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Plant breeding

Environmental effects on hullability of sunflower hybrids

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Summary – Twenty-five sunflower hybrids were grown in 5 environments in order to determine environmental effects and genotype x environment interactions on hullability. Cropping conditions had significant effects on hullability. A water deficit, in particular during seed maturation, resulted in a considerable increase in hullability. Although highly significant, the genotype x environment interaction was quite small with significant correlations between genotype rankings in the different environments. Fractionation of the interaction following a multiplicative model showed that the intensity of interaction varied according to genotype. However, a non-parametric test did not show any significant difference between the stabilities of the 25 hybrids studied. It is concluded that efficient breeding for hullability can be carried out using control genotypes in quite a small number of locations.

hullability / sunflower / genotype x environment interaction / stability / non-parametric test

Résumé – Effets de l'environnement sur l'aptitude au décorticage d'hybrides de tournesol. *Une étude de 25 hybrides de tournesol expérimentés dans 5 milieux a été entreprise pour estimer l'action du milieu et l'importance des interactions génotype x environnement sur leurs aptitudes au décorticage. Les conditions de culture peuvent avoir une incidence très importante sur ce caractère. Un déficit hydrique, notamment durant la phase de maturation des akènes, peut se traduire par une nette augmentation des taux de décorticage. Bien que hautement significative, l'interaction avec le milieu apparaît modérée, les classements des génotypes pour les différents essais étant corrélés significativement. Sa décomposition selon un modèle multiplicatif a permis de montrer qu'elle est plus ou moins prononcée selon les génotypes étudiés. Toutefois, aucune différence de stabilité entre les 25 hybrides n'a été révélée par le test non paramétrique utilisé. Il est conclu qu'une sélection pour l'adaptation générale utilisant des témoins et réalisée sur un nombre limité de lieux devrait être efficace.*

aptitude au décorticage / tournesol / interaction genotype x environnement / stabilité / test non paramétrique

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INTRODUCTION

Most sunflower seedmeal is characterised by a high content of poorly digestible fibre derived from the hulls, which constitute about 20% of the whole seed; protein contents form only about 30 to 33% (Burghart, 1992). For sunflower meal to compete with other protein sources such as soybean for use in animal feeds, it would need to have a protein content of about 40% (Bourdon, 1985; Signoret and Evrard, 1987). At least partial hulling before oil extraction could provide this result. Up to now, the ease with which hulls can be removed from seed (or hullability) has not been included in sunflower breeding programmes and commercial crops show very varying levels, from approximately 20 to 60% (Merrien *et al*, 1992). In order to make large-scale industrial hulling a viable proposition it is necessary to have known and good hullabilities. Studies have therefore been made to determine whether it is possible to select sunflower genotypes which can be hulled easily. Denis *et al* (1994) showed that narrow sense heritability of this character is quite high (70–80%), similar to that of seed oil content, but environmental effects also appeared to be important.

A series of hybrids showing a wide range of hullabilities was grown in diverse environments in order to determine the effect of the environment on hullability and estimate genotype x environment interactions and stability of individual genotypes. In trials of different genotypes in different environments, the 2 sources of variation are rarely additive. A genotype x environment interaction may be due either to different variances in the different environments or, giving more problems for the breeder, to a lack of correlation between results in different environments (Gallais, 1992a). Strategies for breeding programmes will depend both on the size of such an interaction and its causes.

MATERIALS AND METHODS

Sunflower genotypes

Twenty-five F_1 hybrids were produced by a factorial cross of 5 male sterile (female) inbred lines (ZF, CAJ, RC, UD, CD) and 5 restorer (male) lines (PBP4, 89HR2, PB3, PSC5, HA61). CD, a form of HA89, and HA61 were bred by the USDA, Fargo, USA; the other lines were bred by INRA, France.

