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WILD *Helianthus annuus* FOR SUNFLOWER IMPROVEMENT

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SUMMARY

A study of diversity was performed on 81 wild *Helianthus annuus* populations sampled from North America. Morphological and development traits were evaluated for different organs. Principal component analysis of quantitative traits associated the first components 1) to precocity-related traits in agreement with the geographical origin of the populations and 2) to domestication traits. We did not find any structure of qualitative traits by correspondence analysis. A sub-sample of twenty-one contrasted populations was observed for RAPD in comparison with twelve cultivated sunflower inbred lines. One hundred and seventy four polymorph fragments were revealed using nine primers. Cultivated inbred lines were unambiguously separated from wild populations by any analysis. Using RAPDs, much more diversity of wild *Helianthus annuus* appears in comparison with cultivated sunflower inbred lines. Among these populations, no reliable structure or clusters were found. We inferred from these results that a great deal of polymorphisms among wild *Helianthus annuus* remains to be investigated for possible use in sunflower breeding. We inferred also that it was not possible to ascertain clear structures of any qualitative traits and RAPD for wild *Helianthus annuus* populations. This absence of structure could be related with the dispersal of these wild resources when used by nomadic early Americans.

Key words: **Genetic resources, *Helianthus annuus*, sunflower, polymorphism, RAPD**

INTRODUCTION

Wild *Helianthus annuus* are supposed to be the main progenitor of cultivated sunflower forms. The habitat of wild *Helianthus annuus* has occurred primarily in Western North America, in sympatry with ten other annual species of *Helianthus* with more restricted habitats. Crosses and introgressions from other sympatric

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wild annual species have been suggested to occur frequently (Heiser *et al.*, 1969). These crosses might be at the origin of hybrid species such as *Helianthus anomalus* (Rieseberg *et al.*, 1995). Cultivated forms of sunflower are very common in wild *Helianthus annuus* habitat and gene flow from cultivated to wild *Helianthus annuus* is likely (Whitton *et al.*, 1997). Wild *Helianthus annuus* are used in sunflower breeding. Lines with restorer genes of PET-1 cytoplasm leading to male sterility (Leclercq, 1969) have been developed without apparent restriction to crossing and recombination from crosses between wild *Helianthus annuus* and cultivated sunflower. Some of these lines are efficiently combined with sunflower classical material (Fick *et al.*, 1975) in heterotic F_1 hybrids. Moreover, they often present a genetically recessive branching pattern, favorable to hybrid seed production, when used as pollinator. Four different types of cytoplasmic male sterility and associated restorer factors were discovered in wild *Helianthus annuus* (Serieys, 1994). Downy mildew (*Plasmopara halstedii* (Farl.) Berl.) resistance was conversely developed from wild *Helianthus annuus* into popular breeding materials (Fick *et al.*, 1975). Different sources of rust (*Puccinia helianthi* Schw.) resistance were discovered in wild *Helianthus annuus* (Quresh *et al.*, 1993).

Wild traits have to be eliminated for domestication: branching (usually it is genetically dominant but in some cases it is recessive), small seed, seed dormancy, low oil content.

In order to gather more informations about wild *Helianthus annuus* genetic resources variability, we tried to analyse some populations yet maintained as genetic resources for morphological and development traits as well as molecular DNA markers using RAPD. Moreover, pollen viability of hybrid combinations with cultivated type lines was also evaluated for these populations.

MATERIAL AND METHODS

GENOTYPES

1) Populations

The eighty-one populations studied were issued from a sampling for contrasting characters in evaluation of introduced material and diversity of geographical origin (Table 1).

2) Cultivated lines (Helianthus annuus var. *macrocarpus):*

Twelve inbred lines were chosen in order to represent a broad-based recent variability (Table 2).

TRAITS

We performed a preliminary study on eighty-one populations from direct collection in North America (sample of five plants in one location) in 1996 (Serieys *et al.*, 1997).

