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Heterosis and genetic distance in rapeseed (*Brassica napus* L.). Use of different indicators of genetic divergence in a 7×7 diallel

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SUMMARY

The paper deals with a comparison of different indicators of genetic divergence between rapeseed parental lines : the relationship coefficient defined by MALECOT, the generalized distance D^2 of Mahalanobis, and a new G^2 parameter close to HANSON & CASAS' R^2 . The purpose of the authors is to discuss the advantages of their simultaneous use in the prediction of both heterosis values and F1 performances of hybrids from parental lines. Relationships between heterosis values and genetic distances were established for height at flowering and seed yield. Seven lines, more or less related two by two, were crossed following a diallel design. All varieties were tested in a 4-block design at the Plant Breeding Station of Le Rheu (I.N.R.A., France) in 1983. Estimates of correlations between the three distance parameters 2 by 2 were low. This result suggests that the three parameters did not supply the same type of information. Simple linear relationship between any of the distance predictors and either heterosis or F1 performance, was better than or equal to logarithmic and exponential relationships. The simultaneous use of the three distance parameters seemed to be efficient only to predict F1 hybrid yield. However, the relative efficiency of the different predictors depended on the character considered, and, for seed yield, correlations were much higher when the average general combining abilities of parents was added to the predictors.

Additional key words : *F1 performance, prediction.*

RÉSUMÉ

Hétérosis et distance génétique chez le colza (Brassica napus L.). Utilisation de plusieurs indices de divergence génétique chez un diallele 7×7 .

Cet article s'intéresse à la comparaison de trois indices mesurant la divergence génétique entre lignées de colza : le coefficient de parenté défini par MALECOT, la distance généralisée D^2 de Mahalanobis et un nouvel indice G^2 proche de la distance R^2 de HANSON & CASAS. Les auteurs ont alors étudié l'intérêt d'utiliser simultanément ces trois indices pour prédire l'hétérosis et la valeur en croisement des hybrides issus de ces lignées, pour deux caractères agronomiques : la hauteur à la floraison et le rendement en grains.

Sept lignées de colza, plus ou moins apparentées deux à deux, (au sens de MALECOT), ont été croisées à la main selon un plan de croisement diallele. Les hybrides et leurs parents ont été testés en 1983 selon un dispositif randomisé à 4 blocs, à la Station d'Amélioration des Plantes I.N.R.A. du Rheu (Ille et Vilaine).

Les estimations des corrélations 2 à 2 entre les trois indices de distance sont faibles ; ce résultat suggère que les trois indices apportent des informations différentes. Par ailleurs, la comparaison de différents types de relations entre les indices d'un côté et l'hétérosis ou la valeur des croisements de l'autre, conduit à retenir une relation linéaire simple plutôt qu'une relation logarithmique ou exponentielle.

L'utilisation simultanée des trois paramètres de distance semble surtout efficace pour prédire le rendement des hybrides F1. La vigueur hybride observée pour le rendement ou la hauteur est prédite de manière similaire avec deux ou trois indices. Dans le cas du rendement, la prédiction de la vigueur hybride ou de la valeur en croisement semble nettement améliorée lorsqu'on utilise pour prédicteurs, en plus des indices de distance, la demi-somme des aptitudes générales à la combinaison des lignées parentales. L'efficacité relative des différents prédicteurs dépend du caractère étudié.

Mots clés additionnels : *Valeur du croisement, prédiction.*

I. INTRODUCTION

The use of a good predictor for either heterosis or cross values of hybrid varieties could be very useful to plant breeders. It could improve genetic gain per unit of time or means in many breeding programmes. Many authors have searched, more and less successfully, for a relationship between heterosis of agronomic characters and different indicators of genetic divergence with both autogamous and allogamous plants (see LEFORT-BUSON, 1985*a* and *b* or a review). In some studies, correlations between different estimates of genetic distance have been calculated (BRANLARD & CHEVALET, 1984 ; COX *et al.*, 1985), but the simultaneous use of several indicators in the prediction of heterosis has not often been considered. Moreover, very few results are known concerning the prediction of F1 or cross value from indicators of genetic distance, even if this is of utmost importance for breeding purposes.

