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Combining-groups in cultivated sunflower populations (*Helianthus annuus* L.) and their relationships with the country of origin

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Abstract. Using four tester lines an analysis of combining abilities for seed yield, seed moisture content and seed oil content was performed on 39 cultivated sunflower populations originating from ten countries. A between-populations structure based on specific combining abilities (SCA) was designed, defining separate combining-groups for each of the four testers. This structure corresponds to the country in which the populations originated.

Key words: Genetic variability – Heterosis – Combining abilities – Combining groups – Sunflower

Introduction

Like most allogamous plants, the cultivated sunflower, *Helianthus annuus* L., shows strong inbreeding depression and, therefore, strong heterosis when outcrossed. Selection must be accomplished in such a manner as to maximise heterosis, utilising hybrid combinations. This can be achieved by defining combining-groups according to allelic pools that have to be as different as possible, such as in the flint and dent groups in maize (*Zea mays* L.). Cytoplasmic male sterility due to PET1 cytoplasm, used since 1970, has led sunflower breeders to structure genetic variation into two groups, according to maintainers of cytoplasmic male sterility and fertility restorers of male sterility (Leclercq 1969). Hybrid cultivars commercialized during recent years are closely related, thus indicating limited exploitation of genetic variability (Vranceanu 1985). Little research concerning sunflower genetic variability has been published (Anashenko 1972; Yavada and Singh 1985; Bazan et al. 1988). Only two of these publications were based on the values of offspring obtained from crosses. The objective of the present study was designed to examine the values of offspring from a collection of 39 sunflower populations originating from ten different countries test-crossed with four homozygous inbred lines of cultivated sunflower in order to define combining-groups in this species. Using the Mandel analysis, we found a between-population structure based on specific combining abilities. Each tester defines a separate group of combinations. The Mandel analysis, the Euclidean distances, and a principal component analysis (PCA) allow us to recognize three major groups: the Russian group, the Moroccan group, and the French group, which cannot be separated from the Turkish, Argentinian, Italian and Egyptian populations. African, Indian and Hungarian populations are close to the Moroccan group.

Materials and methods

Materials

Thirty-nine different populations of cultivated sunflower originating from ten different countries distributed across the world were studied (Table 1). Four pure lines were used as testers: HA89, RHA274, XK and 85A1. In order to make crosses between populations and testers we used the cytoplasmic male-sterile form of the testers. The pure lines HA89, XK and 85A1 were on PETI cytoplasm and the pure line RHA274 was on PEF1 cytoplasm (Serieys and Vincourt 1987).

Methods

To highlight different combining groups, the genomes of testers have to be as different as possible from each other. The HA89 and RHA274 lines were chosen because they are derived from

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traditional combining-groups used by sunflower breeders, either maintainers of cytoplasmic male sterility, usually named "Russian maintainers", or fertility restorers of male sterility, usually named "American restorers", respectively. Furthermore, the selection of 85A1 and XK lines was done in such a way that the four tester lines are of a different genetic origin and display polymorphisms in phenotypic traits.

The 156 hybrid combinations resulting from testcrosses of populations by testers were studied as part of a network named PROTOURNESOL, which involves INRA and 18 other French private institutes of sunflower breeding. The experimental design was a lattice with two replicates of 100 plants, planted in three geographical locations: west, southwest and central France. Three French commercial varieties, Mirasol, Frankasol and Topflor, were used as controls and included in the trial. Mirasol was replicated in each sub-block to improve the accuracy of the experimental design. Three agronomic characters were measured: seed yield, seed moisture content at harvest, which is a measure of early maturity, and seed oil content.

Statistical methods

Pondered mean coefficient. The seed yield was estimated by a Pondered mean coefficient (PMC):

$$\mathrm{PMC} = \frac{1}{K}\sum_{1,K} \frac{X_k - T_k}{\sqrt{\frac{\sigma_e^2(k)}{n_k}\left(1+\frac{1}{n_t}\right)}}$$

with

K = trial location number,
k = trial location index,
X_k = mean yield in trial location k,
T_k = average control yield in trial location k,
n_t = number of controls,
n_k = number of replications in trial location k.