Table 1: Identity and collection site of wild *Helianthus annuus* populations

INRA Number	USDA PI Number	USDA ANN Number	State of collection	RAPD Study
209	435415	371	Texas	* Jlt
211	435540	627	Illinois	* Haa
351	413011		Missouri	* Haa
358	413018		Wyoming	
361	413021		Wyoming	* Jlt
363	413023		Colorado	
378	413038		South Dakota	* Haa
383	413043		Arizona	
386	413046		Arizona	
388	413048		South Dakota	
410	413070		California	* Jlt
421	413081		California	
435	413095		California	
437	413097		California	
446	413106		California	
458	413118		California	
461	413121		New Mexico	
463	413123		New Mexico	
468	413128		California	
509	413169		Texas	
511	413171	*H.argophyllus* ?	Texas	
519	413180	*Helianthus sp.* ?	Arizona	* Jlt
646	Ames6911	1114	Arkansas	
647	468447	1149	Texas	
648	468450	1160	Texas	* Jlt
649	468468	1184	New Mexico	
650	468473	1193	Texas	
651	468492	1279	Oklahoma	
652	468516	1320	Texas	
654	468576	1430	Arizona	
658	468609	1479	Utah	
660	468621	1511	Colorado	
661	468628	1522	New Mexico	
662	468632	1529	Oklahoma	
665	597895	1753	Iowa	* Haa
733	435557	1956	Kansas	
734	468462	1174	Texas	* Jlt
774	435575	756	Utah	
775	435581	762	Nevada	
822	468619	1507	Utah	
826	468620	1510	Utah	* Jlt

Table 1: Identity and collection site of wild *Helianthus annuus* populations

INRA Number	USDA PI Number	USDA ANN Number	State of collection	RAPD Study
829	597898	1757	Iowa	* Haa
833	468581	1438	California	
928	586807	2101	North Dakota	* Haa
929	586808	2102	North Dakota	
931	586809	2104	North Dakota	* Haa
933	586810	2106	North Dakota	
939	586814	2112	North Dakota	*
943	586816	2116	Montana	
945	586817	2118	Montana	* Jlt
948	586818	2121	Montana	
954	586821	2127	Montana	
955	586822	2128	Wyoming	
963	586828	2136	Wyoming	
966	586831	2139	Wyoming	
970	586834	2143	South Dakota	
974	586836	2147	Wyoming	
975	586837	2148	Wyoming	
980	586840	2153	Colorado	
989	586844	2162	Colorado	* Jlt
996	586847	2169	Colorado	
997	586849	2171	Kansas	
998	586850	2172	Kansas	
999	586852	2174	Kansas	
1000	586853	2175	Kansas	
1007	586860	2183	Kansas	
1011	586864	2187	Kansas	
1012	586865	2188	Nebraska	* Haa
1016	586867	2192	Nebraska	* Haa
1018	586869	2194	Nebraska	
1023	586873	2199	Nebraska	
1030	586877	2206	Nebraska	
1042	586882	2218	South Dakota	
1047	586884	2223	South Dakota	
1055	586887	2231	South Dakota	
1136		INRA 1991 EB P5	South Dakota	
1147		INRA 1991 EB P16	Colorado	
1148		INRA 1991 EB P17	Colorado	
1149		INRA 1991 EB P18	Utah	
1150		INRA 1991 EB P19	Montana	* Jlt
1151		INRA 1991 EB P20	North Dakota	* Haa

Haa indicates a collection in the central Plains region, possibly *Helianthus annuus* var *annuus* of Heiser, 1965 and Heiser *et al.*, 1969. Jlt indicates a collection in the western and south-western states, including California and Texas, possibly *Helianthus annuus* ssp. *jaegeri*, *Helianthus a.* ssp. *lenticularis*, and *Helianthus a.* ssp. *texanus* of the same authors.

Table 2: Identity, pedigree, origin and reference of cultivated lines

Name	Pedigree	Origin	Reference
90R19	NSH45 hybrid from Yugoslavia	INRA	
RT1B11	Broad based Synthetic population	INRA	
89HR2	R2D pool of Pet1 cytoplasm restorers	INRA	
2603	Cultivated population from Morocco	INRA	
83HR4	M5NV//M5.1.6/RHA274	INRA	
92B6=AA7.2.4	*H.argophyllus*/ Sunflower pool	INRA	Griveau *et al.*, 1996
FS20	Cernianka/ Sunrise	INRA	
HA335	HA89*3/wild *H. annuus* 423	USDA NDSU	Miller and Gulya, 1988
HA89	VNIIMK 8931		
LR1	85B6 / *Helianthus debilis* 215	INRA	
LR2	FS20 / *Helianthus argophyllus*	INRA	Besnard *et al.*, 1997
RHA274	PI343765/HA119// HA62-4-5	USDA,NDSU,Texas	Fick *et al.*, 1975