Experimental design

The hybrids were grown in randomised block design trials with 3 replications, in 3 locations in 1991: Clermont-Ferrand, Puy-de-Dôme, France (CL91); Cognat-Lyonne, Allier, France (CO91); and Carmona, Seville, Spain (ESP91). There were 2 locations in 1992: Clermont-Ferrand, Puy-de-Dôme, France (CL92); and Cognat-Lyonne, Allier, France (CO92).

The French trials were characterised by regular rainfall during the growing period, with more in 1992 than 1991 (CL91: 221 mm; CO91: 251 mm; CL92: 580 mm; CO92: 500 mm). Maximum daily temperatures rarely exceeded 30°C. The soil was deep clay at Cognat-Lyonne and chernozem at Clermont-Ferrand. The Spanish trial had much less rainfall (80 mm) with none during maturation (July and August), and very high maximum daily temperatures, often exceeding 35°C. The data necessary to calculate quite complete water balances (rainfall, usable soil reserve, potential evapotranspiration) were not always available.

The plots consisted of 2 rows with about 25 plants/plot and plant densities of between 53 000 and 69 000 plants/ha. The plants were open pollinated but the capitula were protected from bird damage after flowering by greaseproof paper bags. Seed was harvested at about 10% water content and dried at 30°C. Before measurements of hullability, water contents were homogenised at 4–6% by drying in an incubator at 35°C overnight.

Measurements of hullability

Hullability is defined as the proportion of hulls removed by a mechanical huller, compared with the total hull content (HC) of the seed. HC was determined after manual hulling of a random sample of 50 seeds. The percentages of hulls removed by a laboratory huller (MH), with a disc spinning at 3 800 rpm, were measured on 10 g samples of seed. Hullability (H) was calculated as (MH/HC) x 100.

Statistical analyses

The multilocal data were analysed by analysis of variance for a fixed effects model:

$$P_{ijk} = \frac{\mu + E_j + B_k}{E_j + G_i + G_i * E_j + e_{ijk}}$$

with

P_{ijk}: phenotypic value;

μ: general mean;

E_j: environmental effect j; $j = 0$ to J;

B_k/E_j: effect of replication k in environment j; $k = 0$ to K;

G_i: effect of genotype i; $i = 0$ to I;

$G_i * E_j$: genotype x environment interaction;
e_{ijk} : residual effects.

After testing the significance of the genotype x environment interaction, it was divided into several multiplicative terms with the form:

$$\theta^m * \gamma_i^m * \delta_j^m$$

They include 1 sub-term associated with the genotypes (γ) and another (δ) associated with the environments. Their maximum number is the minimum of ($I - 1$) and ($J - 1$). The sums of squares of the multiplicative terms are related to the parameters θ by $SCE_m = K (\theta^m)^2$ (Denis and Vincourt, 1982).

The model used requires the following conditions for the parameters that are estimated from the matrix of residues of the additive model:

Centred main effects:

$$\Sigma E_i = \Sigma G_j = 0$$

Centred, normalised and orthogonal interaction terms:

$$\Sigma \gamma_i^m = \Sigma \delta_i^m = 0$$

$$\Sigma \gamma_i^m \gamma_i^{m'} = \Sigma \delta_j^m \delta_j^{m'}$$

$$= 0 \text{ if } m \approx m' \text{ or } = 1 \text{ if } m = m'$$

The stability of individual hybrids was determined using the non-parametric method advocated by Nassar and Hühn (1987) and modified by Hühn and Nassar (1989). This estimation is based on the ranking of each genotype in each environment. A genotype can be considered as stable if its rank is always the same or similar in the different environments, according to the dynamic concept of stability defined by Becker and Leon (1988).

Among the different parameters permitting measurement of the dispersion of ranks, following the recommendations of Huehn (1990a), only the mean of the absolute rank differences is taken into account. To estimate phenotypic stability independently of genotypic effects, rank depending only on the genotype x environment interaction and on residual variance, the original data (means of K replications) were first corrected in the following manner:

$$P_{ij.}^* = P_{ij.} - (P_{i..} - P_{...})$$

with

$P_{ij.}$: phenotypic value of genotype i in environment j (i = 1 to I ; j = 1 to J);

$P_{i..}$: marginal mean of genotype i;

$P_{...}$: overall mean.

