeño tamaño, mientras que las españolas se caracterizaron por tallos más robustos, capítulos más grandes con lígulas y filarias (brácteas) más anchas. Las plantas fueron más bajas y las hojas de mayor tamaño en Girona que en Andalucía. El análisis multivariado diferenció las poblaciones de Argentina y España por muchos rasgos. El flujo génico cultivo-silvestre es probablemente la fuente de variación genética entre ellas. En Argentina, las poblaciones mantienen el aspecto de las antiguas introducciones silvestres, mientras que las poblaciones españolas son más de tipo malezoide y probablemente se originaron en contaminación de semilla comercial por polen de plantas silvestres o híbridos cultivo-silvestre.

POPULATIONS ENVAHISSEURS DE *Helianthus annuus* EN ARGENTINE ET EN ESPAGNE

RÉSUMÉ

Helianthus annuus sauvage il est originaire d'Amérique du Nord mais il se trouve aussi dans d'autres parties du monde. L'origine des populations exotiques est incertaine et probablement ont évolué très diversement dans les différents pays. Pour effiler l'origine des populations envahisseurs en Argentine et en Espagne, se on des données morphologiques et agro-écologiques de neuf populations de la région centrale de l'Argentine, six populations d'Andalousie et une de Girona, dans son habitat naturel, pendant trois voyages d'exploration en 2007 et 2008. En Argentine, *H. annuus* sauvage il a été trouvé principalement dans des secteurs perturbés entre des chemins et clôturés. Dans quelques cas les populations sont trouvaient localisées dans les marges de domaines cultivés. Les populations argentines ont atteint plus de 50.000 m^2 et une densité d'autour de 25 plantes/m^2. En Espagne, les populations se sont trouvées principalement dans des terres cultivées. Celle de grande taille couvrait d'autour 1500 m^2 et il contenait non plus de 200 plantes. Les populations argentines ont montré des plantes plus hautes avec un plus grand nombre de capitules de petite taille, tandis que les Espagnols se sont caractérisées par des tiges plus robustes, des capitules plus grands avec ligules et bractées plus larges. Les plantes ont été plus faibles et les feuilles de grande taille en Girona qui en Andalousie. L'analyse variable a différencié les populations l'Argentine et de l'Espagne par beaucoup de caractéristiques. Le flux des génes cultivé-sauvage est probablement la source de variation génétique entre elles. En Argentine, les populations maintiennent l'aspect des anciennes introductions sauvages, tandis que les populations espagnoles sont plus type mauvaise herbe et probablement en pollution de semence commerciale par pollen de plantes sauvages ou hybrides cultivé-sauvage.