PMC is the mean pondered determined by deviation with respect to controls. This coefficient gives a lesser weight to experiments having the largese coefficients of variation, thus

Table 1. Name, origin and general combining abilities (GCA) of populations

Code	Origin	Name	GCA seed yield (PMC)	GCA seed moist cont. (%)	GCA seed oil content (%)
Af1	Africa	ZAMBIA PI 480473	1.21	14.07	46.67
Af2	Africa	ZAMBIA PI 480472	0.31	12.20	47.11
Ar3	Argentina	CORDOBES*YENISSEI	−0.08	9.71	45.08
Ar4	Argentina	PUNTANO*SMENA	0.32	9.55	45.84
E5	Egypt	GIZZEH	0.98	10.52	42.41
F6	France	GRIS STRIE PA. 164	−1.56	10.08	41.57
F7	France	P.I.F. FAUX ISSANKA	−1.37	6.39	47.35
F8	France	P.I.C. FAUX ISSANKA	−2.10	6.73	47.86
F9	France	GRIS STRIE PROVENCE	−0.94	11.42	42.15
F10	France	ISSANKA	−1.72	6.88	47.84
F11	France	POPULATION CLAPIERS	−1.11	7.28	48.26
F12	France	NAIN ROUGE	−1.79	12.04	41.92
H13	Hungary	LOVASPATONAï	−1.47	14.39	46.45
In14	India	INDIA COMPOSITE	−0.87	10.28	53.80
It15	Italy	MOTTA DI LIVENZA	0.12	9.18	43.27
It16	Italy	MOïMACCO	−0.90	8.26	43.24
M17	Morocco	H101.113	0.86	12.55	46.38
M18	Morocco	S13.P3.1.N197	−2.05	9.32	51.27
M19	Morocco	86.DB.1.369	−1.94	8.83	52.00
M20	Morocco	S 659.4.373	−2.60	8.68	51.28
M21	Morocco	H40.12.A01.N115	−2.10	9.08	49.45
M22	Morocco	H112.122.235	−1.94	10.32	49.28
M23	Morocco	SB.P4.1.198	−2.09	10.11	49.97
M24	Morocco	R 1875.P2.1.196	−1.42	9.60	49.51
R25	Russia	ZARIA	−1.96	8.15	48.44
R26	Russia	PEREDOVIK KRASNODAR	−0.12	9.31	51.07
R27	Russia	TCHAKINSKI 269.433	−1.54	7.85	49.93
R28	Russia	NOVINKA.2079	−2.10	8.61	48.81
R29	Russia	KARKOVSKI.50.2080	−1.41	8.65	52.52
R30	Russia	VNIIMK 8931.1221	−1.35	8.62	50.15
R31	Russia	ARMAVIR 3497.5.3.1.1.1345	−1.93	7.96	50.96
R32	Russia	RACVIET 2.1412	−0.91	10.33	51.59
R33	Russia	KHARKOV 101	−0.42	7.82	52.42
R34	Russia	PROGRESS	−0.28	11.51	48.02
R35	Russia	VNIIMK 1646.2.1.1.2.1492	−1.30	7.85	50.45
R36	Russia	VOLGAR CODISOL.1695	−0.57	8.62	49.13
T37	Turkey	BILECIK	0.63	9.08	40.54
T38	Turkey	CANAKALLE	−0.91	7.76	42.77
T39	Turkey	IZMIR	−0.24	8.51	41.74

permitting us to take this information into consideration without resulting in a significant bias in the resulting calculations.

Analysis of variance of the linear model permitted us to calculate the general (GCA) and specific (SCA) combining abilities. The GCA of one population is the mean value, calculated in the four testcrosses, of this population. It represents the summed additive effects. The GCA represents about 80% of the phenotypic value of hybrids, and is related to the material per-se value (Tables 1–3). The SCA is the difference of a specific crossing with the value computed from the GCA of its parents. It is an interaction between one population and a specific tester.

Because the SCA effects could be correlated among each other, they were studied using the method of Mandel which allows an examination of the interaction with a method similar to a principal component analysis (Mandel 1971). Thus we obtained three independent Mandel components.

Euclidean distances. The Euclidean distances were calculated from the specific combining abilities (SCA) of the three agronomic characters. We thus obtained 12 variables (four testers by three agronomic characters).

Principal component analysis. The principal component analysis was computed with the same 12 variables.

Results and discussion

The population effect (GCA) and the effects resulting from population-tester interaction (SCA) were significant at the 1% level (F test of Fisher).

General combining ability analysis

For country origins where populations are the most numerous, the GCA effects indicate that the Russian populations have a higher level of seed yield and seed oil content than the French populations, while Moroccan populations are intermediate for seed oil content and have a high level of seed water content, which implies late maturity (Table 3).

Specific combining ability analysis

Mandel analysis. This analysis is similar to a principal component analysis where populations are observations while testers are variables. The Mandel components are computed as linear combinations of variables and are not correlated with each other.