Morphophysiological quantitative traits of growth and development and passport traits were observed:

- collection latitude and longitude;
- plant height;
- length of longest lateral branch;
- maximum leaf blade and petiole length;
- basal, stem and head branching intensity (scaled from 1 to 5);
- days to flowering;
- head diameter;
- achene length, width, weight and oil content.

Morphophysiological qualitative traits of shape and color of organs were also observed in accordance with IPGRI-IBPGR (1985) :

- leaf shape (6 classes);
- leaf anthocyanin (4 classes);
- leaf margin (3 classes);
- shape of cross section of leaf (2 classes);
- leaf blistering (3 classes);
- head erectness (4 classes);
- flower anthocyanin (3 classes);
- presence or absence of male sterility of some plants;
- bract width (6 classes);
- bract length (2 classes);
- bract shape (2 classes);
- bract peak (5 classes);
- achene: main colour (7 classes), presence or absence of stripes, presence or absence of mottling.

Twenty-one populations (asterisk) and twelve inbred lines were studied for RAPD. DNA was prepared with CTAB detergent (Hoisington *et al.*, 1994). DNA preparation was made on 3 bulks of leaves from 10 plants for each population representing 30 individuals. RAPD was produced according to Besnard *et al.* (1997) with nine primers confirmed for discrimination in sunflower (Besnard *et al.*, 1997; Tersac *et al.*, 1993)

Pollen viability of hybrids: all populations were found self-sterile and pollinated with sunflower tester 90R19, RT1B11, 89HR2. The testcrosses were checked for pollen viability using Alexander (1969) iodine coloration method.

STATISTICAL ANALYSIS

Genetic distances between bulks and between populations were computed using Jaccard (1906) distances more adapted to dominant RAPD markers. SAS Institute (1992) STAT package was used for principal component analysis and correspondence analysis (Benzécri, 1982). Classifications were built for RAPD fragments using PHYLIP package (Felsenstein, 1993).

RESULTS

The results of the study of morphological and physiological traits have been detailed in our preceding publication (Serieys *et al.*, 1997). Within population polymorphism is comparable to between-population diversity. Principal component analysis reveals a strong structure of morphological and physiological quantitative traits supposed to be submitted to strong selection effects: flowering date, height, branching. Two main axes describe 60% of variation. The first axis is related to early or late types, plant height, and latitude and soil fertility of prospecting site. The second axis deals with traits related to domestication: seed and head sizes, intensity of branching.

Qualitative characters of organ color and shape were evaluated with correspondence analysis. No consistent structure was evidenced, with some erratic points possibly related with inter-specific introgressions.

RAPDs: One-hundred and seventy four polymorphic fragments were observed between bulks and lines evaluated (Figure 1). The incidence matrix was analyzed by correspondence analysis (Figure 2) and Jaccard distances between bulks (Figure 3). In these analyses, no evident structure or cluster between populations was revealed. However, variation between bulks of the same population appeared much less frequent than variation between populations. The only ambiguous classifications through PHYLIP diagrams were for #1150 and #1151 population bulks. The dispersion of observations in the main axes of correspondence analysis is considerably higher in wild populations than in cultivated lines. Cultivated lines were grouped in these diagrams and moreover very distinct from wild populations.