The ranks of the I phenotypic values were calculated for each environment separately; rank 1 given to the lowest value. The mean of the absolute rank differences was determined from:

$$S_i = \frac{\Sigma j < j' \mid r_{ij} - r_{ij'} \mid}{J(J-1)/2}$$

r_{ij}: rank of the genotype i over the environment j.

The test of the hypothesis H0, *ie* that all the genotypes have the same stability for their phenotypic values, was calculated from

$$Z_i = [S_i - E(S_i)]^2 / V(S_i)$$

where

$$E(S_i) = (I^2 - 1) / (3I)$$

and

$$V(S_i) = \{(I^2 - 1)[(I^2 - 4)(J + 3) + 30]\} / [45I^2J(J - 1)]$$

Comparison between the χ^2 value with I degrees of freedom and the quantity $S = \Sigma Z_i$ shows whether significant differences in stability exist between genotypes. If the hypothesis is rejected, the stability analysis is continued for each genotype. Z_i follows an approximate χ^2 distribution with 1 degree of freedom and makes it possible to test the null hypothesis that genotype i is stable. Z_i can be significant both if r_i is significantly greater than its theoretical value (an unstable genotype compared with the others) and if it is significantly lower (for a particularly stable genotype) (Krenzer *et al*, 1992).

The analyses of variance were carried out with the software Statgraphics (version 5.0). The software Intera was used to analyse the genotype x environment interaction (Decoux and Denis, 1992).

RESULTS

For each trial, the mean hullabilities of each of the 25 hybrids are presented in table I. There were considerable differences between genotypes, which ranged from 27.3 (CO92) to 38.9 (CL91) percentage points. The analyses of variance for each location showed highly significant genotype effects. The coefficients of variation varied from 6.3 to 20.8%, the same level as those generally observed for sunflower yield trials.

The trial carried out in Spain in 1991 (ESP91) gave a much higher mean level of hullability (68.8%) than in France, where similar figures were obtained for the 2 locations and 2 years (27.3 to 38.3%). The environment effect (F = 817.6), genotype effect (F = 44.5) and genotype x environment interaction (F = 4.8) were highly significant (table II) but the main effects (genotype and environment) explain a much greater part of the variation than the interaction.

Table I. Hullabilities (in %) of 25 sunflower hybrids studied in 5 environments.

Female parent	*Male parent*	*Code*	*Environment*				
			CL91	*CL92*	*CO91*	*CO92*	*ESP91*
ZF	PBP4	A1	18.0	33.6	20.3	30.4	70.1
ZF	89HR2	A2	9.4	22.5	14.2	19.0	52.1
ZF	PB3	A3	12.6	29.3	15.4	26.1	53.0
ZF	PSC5	A4	33.6	39.3	32.9	24.6	67.4
ZF	HA61	A5	28.2	54.3	31.9	43.3	66.6
CAJ	PBP4	B1	35.5	35.6	34.9	28.3	69.5
CAJ	89HR2	B2	19.9	30.0	17.5	20.2	61.1
CAJ	PB3	B3	21.6	24.4	17.1	27.6	52.9
CAJ	PSC5	B4	48.3	37.5	51.8	25.2	70.8
CAJ	HA61	B5	48.1	59.9	41.2	38.9	67.1
RC	PBP4	C1	38.3	47.6	47.0	31.6	79.7
RC	89HR2	C2	26.1	26.1	18.8	16.3	70.9
RC	PB3	C3	22.5	36.8	25.1	19.7	60.0
RC	PSC5	C4	42.0	44.7	37.8	16.0	84.9
RC	HA61	C5	40.6	59.6	47.9	27.4	77.9
UD	PBP4	D1	32.1	46.8	31.2	38.7	83.6
UD	89HR2	D2	38.3	42.3	29.8	30.7	84.8
UD	PB3	D3	28.0	30.6	23.5	23.3	75.0
UD	PSC5	D4	41.4	48.3	44.7	34.6	81.0
UD	HA61	D5	39.0	53.2	51.1	41.4	81.3
CD	PBP4	E1	27.8	26.7	32.4	20.1	60.6
CD	89HR2	E2	24.4	21.4	26.8	16.7	64.9
CD	PB3	E3	16.9	26.9	22.5	21.7	54.6
CD	PSC5	E4	44.2	39.3	39.5	28.0	66.3
CD	HA61	E5	34.3	41.9	42.6	32.7	62.9
Mean			30.8	38.3	31.9	27.3	68.8
Range			38.9	38.5	37.6	27.3	32.8
Coefficient of variation			13.9	15.1	20.8	14.6	6.3