This paper is a contribution to the study of the relationship between either heterosis or F1 values and genetic distance in winter rapeseed. In France, rapeseed breeders have improved selfed lines. However, recent studies have pointed out the economic advantage of F1 hybrid varieties (LEFORT-BUSON & DATTÉE, 1985*a*) and the possible use of male sterile systems for commercial production of hybrids (ROUSSELLE, 1982 ; ROUSSELLE & RENARD, 1982). The authors of this paper have intended to use both *a priori* and *a posteriori* information as indicators of genetic distance, the latter being estimated from either selfed lines or F1 hybrids. For each indicator, they have first compared various kinds of relationships between the two parameters. Then, they have simultaneously introduced several indicators of genetic distance and average parental values when inbred or crossed to ensure the best prediction of both heterosis and F1 values.

The paper deals with results of a one-year trial, and practical conclusions are limited. However, the authors' first aim was methodological : they wanted to examine the advantage of simultaneous use of different indicators of genetic divergence.

II. MATERIAL AND METHODS

A. Material ; experimental design

A (7 × 7) complete diallel with selfed-lines more and less related was performed in the greenhouse at the Plant Breeding Station of Le Rheu (I.N.R.A.) in 1982. Parental lines were selfed for at least eight generations and assumed to be genetically fixed ; six of them, R 41, R 332, Kara, Expor, 61.4 H and 70.14, came from Europe, while the seventh, Hokkaido, came from Japan. F1 hybrids and parental lines were sown at Le Rheu following a randomized 4-block design. Plots had 5 rows, 3 m long with 0.30 m between rows.

Plot height and plot leaf canopy at flowering, mean weight of seeds per pod, average 1000-seed weight and seed yield at maturity were measured. Five 50-pod

samples were harvested for estimation of mean weight of seeds per pod. Three samples of about 1000 seeds were harvested, numbered and weighed for determination of 1000-seed weight. Only the three inner rows were harvested for plot seed yield to avoid competition effects (AZAIS *et al.*, 1986).

B. Method

Many estimations of multicharacter genetic distance can be obtained : see VINCOURT & HÉBERT (1985) for a review. We chose three of them, one using pedigree information (the complement to 1 of kinship coefficient, $1-\psi$), one using information on parental lines (generalized distance D^2 of Mahalanobis), and one using values of parents when crossed and close to HANSON & CASAS' R^2 (1968). The $(1-\psi)$ distances have been estimated from pedigrees of parental lines : they are given in table 1. The distances D^2 of Mahalanobis have been calculated from both vectors X_i and X_j including data on parental lines I and J (height and leaf canopy at flowering, mean weight of seeds per pod, 1000-seed weight and seed yield), and according to the formula given by ANDERSON (1958) :

$$D^2 = (X_i - X_j) W^{-1} (X_i - X_j)'$$

where W^{-1} is the variance/covariance matrix for residuals.

The R^2 distances were estimated from specific combining ability values (SCA or S_{ij}), with the statistic (HANSON & CASAS, 1968) :

$$\hat{R}_{ii'}^2 = \sum_j (\hat{S}_{ij} - \hat{S}_{i'j})^2 - 2(n^2 - n + 1) \sigma^2/n, \quad i \neq i',$$

where n is the number of parents in the diallel and σ^2 the residual variance for the character considered.

In the case of rapeseed where SCA variance often represents a small part of total genetic variance, we have substituted whole genotypic values \hat{Y}_{ij} for \hat{S}_{ij} values in the above formula ; also, parental values have been excluded from the calculation. The new distance so calculated for one character k is named \hat{d}_k^2 in the following. Its meaning is different from that of R^2 : in the first case, differences between lines are based on genotypic values (average and specific), whereas in the second case differences are based only on specific combining abilities. Then, in order to take into account information from all five characters, distances \hat{d}_k^2 were first standardized by genotypic variability ($\hat{\sigma}_k^2$) of character k and them summed over all characters to give a new distance

$$\hat{G}^2 = \sum_{k=1}^5 (\hat{d}_k^2 / \hat{\sigma}_k^2).$$

This new distance was multivariate like Mahalanobis D^2 ; however, it did not take into account correlations between characters.