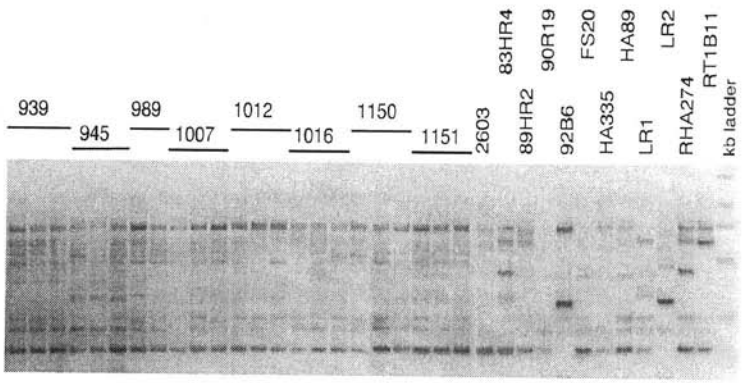

Figure 1: Polymorphysm for fragments obtained with J14 primer

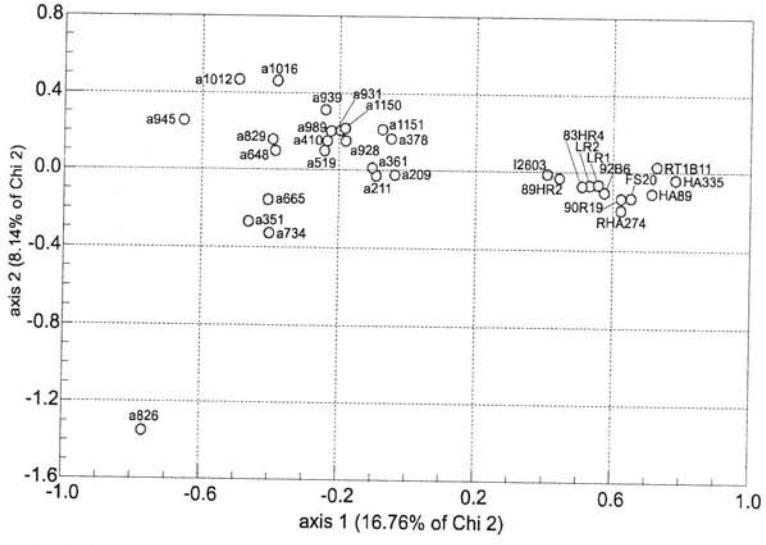

Figure 2: Correspondence analysis of RAPD

Another approach was performed in relation with the results of Cronn *et al.* (1997). Total number of polymorphic fragments and 'unique' fragments were computed for eleven "Plains" populations, ten "Western and Range" populations and twelve cultivated lines. Out of one-hundred and seventy-four polymorph fragments we found one-hundred and sixty-two fragments on "Plains" populations, one-hundred and sixty-three fragments on "Western and Range" populations and one-hundred and twenty-five fragments on cultivated lines. We observed six unique

fragments in "Plains" populations, six unique fragments in "Western and Range" populations and one unique fragment in the twelve cultivated lines (Table 3).

Table 3: Number of polymorph RAPD fragments of different germplasm origins

Hypothetical origin and classification of populations and lines	Number of populations or lines	Total polymorph RAPD fragments	Fragments unique to the class
Helianthus annuus annuus (Plains populations)	11	162	6
Helianthus annuus var *macrocarpus* (cultivated lines))	12	125	1
Helianthus annuus ssp. *jaegeri*?, *Helianthus* a. *lenticularis*?, *Helianthus* a. *texanus*?. (Western and South-western populations)	10	163	6

Pollen viability was rated by pollen staining averaging 70 to 100% in all the combinations between the populations and sunflower line testers, except accession #383 which was itself previously observed partially male sterile.

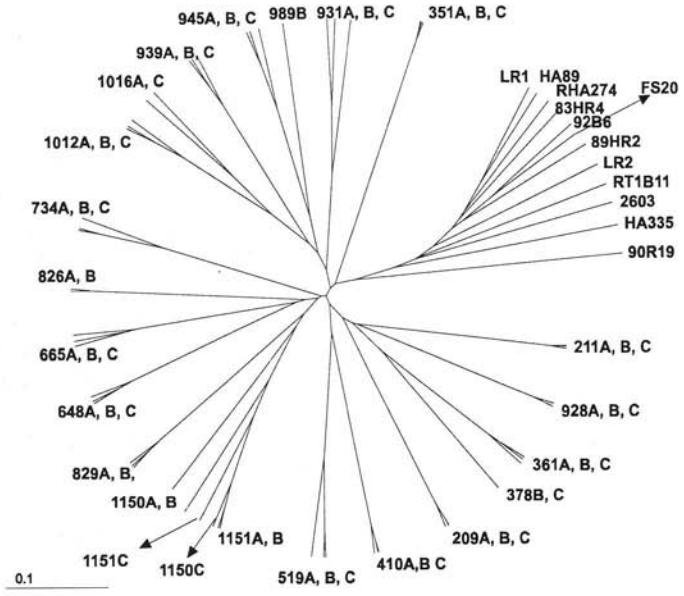

Figure 3: UPGMA diagram of Jaccard distances between wild populations, bulks and cultivated inbreds