In the Mandel analysis, computed on SCA, the two first Mandel components represent percentages of the total inertia which are respectively 84%, 74.5% and 87.2% for the three agronomic characters studied. The graphical representation of the first two Mandel components clearly discriminates between the four variables of the analysis, represented by testers (Figs. 1–3). Because testers are clearly separated (one tester per quadrant), this approach allows us to define, for each agronomic character, four groups of combinations

Table 2. Origin and general combining abilities (GCA) of testers

Code	Origin	Name	GCA seed yield (PMC)	GCA seed moist. cont. (%)	GCA seed oil content (%)
T1	INRA (France)	85A1	−2.74	9.54	45.74
T2	USDA (USA)	(Cms-PEF1) RHA274	−1.60	7.10	45.17
T3	USDA (USA)	HA89	−0.49	9.72	49.24
T4	INRA (France)	XK	1.45	12.14	49.42

Table 3. Mean values of general combining abilities (GCA) by country of origin

Origin	Number of populations	GCA seed yield (PMC)	GCA seed moist. cont. (%)	GCA seed oil content (%)
Africa	2	0.76	13.13	46.89
Argentina	2	0.12	9.63	45.46
Egypt	1	0.98	10.52	42.41
France	7	−1.51	8.69	45.28
Hungary	1	−1.47	14.39	46.45
India	1	−0.87	10.28	53.80
Italy	2	−0.39	8.72	43.25
Morocco	8	−1.66	9.81	49.89
Russia	12	−1.16	8.77	50.29
Turkey	3	−0.17	8.45	41.68

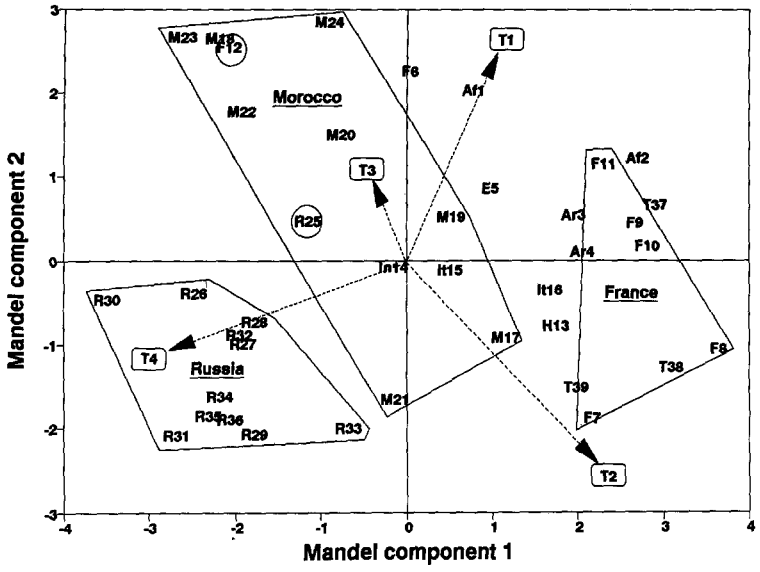

Fig. 1. Mandel analysis computed on the SCA of seed yield of 39 cultivated sunflower populations with four testers. Plot of Mandel components 1 and 2: variables, *T1–T4*, tester 1 to tester 4; observations, *Af1–T39*, sunflower populations (see Table 1)

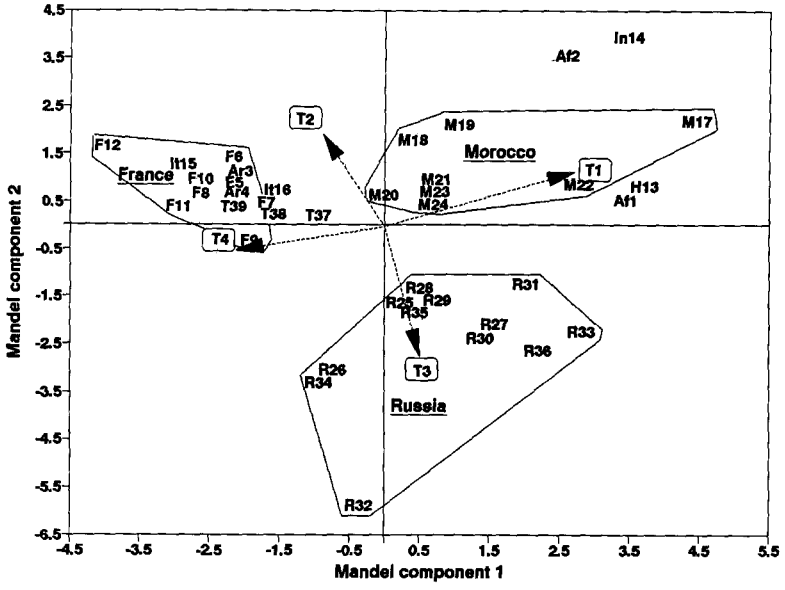

Fig 2. Mandel analysis computed on the SCA of seed moisture content of 39 cultivated sunflower populations with four testers. Plot of Mandel components 1 and 2: variables, *T1–T4*, tester 1 to tester 4; observations, *Af1–T39*, sunflower populations (see Table 1)

based on crossing values of the material studied with each of the four testers.

