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High infraspecific diversity of wild sunflowers (*Helianthus annuus* L.) naturally developed in central Argentina

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ABSTRACT

The sunflower's wild relative *Helianthus annuus* L. is a non-native invader in several regions of the world. It was introduced as an experimental forage plant in central Argentina six decades ago where it probably escaped and developed extended populations coexisting with the sunflower crop. If the invasive taxon was diffused without modifications, it would be expected to have phenotypic similarities with its parental sources. Nine populations representative of different geographic regions of central Argentina were compared with 17 populations from the USA (center of origin) in a common garden study at Bahía Blanca, Argentina using 47 phenotypic traits. The nine invasive wild populations were differentiated among themselves and from the native populations by plant form and life cycle traits, oil composition, inflorescence, and achene morphology. Populations from both continents shared traits related to domesticated sunflower, such as bract width over 0.8 cm, but the frequency of this trait was higher in populations from Argentina. The high variability of wild *H. annuus* populations from Argentina did not reveal any founder effects. The diversity found in the invasive populations reflected about three-fourths of the phenotypic variability of those from the center of origin, even though the environmental conditions of the Argentine habitats represented only half of the variability present in the North American habitats. The current findings demonstrated that the invasive wild sunflower populations have developed within few decades a high degree of variability, which could be a source of a novel biodiversity useful as a genetic resource for sunflower crop improvement.

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1. Introduction

Due to genetic and evolutionary implications, species under cultivation and their wild relative complexes have been extensively researched by the historians of domestication and agriculture (Harlan, 1992). The release of modern crop varieties, including new traits obtained by mutagenesis or bioengineering, has changed the focus on the wild-crop relatives study because gene flow could promote the development of new and more complex weeds (Gressel, 2005). In this area of research, the wild and weedy crop relatives are also generating interest due to their potential value as a genetic resource.

It is generally accepted that the sunflower crop, *Helianthus annuus* var. *macrocarpus* L. (Asteraceae), was domesticated around 4000 years ago in North America, the center of origin of the genus, where wild native populations are still found today (Harter et al., 2004). Russian breeders significantly improved the crop species during the 19th century using selected germplasm introduced into Europe as ornamentals, creating oil seed varieties that were successfully adopted by farmers' worldwide (Heiser, 1954; Schilling, 2006; Seiler and Rieseberg, 1997). The negative consequence of the global spread of the *Helianthus* genus was the diffusion of some wild populations of *H. annuus* that behave as a non-native invader in several regions of the world (Bervillé et al., 2005; Dry and Burdon, 1986).

In Argentina, the sunflower crop was introduced in the 1930s through domestic populations brought by European immigrants (Bertero de Romano and Vazquez, 2003). The first report of wild sunflower introductions was one decade later, when it was found as an experimental forage crop (Bauer, 1991). It is unknown how

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Nomenclature

CIC	days from transplant to end of flowering
DIB	days from transplant to 10% of flowering
HNU	head number
LLG	leaf length (cm)
LNU	leaf number
LSI	leaf width × length (cm^2)
PHT	plant height at begin of flowering (cm)
LWI	leaf width (%)
PLG	petiole length (cm)
SDI	stem diameter at mid-height (cm)
AEF	anthocyanin stigma frequency
APF	anthocyanin pale frequency
BIN	bract length: width relationship
HDI	head disk diameter (cm)
HLF	heads with leaf on the back frequency
RDF	red disk frequency
BSF	black stripes frequency
GPF	grey pericarp frequency
OSF	ovoid shape achene frequency
SFW	achene fresh matter weight (mg)
STH	achene thickness (mm)
SWT	achene width (mm)
C181	oleic acid content (%)
C182	linoleic acid content (%)
C220	behenic acid content (%)
C240	lignoceric acid content (%)
C832	linoleic/oleic relationship
YOI	iodine index

in the following 60 years the wild sunflower spread throughout central Argentina and colonized well-defined agro-ecological habitats (Cantamutto et al., 2008). At present, the wild populations are mostly located west of the more suitable area for the sunflower crop (de la Vega and Chapman, 2006).

The coexistence of the crop and wild sunflowers makes it difficult to disregard the existence of exo-ferality in the diffusion processes (Gressel, 2005; Poverene et al., 2004; Ureta et al., 2008). The use of wild sunflower as a genetic resource, ornamental, or as a contaminant of crop and forage seeds could be some other possible ways of intentional or unintentional introductions into different places in central Argentina.