DISCUSSION

Few studies about wild *Helianthus annuus* diversity have been published. Heiser (1954) evaluated eighty populations and was able to divide the species into three subspecies and a variety. Then Heiser *et al.* (1969) described six forms of

non-cultivated sunflower related to geographic origin. Seiler (1984) found extensive variation for morphological characters in ninety populations collected in USA. Rieseberg and Seiler (1990) compared domesticated and wild sunflowers for isozyme and chloroplast DNA. They found good similarity between wild and domesticated forms, extensive polymorphism in wild forms and virtual monomorphism in domesticated forms. In 1995 Arias and Rieseberg compared the same sample for RAPDs. They found high identity parameters between wild and domesticated *Helianthus annuus*. However, in contrast with the preceding study, they found that the modern cultivars are not genetically cohesive, perhaps due to the extensive intraspecific and interspecific hybridization. They observed little concordance between the geographical origin and genetic clustering of wild populations. They proposed to explain this finding "by the weedy, human dispersed nature of wild *Helianthus annuus* populations". Cronn *et al.* (1997) studied one-hundred and forty-six accessions of wild and domesticated sunflower for allozyme diversity. They found that samples from the Great Plains region of the United States were genetically divergent from accessions from California and the South-western United States. How domestication has taken place is however difficult to ascertain. Heiser (1985) suggested that wild *Helianthus annuus* was used by early Americans as food, then became a companion plant in the precarious settlements. It was further introduced from Western North America to Central U.S.A. and Canada. Seed dormancy allowed wild *Helianthus annuus* to survive and precede early American settlements and a return to sub-spontaneous wild or weedy forms.

In our study (detailed in Serieys *et al.*, 1997), a clear structure was observed for continuous traits of growth and development (size of vegetative and reproductive organs, timing of development). Two axes of principal component analysis were evidently in relation with external factors. The first axis was related with developmental precocity and collection place. The northern populations were earlier, with shorter growth characteristics and smaller organs. However, the latest types were found in central states such as Nebraska, Kansas where deep rich soil conditions could allow a long growth and development period. The second axis was related with branching and reproductive organs and possibly related with domestication breeding effects, in relation with ancient use of *Helianthus annuus* by early Americans in proto-historic times, or more commonly by pollution of wild self-sterile *Helianthus annuus* by cultivated sunflower pollen.

In contrast with these relatively clear and simple results, we did not find any consistent structure in the samples studied for qualitative morphological characters and RAPD. This is in accordance with Arias and Rieseberg (1995) who did not observe a good concordance between the geographical origin and genetic clustering of wild populations. However, with isozyme neutral markers, Cronn *et al.* (1997) found a geographical divergence between populations and more diversity in "Plains" material. "Plains" populations are possibly related with *Helianthus annuus* var. *annuus* (Heiser, 1969), "Western and Range" populations are possibly related with *Helianthus annuus jaegeri*, *Helianthus annuus lenticularis* and *Helianthus annuus texanus* (Heiser, 1969); cultivated material is typically *Helianthus annuus* var. *macrocarpus*. In order to verify this finding we interpreted our results using 3 classes of origin in RAPD studies (Table 3):

4. "Plains" populations from Illinois, Iowa, Missouri, Nebraska, North Dakota, South Dakota,
5. Other "Range" populations, Western and South-western collected populations (Arizona, California, Colorado, Montana, Texas, Utah, and Wyoming),
6. Cultivated lines very distinct from the other groups, with restricted variability.

Plains populations are not differentiated from other wild populations in the correspondence analysis. Plains populations do not appear more polymorph than other (one-hundred and sixty-two fragments against one-hundred and sixty-three). They do not appear very divergent (one-hundred and fifty-six fragments in common for both wild "groups"). This can be explained by the continuous habitat (no isolation), but also by human factors yet explained. Some discrepancies could be due to divergence of population sampling, traits observed and molecular tools used.