The observations of the Mandel analysis, represented by populations, reveal a structure according to the country of origin of the populations, in particular for the French, Moroccan and Russian populations which are the most numerous. These results are in agreement for each of the three agronomic characters measured.

Examining each agronomic character we conclude that:

(1) Russian populations are characterized by interactions with the T4 tester for seed yield, the T3 tester for seed moisture content, and the T1 tester for seed oil content.

(2) Moroccan populations are characterized by interactions with the T1 tester for seed moisture content and the T4 tester for seed oil content.

(3) French populations are characterized by interactions with the T2 tester for seed yield, the T4 tester for seed moisture content, and the T3 tester for seed oil content.

Euclidean distances. Euclidean distances between populations were computed, using specific combining values (standardized values) for each tester and for each agronomic character as variables. We thus obtained 12 variables (four testers by three agronomic characters). These distances were represented as a dendrogram (ascending hierarchical cluster analysis).

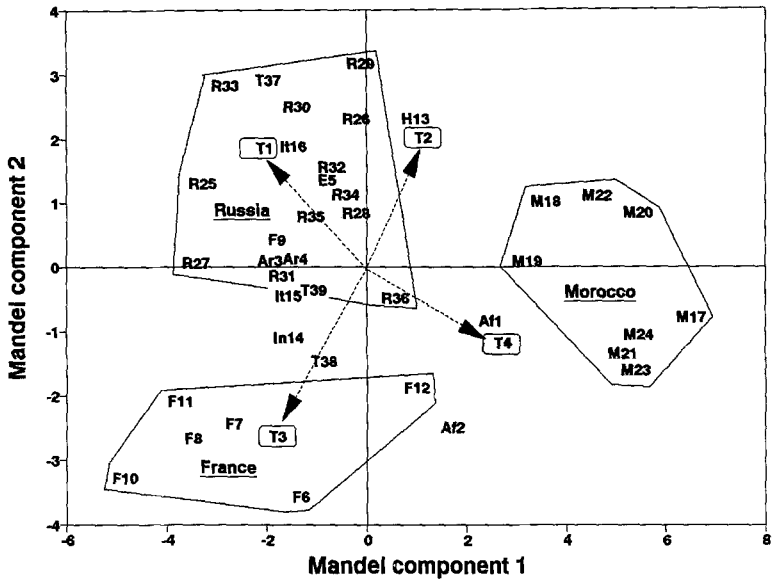

Fig. 3. Mandel analysis computed on the SCA of seed oil content of 39 cultivated sunflower populations with four testers. Plot of Mandel components 1 and 2: variables, *T1–T4*, tester 1 to tester 4; observations, *Af1–T39*, sunflower populations (see Table 1)

This dendrogram also shows a clustering of the populations by country of origin at the level of certain nodes (Fig. 4). We noted three major groups:

(1) The Russian populations, which constitute an homogeneous group.
(2) The Argentinian, Egyptian, Italian, Turkish and French populations.
(3) The Moroccan, African, Indian and Hungarian populations.

In groups 2 and 3 populations are clustered in subgroups according to the country of origin.

Principal component analysis (PCA). The principal component analysis based on the same 12 variables, as described above, were computed. The percentage of the total inertia for the two first components is 56% (30% for axis 1 and 26% for axis 2). The graphical representation of the first two components clearly shows a structure of populations by country of origin (Fig. 5). This result agrees with both the Mandel analyses and the Euclidean distances. The Moroccan group is now homogeneous.

This analysis highlights the following structuring variables:

(1) The Russian group is defined by interactions with the T4 tester for seed yield, with the T3 tester for seed moisture content, and with the T1 tester for seed oil content.
(2) The Moroccan group is essentially defined by interactions with the T4 tester for seed oil content.