Code: as used for genotype identification in figure 1.

Table II. Study of 25 sunflower hybrids in 5 environments using an analysis of variance with interaction divided into 3 multiplicative terms.

Source of variation	*SS*	df	*MS*	F *test*
Total	132 917.6	374		
Environment (E)	85 426.2	4	21 356.6	817.6**
Block/environment	1 388.4	10	138.8	5.3**
Genotype (G)	27 890.1	24	1 162.1	44.5**
Interaction G x E	11 943.4	96	124.4	4.8**
Multiplicative term 1	5 344.0	(27)	197.9	7.6**
Multiplicative term 2	3 858.3	(25)	154.3	5.9**
Multiplicative term 3	1 811.2	(23)	78.7	3.0**
Rest of the interaction	930.0	(21)	44.3	1.7*
Residual	6 269.4	240	26.1	

df: in case of multiplicative terms, there are no classic degrees of freedom associated with the sum of squares but parametric dimensions (Denis, 1992). ** Highly significant ($P < 0.01$); * significant ($P < 0.05$).

The 3 multiplicative terms obtained by fractionating the genotype x environment interaction were highly significant. They explained 44.7, 32.3 and 15.2% of the interaction respectively. The rest of the interaction (which is the fourth term in this example with 5 environments), 7.8% of the total, was significant. Graphic representation of the residues does not show any reason to question use of this model.

The graphs in figure 1 represent the first 2 sub-terms (multiplied by the corresponding θ value) of the multiplicative model associated respectively with the environments (fig 1a) and with the genotypes (fig 1b). Axis 1 (first mutiplicative sub-term) clearly opposes the environments CO92 and CL91. The environments corresponding to the 2 years of the trials are separated by axis 2 (second multiplicative sub-term), which is mainly defined by the Spanish environment. The genotypes showed a similar behaviour in trials CL91 and CO91. The environments that are closest on this plane, which represents 77% of the interaction, are those best correlated with each other (table III). The Spearman rank correlations between the results in the different trials have similar values and are generally quite high; they are somewhat lower when the trial CO92 is involved.

A comparative analysis of the environment and genotype planes makes it possible to distinguish the most unstable genotypes and to predict their behaviour in the different locations. There is no clear structuring of the genotypes into groups (fig 1b). The genotypes RC x PSC5, RC x 89HR2, UD x 89HR2, UD x PB3, UD x PBP4 and ZF x PBP4 had a particularly good hullability in Spain compared with that predicted by the additive model ($\mu + G_i + E_j$, the main effects being centred). RC x PSC5 is differentiated from ZF x PBP4 by its behaviour at Cognat-Lyonne in 1992, the interaction being negative for RC x PSC5 and positive for ZF x PBP4. In contrast, CD x HA61 and CAJ x HA61 hulled particularly badly in Spain, compared with their average behaviour over all the environments. CAJ x PSC5 was characterised by a good hullability for CO91 and CL91. ZF x HA61, ZF x PB3, ZF x 89HR2 and ZF x PBP4, all with the same female parent, showed a positive interaction with the environment CO92. The genotypes with a central position were the most stable. Among these, UD x PSC5, UD x HA61 and RC x PBP4 showed the best hullabilities.