Genotypic values and the variance of F1 hybrids and parental lines were estimated from an additive 2-way analysis of variance : genotype and block. Two different characters, height at flowering (rather simple) and plot seed yield (rather complex), have been

TABLE 1

Matrix of (1- ψ) distances between parental lines.
Matrice des distances (1- ψ) entre lignées parentales.

	R 332	Expor	European lines			Asiatic line Hokkaido
			61.4 H	70.14	Kara	
R 41	0.96	0.53	0.99	0.98	1	1
R 332		0.82	0.88	0.97	1	1
Expor			0.75	0.62	1	1
61.4 H				0.44	1	1
70.14					1	1
Kara						1

retained for the study of the relationship of genetic distance to either heterosis or F1 values ; others were only used for estimation of the multicharacter genetic distances D^2 and G^2 . For height and yield a second analysis of variance following GRIFFING'S method 3 (1956) was performed on genotypic means to confirm the minor part of SCA effects in the total genotypic variance.

The study of the relationship between the above parameters was carried out in two steps : the first was to compare different kinds of relationships, and the second to get the best prediction of the two heterosis values referred to mean (He_{MP}) and best (He_{pmax}) parent respectively and of F1 performance with different predictors. Three kinds of relationship, linear, logarithmic and exponential were compared : d being the genetic distance, correlations between d and F1, log d and F1, d and log F1, were calculated. In the search for best prediction, we used the three genetic distance parameters and both the mean parental value [$(1/2)(P_i + P_j)$] and the average general combining ability (GCA) of the two parental lines [$(1/2)(GCA_i + GCA_j)$]. Various multiple correlation coefficients were calculated, first with parental information alone, and then with all information. In the first case, there is statistical independence between predictors (measured on parents) and variables to be predicted (measured

on F1 hybrids). However, results of a diallel table are related : in a (7×7) diallel there are at least seven independent pieces of information ; so, in the simple correlation tests, we used five degrees of freedom (n-2), as done by BRANLARD & CHEVALET (1984).

When total information is considered, there is no independence between predictors and variables to be predicted : no test has been done, of course, and results are just given for information.

III. RESULTS AND DISCUSSION

A. Analysis of variance

Results indicated a significant effect of genotypes for both F1 hybrids and selfed lines, whatever the character. So, genetic distances were estimated with parents either inbred or crossed. GRIFFING'S decomposition of variability showed a significant effect for both SCA and GCA values in case of height (table 2) ; however, the variability of GCA effects was three times as great as that of SCA effects. For seed yield, only GCA effects were significant (table 3), as was expected from previous studies (LEFORT-BUSON &

TABLE 2

Breakdown of variability for plot height and yield, following GRIFFING'S method 3 (1956).
Décomposition de la variabilité selon la méthode 3 de GRIFFING (1956) pour la hauteur et le rendement en grains.

Height at flowering					
Variation	df	MS	F-value		
G.C.A.	6	357.85	28.7**	$\sum_i g_i^2/6 = 34.54$	
S.C.A.	14	37.00	2.96**	$\sum_i s_{ij}^2/14 = 12.26$	
R.E.	21	13.16	1.05	$\sum_{ij} r_{ij}^2/21 = 0.34$	
Error	111	12.48	/	$\sigma_e^2 = 12.48$	

Seed yield					
Variation	df	MS	F-value		
G.C.A.	6	39.31	5.20**	$\sum_i g_i^2/6 = 3.18$	
S.C.A.	14	7.66	1.01	$\sum_i s_{ij}^2/14 = 0.06$	
R.E.	21	10.71	1.42	$\sum_{ij} r_{ij}^2/21 = 1.57$	
Error	111	7.56	/	$\sigma_e^2 = 7.56$	

DATTÉE, 1985*b*). So, in both cases, estimation of genetic divergence with SCA values was not interesting and has been carried out with global genotypic values : G^2 statistics have been used rather than R^2 .