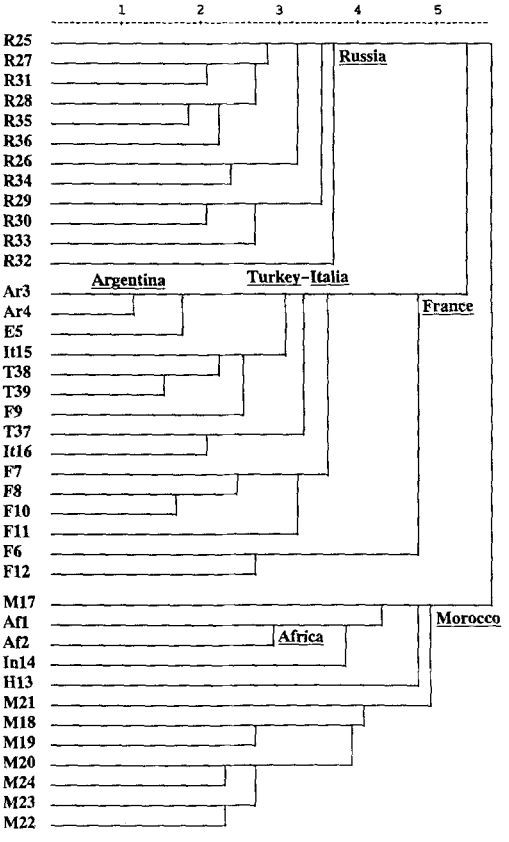

Fig. 4. Euclidean distances computed on the SCA of 39 cultivated sunflower populations with four testers for seed yield, seed moisture content and seed oil content (ascending hierarchical cluster analysis)

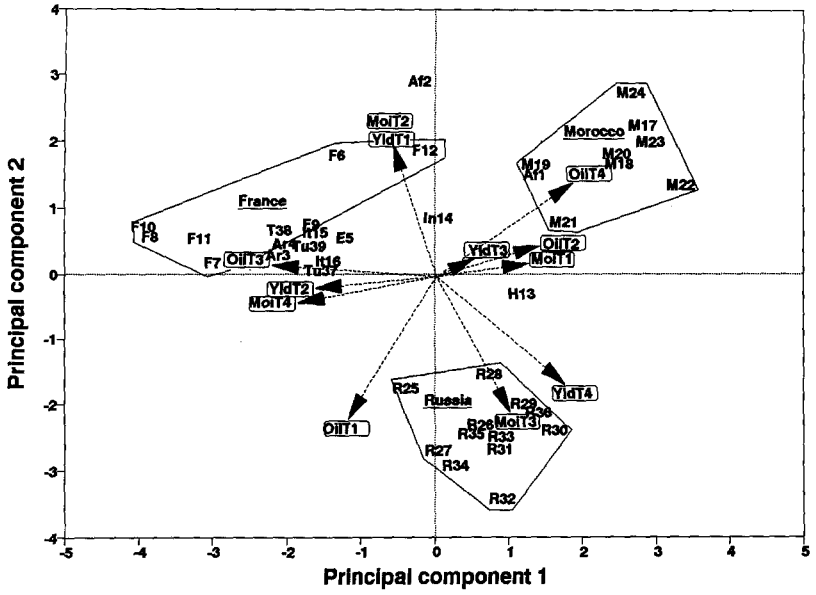

Fig. 5. Principal component analysis on SCA of 39 cultivated sunflowers populations with four testers. Variables: *YldT1– YldT4*, SCA for seed yield of populations with tester T1 to tester T4; *MoiT1–MoiT4*, SCA for seed moisture content of populations with tester T1 to tester T4; *OilT1–OilT4*, SCA for seed oil content of populations with tester T1 to tester T4. Observations: *Af1–T39*, populations (see Table 1)

(3) The French group is defined by interactions with the T2 tester for seed yield, with the T4 tester for seed moisture content, and with the T3 tester for seed oil content. This group cannot be separated from the Turkish, Argentinian, Italian and Egyptian populations.

Conclusion

Mandel analysis permitted us to define four separate combining groups corresponding to the four testers. The Mandel analysis, Euclidean distances, and principal component analysis agree with a structure of sunflower populations corresponding to the country of origin. We conclude that populations from different countries are different for their interactions with testers and, therefore, different at least for part of the genes involved in these interactions. Since our knowledge about the genetic origins of populations is very limited we cannot use any historical lineage. However, two hypothesis are possible: either the methods used by breeders, and in particular the tester strains that they use in order to improve their stock, differ (in the present study the alleles involved in the elaboration of heterosis would have to be different) or the materials from different geographical origins are largely unrelated and, accordingly, differ for the greater part of their genomes.

One could examine molecular markers to obtain a possible answer to this question. This is what we intend to do in a continuation of this study. This approach might also allow us to propose the possible existence of a relationship between the defined combining-groups and appropriate molecular markers of the genome, thus making it possible to predict heterosis. Predicting heterosis is quite costly to measure by crossing and field evaluation.

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