After transformation of the data and ranking of the 25 hybrids according to their hullabilities in each environment, the means of the absolute rank differences (S_i) and the corresponding statistical tests (Z_i) were calculated: the expected value and variance of S_i were 8.32 and 5.54 respectively. The dispersion of ranks (table IV) varied from 5.0 to 13.6, the most stable geno-

Table III. Spearman rank correlations between hullabilities of 25 sunflowers hybrids studied in 5 environments.

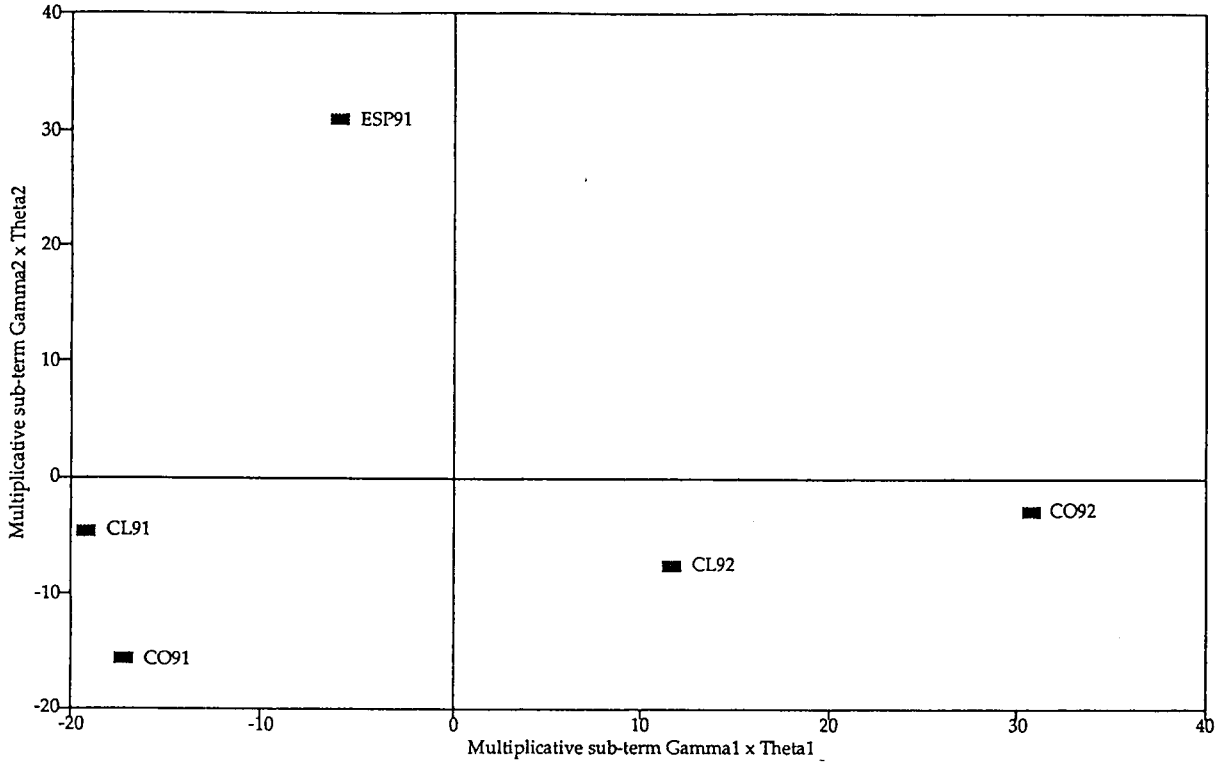
Environment	*CL91*	*CL92*	*CO91*	*CO92*
CL92	0.74**			
CO91	0.89**	0.75**		
CO92	0.41*	0.71**	0.46*	
ESP91	0.66**	0.63**	0.56**	0.32 ns

** Highly significant ($P < 0.01$); * significant ($P < 0.05$); ns: not significant.

Table IV. Means of the absolute rank differences (S_i) and corresponding statistic tests (Z_i) for hullabilities of 25 sunflower hybrids tested in 5 environments.