B. Different kinds of relationships between either heterosis or F1 performance and genetic distance

In almost all cases, the simple linear relationship between genetic distance (d) and either heterosis or cross values was better than or equal to logarithmic or exponential relationships (table 3). In one case only [relation between height mean parent heterosis and distance ($1-\psi$)], the exponential relationship appeared to be better. On the whole, simple linear relationships were retained for following prediction studies.

Few correlations were significant because of the few degrees of freedom (table 3). For plot height at flowering, distance D^2 was a good predictor of both He_{MP} and F1, while distance ($1-\psi$) was a good predictor only for He_{MP} . Distance G^2 was correlated (not significantly but close to the limit) to F1 performance but not to heterosis values. For seed yield, both D^2 and G^2 were correlated with He_{MP} (table 3) : the result was not statistically established in the case of G^2 . None of the indicators of distance were correlated with F1 performance. In the discriminant analysis, variables which have the greatest coefficients on the first axis were W 1000 and yield (the first axis accounted for about 50 % of the variation). So, for yield, it was not surprising to get a good prediction of mean parent heterosis from the distance D^2 , even if the character

was not highly heritable (LEFORT-BUSON & DATTÉE, 1985*b*).

For both characters, the distances \hat{d}_k^2 monocharacter were also estimated and compared to \hat{G}^2 multivariate in the prediction of heterosis or F1 performance. Excluding the prediction of mean parent heterosis for yield, the estimates of correlations between heterosis or F1 performance and distance were similar when using \hat{d}_k^2 or \hat{G}^2 . However, in the case of seed yield mean parent heterosis, the estimation was much higher with \hat{G}^2 than with \hat{d}_k^2 . So, for yield, which is a "complex" character with low heritability, prediction could be more accurate when taking into account information on other characters.

C. Correlations between the three indicators of divergence

Correlations between genetic distance parameters were not significant (table 4) probably because of the few degrees of freedom. However, the homogeneity of estimations for both characters needs to be discussed. Distances D^2 and G^2 were correlated ($\hat{\rho} \simeq 0.69$), while D^2 and ($1-\psi$) were moderately correlated ($\hat{\rho} \simeq 0.40$) and there was no correlation at all between G^2 and ($1-\psi$). COX *et al.* (1985) have obtained similar results concerning the relation between the coefficient of parentage and an index of similarity based on morphological loci, in 115 soybean cultivars : 3 groups of cultivars have been formed and correlation varies from 0.26 to 0.50 in the groups. In wheat, BRANLARD

TABLE 3
Various kinds of relationships between genetic distance (d) and either heterosis values ($He_{\overline{P\overline{A}T}}$, He_{Pmax}) or F1 performance (F1).
Différents types de relations entre la distance génétique (d) et respectivement les valeurs d'hétérosis ($He_{\overline{P\overline{A}T}}$ et He_{Pmax}) et la valeur de l'hybride (F1).

Heterosis referred to mean parent						
d = distance	D ²	Height 1- ψ	G ²	D ²	Yield 1- ψ	G ²
(d, He_{MP})	0.818*	0.638	0.418	0.764*	0.437	0.635
(d, log He_{MP})	0.713	0.776*	0.320	0.603	0.462	0.481
(log d, He_{MP})	0.617	0.615	0.387	0.681	0.433	0.527
Heterosis referred to best parent						
	D ²	Height 1- ψ	G ²	D ²	Yield 1- ψ	G ²
(d, He_{Pmax})	0.251	0.287	- 0.150	0.536	0.377	0.213
(d, log He_{Pmax})		no estimations, because of negative values of He_{Pmax}				
(log d, He_{Pmax})	0.148	0.294	- 0.180	0.464	0.390	0.110
F1 performance						
	D ²	Height 1- ψ	G ²	D ²	Yield 1- ψ	G ²
(d, F1)	0.840*	0.497	0.740	0.249	0.426	0.420
(d, log F1)	0.831*	0.503	0.729	0.236	0.451	0.413
(log d, F1)	0.643	0.388	0.671	0.134	0.431	0.448

NB : The test of significant correlation was made with 5 df and a 5 % risk for both D^2 and $1-\psi$. No test was carried out with G^2 , because of statistical dependence of correlated parameters.