In the invaded habitats, the populations show different life cycles, height, leaf shape, head morphology (Poverene et al., 2002). These could be attributed to phenotypic plasticity in response to environmental and ecological constraints of the different growing places (Richards et al., 2006). In addition, genetic differences between populations may exist. A common garden study minimizing environmental effects (Bender et al., 2002; Sugiyama, 2003) could be used to estimate the real genetic variability of phenotypic traits between populations (Rawashdeh et al., 2007; Soleimani et al., 2007).

We compared the plant morphology, life cycle, and seed oil composition of naturalized *Helianthus annuus* populations from Argentina with populations from the North American center of origin in a common garden study. If the populations from Argentina showed well-defined similarities with populations of wild sunflowers from the center of origin, this would suggest that introductions served as the most probable origin of the Argentine populations. If not, a new biodiversity in the *H. annuus* species must have been developed under the natural conditions of the invaded agro-ecosystem. This fact would indicate an ongoing microevolution giving the Argentine populations the potential value as a new genetic resource for the sunflower crop.

2. Materials and methods

2.1. Plant germplasm sources

Germplasm from Argentina consisted of wild *Helianthus annuus* populations collected in nine locations representative of the geographical different invaded habitats (Cantamutto et al., 2008). The provinces of Córdoba, La Pampa and Buenos Aires contributed two populations each; Rio Cuarto (RCU) (S 33°09′, W 64°20′), Juarez Celman (JCE) (S 33°40′, W 63°28′), Colonia Barón (BAR) (S 36°10′, W 63°53′), Rancul (RAN) (S 35°04′, W64°46′), Adolfo Alsina (AAL) (S 37°16′, W 62°59′) and Carhué (CHU) (S 37°16′, W 62°55′), respectively. Entre Ríos, San Juan and Mendoza provinces contributed one population each; Diamante (DIA) (S 32°03′, W 60°38′), Media Agua (MAG) (S 31°57′, W 68°27′) and Las Malvinas (LMA) (S 34°47′, W 68°15′), respectively.

Wild germplasm from North America was represented by 17 populations. States of origin and passport numbers were: Arizona (AZ) PI 468571, California (CA) PI 468580, Colorado (CO) PI 468621, Illinois (IL) PI 435540, Indiana (IN) PI 468633, Iowa (IA) PI 597901, Kansas (KS) PI 586851, Montana (MT) PI 586821, Nebraska (NE) PI 586867 Nevada (NV) PI 468596, New Mexico (NM) PI 468537, North Dakota (ND) PI 586807, Oklahoma (OK) PI 468483, South Dakota (SD) PI 586835, Texas (TX) PI 468504, Utah (UT) PI 468607, and Wyoming (WY) PI 586824 (for more information see www.ars-grin.gov/cgi-in/npgs/acc/display.pl?1080516). American germplasms are coded in the following by two, Argentine ones by three characters.

Geographic coordinates and altitude of collection sites for all populations were obtained from USDA (2008) and the Argentine passport data. Mean temperature of the hottest and coolest month and the average annual rainfall of the nearest locality, were obtained from www.worldclimate.com and de Fina (1992) for USA and Argentine populations, respectively.

2.2. Plant material studied in the common garden

Seed dormancy was overcome by maintaining seeds in germination paper in a wet chamber at 5 °C for 1 week (ISTA, 2004). Seedlings were grown for 30 days in the greenhouse at 20–25 °C in 28 × 54 cm^2 200-cell plastic trays and then transplanted in rows 2.10 m long with 0.25 m between plants for an equivalent population of 19.047 plants ha^{-1}. Plots at the Agronomy Department, Universidad Nacional del Sur, Bahia Blanca, Argentina (S 38°41′, W 62°14′) were drip irrigated for optimal plant growth. Data were collected from 238 and 248 individuals from Argentina and USA, respectively, during the 2004–2006 summer seasons in experimental plots including 9–24 populations each year. Original seeds were used for the first year, while re-generated achenes were used in subsequent years. Observations, population regeneration, and achene sampling were made on more than 20 individuals per population, except for four USA populations with poor germination which had only 14–18 individuals. Controlled pollinations for seed regeneration were made by hand on heads of sibbed individuals covered with polyamide bags until the end of flowering. Bulked seed lots of open-pollinated mature heads were collected before shattering and used to determine morphological and oil chemical

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