Female parent	*Male parent*	*Code*	S_i	Z_i
ZF	PSC5	A4	5.0	1.99
RC	PB3	C3	5.6	1.34
UD	PSC5	D4	5.8	1.15
CAJ	89HR2	B2	6.2	0.81
CAJ	PBP4	B1	6.4	0.67
CD	PB3	E3	6.6	0.53
ZF	89HR2	A2	6.6	0.53
UD	HA61	D5	7.4	0.15
UD	PB3	D3	8.4	0.00
CD	89HR2	E2	8.8	0.04
RC	PBP4	C1	8.8	0.04
CAJ	PB3	B3	9.2	0.14
CD	HA61	E5	9.6	0.30
CD	PBP4	E1	10.0	0.51
UD	89HR2	D2	10.6	0.94
RC	89HR2	C2	10.6	0.94
CD	PSC5	E4	10.8	1.11
RC	HA61	C5	10.8	1.11
UD	PBP4	D1	10.8	1.11
ZF	PB3	A3	11.2	1.50
CAJ	HA61	B5	11.4	1.71
ZF	PBP4	A1	11.4	1.71
RC	PSC5	C4	11.4	1.71
ZF	HA61	A5	13.6	5.03
CAJ	PSC5	B4	13.6	5.03

Code: as used for genotype identification in figure 1. S_i expected value: $E(S_i) = 9.32$; S_i variance: $V(S_i) = 5.54$; sum of Z_i values: 30.10; not significant.