CONCLUSION

What conclusion can be drawn for the breeder or population geneticist? For direct breeding purpose, extensive sampling of wild *Helianthus annuus* is perhaps not necessary because the variability is so weakly structured. The strategy might be very different for mid-term or long-term genetic resources management. We built a composite population with the 81 wild populations used as females recombined with 3 cultivated inbred lines 90R19, RT1B11, 89HR2. For the geneticist, the markers and traits used in this work are very insufficient for gene flow studies between cultivated and wild *Helianthus annuus*. Cytoplasm organelle DNA markers (chloroplast and mitochondria) could be very useful for this purpose.

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Helianthus annuus SILVESTRE PARA EL MEJORAMIENTO DEL GIRASOL

RESUMEN

La divergencia era investigada para 81 poblaciones del *Helianthus annuus* silvestre que proviene de Norteamerica. Diversas partes de la planta eran evaluadas con respecto a las propiedades evolutivas. El analisis de componentes basicos de propiedades cuantitativas ha liado los primeros componentes con 1) las propiedades de precocidad, conforme al origen geografico de poblaciones, 2) las propiedades de domesticacion. El analisis de correspondencia no indico cualquier estructura de propiedades cualitativas. La submuestra se componia de 21 poblaciones diferentes segun las propiedades y fue investigado para RAPD en comparacion con 12 lineas consanguineas del girasol cultivado. Con la utilizacion de nueve primers fueron encontrados 174 fragmentos poliformes. Las lineas del girasol cultivado eran claramente diferentes de las poblaciones silvestres sin mirar el analisis aplicado. Con la utilizacion de RAPD fue constatada la divergencia considerablemente elevada en las poblaciones silvestres mas que en las lineas del girasol cultivado. Entretanto, no pudieron ser constatadas ciertamente la estructura y tampoco la existencia de grupos en la poblacion. A base de los resultados obtenidos, hemos concluido que hay aun una gran parte de poliformismo entre las especies silvestres de *Helianthus annuus* para ser investigada para la aplicacion posible en la seleccion de girasol. Hemos tambien concluido que no fue posible de constatar cualquier clara estructura de propiedades cuantitativas y de RAPD en las poblaciones silvestres de *Helianthus annuus*. Esta falta de estructura puede ser liada con la diseminacion de esas fuentes silvestres como consecuencia de la utilizacion por los habitantes primitivos de America, los cuales vivian como nomadas.

L'*Helianthus annuus* SAUVAGE ET L'AMÉLIORATION DU TOURNESOL

RÉSUMÉ

Une étude de diversité a été faite sur 81 populations *d'Helianthus annuus* originaires d'Amérique du Nord. Les caractéristiques de développement et les caractéristiques morphologiques des différents organes ont été evaluées. L'analyse des composantes de base des caractéristiques quantitatives a relié les premières composantes 1) aux caractéristiques de précocité, ce qui est en accord avec l'origine géographique des populations, et 2) aux caractéristiques d'adaptation. L'analyse de la correspondance n'a pas montré de structure des caractéristiques qualitatives. Un sous-échantillonnage composé de 21 populations différentes a été examiné pour RAPD et comparé à 12 lignes inbred de tournesol de culture. L'utilisation de neuf primers a révélé 174 fragments polymorphes. Quel que soit le type d'analyse, les lignes de tournesol de culture étaient clairement différentes des populations sauvages. Le RAPD montre une plus importante diversité dans les populations sauvages que dans les lignes de tournesol de culture. Cependant, dans les populations, nous n'avons pu confirmer ni la structure, ni l'existence de groupes avec certitude. Les résultats obtenus nous ont amenés à conclure qu'il reste encore une grande partie de polymorphismes chez les espèces sauvages *d'Helianthus annuus* qu'il faudrait examiner en vue d'une application possible dans la culture du tournesol. De plus, nous avons déduit qu'il n'était pas possible de déterminer une structutre claire des caractéristiques quantitatives et de RAPD dans les populations sauvages *d'Helianthus annuus*. Cette absence de structure pourrait être attribuée à la dispersion des ressources sauvages comme conséquence de la vie nomade des premiers habitants du continent américain.