b. Representation of the multiplicative model parameters for the 25 genotypes

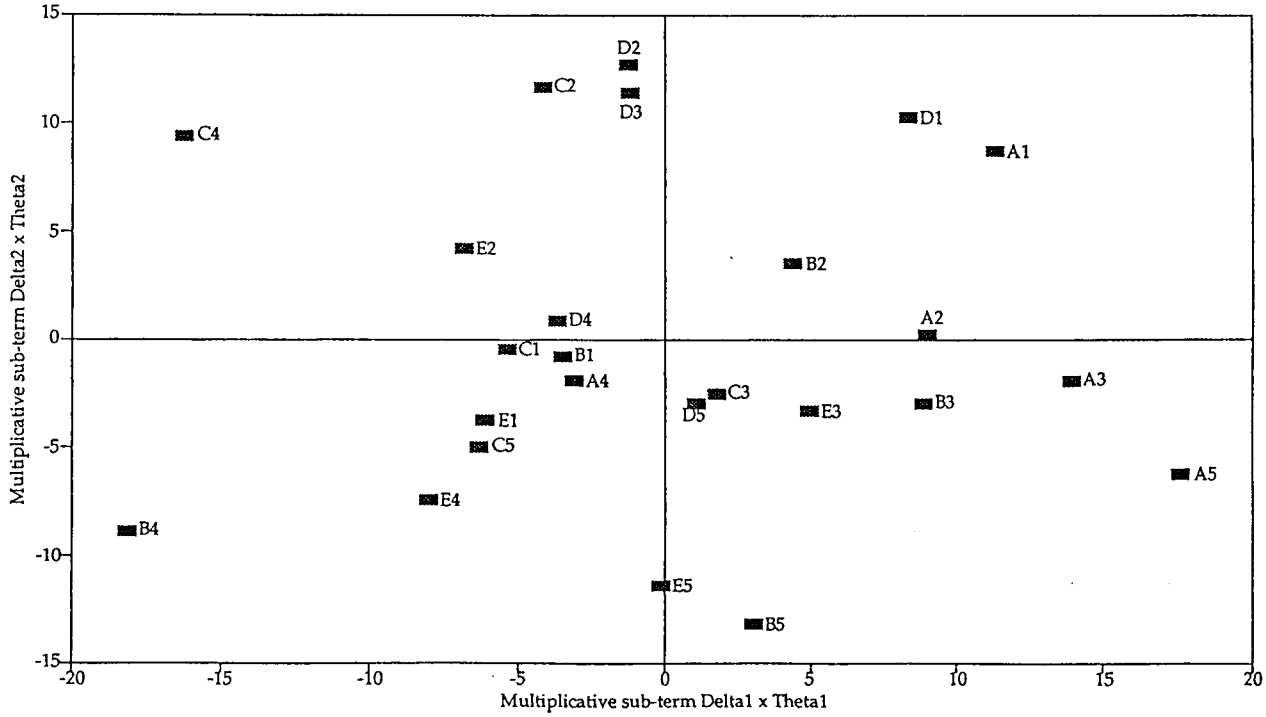


Fig 1. Hullabilities of 25 sunflower hybrids studied in 5 environments. **a.** Representation of the multiplicative model parameters for the 5 environments. **b.** Representation of the multiplicative model parameters for the 25 genotypes. Genotypes codes: ZF (A); CAJ (B); RC (C); UD (D); CD (E); PBP4 (1); 89HR2; PB3; PSC5 (4); HA61 (5).

types being ZF x PSC5, RC x PB3 and UD x PSC5. However, comparison of the $\sum Z_j = 30.1$ with the critical $c^2_{(0.95, 25)}$ value (37.7), indicates that there was no significant difference in stability between hybrids. In addition, there was no correlation between the stability parameter S_j and level of hullability for the 25 hybrids (Spearman rank correlation = 0.29 ns).

DISCUSSION

The 25 sunflower hybrids were grown in trials in regions where sunflowers are normally grown but with very different environments, in particular concerning water stress. This study has shown that hullability may be considerably increased under certain cultural conditions, whilst characters such as oil content are penalised.

The genotype x environment interaction was highly significant, but quite small, the results in different environments being closely correlated. This result was also found for another series of sunflower hybrids, where the rank correlation coefficients were at least 0.70** (Denis *et al*, 1994). The results also agree with those of Champolivier and Merrien (1993) who concluded that "the main element to be taken into account to obtain seed with good hullability is the choice of cultivar, the environment practically not modifying the ranking of hybrids for this character". It would appear that, of the 2 origins of genotype x environment interactions suggested by Gallais (1992a), the interaction for hullability results from different variances in the different environments, such that the ranking of genotypes is not changed but only the extent of distinction between them.

Analysis of the genotype x environment interaction by a multiplicative model showed that there are differences in variability of genotype hullability level about their mean value. Gallais (1990) justified consideration of performances in different environments as different characters by the fact that part of the genotype x environment interaction is due to the expression of different genes or different gene regulation. If the multiplicative terms (orthogonal by definition) are considered as resulting from the expression of independent genes, it would be possible to breed for specific effects in particular types of environment.

The results obtained with the multiplicative model show a very good correspondence with the non-parametric method, agreeing with the observations of Huehn (1990b) and Leon (1985, cited by Becker and Leon, 1988) who found a close correlation between ecovalence, which measures the contribution of a genotype to an interaction, and the parameter S_j. Calculation of the means of the absolute rank differences did not show any significant difference in phenotypic stability between the 25 hybrids. Simple to use, non-parametric tests are also less susceptible to measurement errors than parametric methods (Nassar and Huhn, 1987). However, there is some loss of information when using ranks to estimate stability. The effects of minor interactions may not induce any modification of ranking, whereas large variations in ranking may be observed for rather similar corrected data values.

It appears likely that genotypic differences in hullability may be explained by differences in both hull structure (thickness and degree of lignification and fractionation of the sclerenchyma) and seed density, a space between the hull and the kernel giving good hullability. These 2 factors are influenced by the environment (Beauguillaume and Cadeac, 1992). According to Percie du Sert and Durrieu (1988), lignification of the ovary wall, which partly explains hull thickness, depends on environmental conditions during seed maturation. The formation of pericarp tissues and lignification of sclerenchyma fibres is complete about 30 d after flowering (Perestova, 1976), corresponding to physiological maturity and the beginning of the desiccation phase. Water stress during the 30 d after flowering appears favourable for the development of a thick hull and good hullability (Leprince-Bernard, 1990). Champolivier and Merrien (1993) found that a freely available or only slightly limited water supply reduced hullability.

Denis *et al* (1994) showed, for individual environments, positive correlations between hullability and hull content and negative correlations between hullability and oil content, probably because the oil and hull contents of the seed are also negatively related. They concluded that breeding programmes would require use of an index involving both hullability and oil content.

Crop environment influenced not only hullability but also other seed characteristics. Compared with the results in the French trials, the environmental conditions in the Spanish trial gave an increase of about 4 percentage points in hull content and a reduction of 9 points in oil content. The very high level of hullability shown by the Spanish trial can probably be explained by the absence of rain during maturation and by very high maximum daily temperatures. Greater avail-

ability of water in the French trials, in particular during seed maturation may have favoured better seed filling, giving lower hull content and poorer hullabilities. In the same way, the difference between mean hullabilities of the hybrids tested in 1992 at Clermont-Ferrand and Cognat-Lyonne may be due to differences in conditions during the maturation period; achene maturation was much more rapid at Clermont-Ferrand than at Cognat-Lyonne. Since rainfall and potential evapotranspiration were similar in the 2 environments, the cause was probably related to different soil water retention capacities. In 1992, the plants suffered from an excess of water during May and June, especially at Cognat-Lyonne, which resulted in a reduction of height. This trial was, thus, not representative of normal sunflower culture conditions in the region where most crops showed, as at Clermont-Ferrand, a luxuriant vegetation.

According to Gallais (1992b), 'poor' environments with limiting factors make interactions evident, since the different genotypes do not have the same needs. The hybrids which showed a strong positive interaction with the Spanish environment may be considered as relatively susceptible to drought, their achenes being less well filled than the mean, giving increased hullability. In contrast, a strong negative interaction with ESP91 could be interpreted as indicating some drought tolerance. However, such a hypothesis needs to be confirmed by additional testing and measurements of characters such as seed yield and plant height which are generally affected by drought.

It has been possible to identify genotypes with both good hullability and good stability for this character. The size of the genotype x environment interaction and the relatively small variation in stability should be confirmed on a large network of trials. Such a programme would make it possible to decide on the need to take stability into account in a breeding programme. This would be difficult on segregating material since the amount of seed available is generally limited, but during the final selection of hybrids and trials for registration in official catalogues, estimation of performance in several environments would provide more valid judgement of hullability in the case of the most unstable genotypes. At present, following the results reported above, it does not appear necessary to envisage breeding for specific adaptation. Breeding for improved hullability in a limited number of locations should be sufficient to develop lines or hybrids with generally good hullabilities. The use of controls, inbred lines or hybrids, which are reasonably stable and with different hullablities, will be necessary. Since dry conditions give high levels of hullability, whatever the genotype, it is preferable to perform breeding programmes under conditions in which water is not a limiting factor.

Knowledge of drought tolerance could be useful to help understanding of environmental effects and their interactions with genotype effects. It would be interesting to determine whether there is any relationship between seed yield and hullability for given genotypes and also to compare the effects of different environmental conditions during floret initiation, flowering and seed filling, the periods when seed yield is determined (Blanchet *et al*, 1985; Merrien, 1986; Blanchet, 1987). It would be possible to do this using staggered sowing dates. In addition, studies of seed protein content appear to be necessary.

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