TABLE 4

Correlations between predictors of genetic divergence.
Corrélations entre plusieurs prédicteurs de la divergence génétique.

		D ²	1- ψ	G ²
			Height	
D ²	y	/	0.410	0.695
	i			
1- ψ	e	0.398	/	0.064
	l			
G ²	d	0.685	0.064	/

\hat{p} (5 df ; 5 %) = 0.754.

& CHEVALET (1984) found also a positive correlation between genetic distance (1- ψ) and a χ^2 distance based on agronomic and morphological characters of 78 cultivars, but it was very low (\hat{p} = 0.150).

To summarize, correlations between the three indicators of divergence were not very strong : the information brought by each of them was probably different.

D. Multiple correlations between genetic distance and both heterosis and F1 values (table 5)

For both yield and height, parental predictors accounted for a large part of the variation in heterosis values : about 60 % and more than 70 % for He_{MP} and He_{Pmax} respectively. They were also efficient for prediction of F1 performance in case of height (74 %) but not in case of yield (34 %). So, for yield, parental information might help in prediction of heterosis, but it was not sufficient for prediction of F1 performance ; the latter parameter may depend first on GCA values of parents in this considered group of F1 hybrids. In case of height, only predictors D² and

(1- ψ) were efficient for both He_{MP} and F1 predictors, but not for He_{Pmax} prediction. In conclusion, parental information was efficient in prediction of cross value for a simple character such as height, but not for a complex character such as seed yield. On wheat, SHAMSUDIN (1985) also found a good correlation between distance D² and both heterosis and SCA effects for grain yield (\hat{p} \approx 0.44) in a (10 \times 10) half diallel including spring varieties.

In the case of height, distance G² was not very informative (after introduction of both D² and (1- ψ) distances) for prediction of either heterosis or F1 values. However, it appeared valuable in the case of yield for prediction of F1 performance : the use of both G² and 1- ψ gave a higher estimate of correlation (\hat{p} = 0.64) than the use of both D² and 1- ψ (\hat{p} = 0.565).

For height, the use of average GCA instead of mean parent value was not better for prediction of any of the three parameters (table 5). Again, for a simple character with medium heritability, predictors measured on inbred values were at least as good as predictors measured on crossbred values.

However, for yield, the use of average GCA rather than mean parent value was more informative in particular for F1 prediction. So, for a complex character such as yield with low heritability, the use of predictors built up with cross-values of parental lines (GCA, G²) appeared necessary for a good estimation of F1 performance : more than 70 % of F1 yield variation was explained with GCA, G² and 1- ψ . Average GCA parameter was also important in case of yield heterosis prediction, but its combination with D² rather than G² seemed more efficient.

MARCHAIS (1978) obtained higher correlations between mean parent heterosis and HANSON & CASAS' R² distance in *Pennisetum typhoides*, for different morphological and yield characters : \hat{p} varied from 0.80 to 0.97 for ten characters. And, except for seed yield,

TABLE 5

Estimates of multiple correlation coefficients (\hat{p}) between predictors and both heterosis values (He_{MP} , He_{Pmax}) and F1 performance (F1).
Estimation des coefficients de corrélation multiple (\hat{p}) entre différents prédicteurs et, d'une part, les valeurs d'hétérosis (He_{MP} , He_{Pmax}), d'autre part, la valeur de l'hybride (F1).

Predictors		\hat{p} (He_{MP})	\hat{p} (He_{Pmax})	\hat{p} (F1)
Measured on selfed-lines				
D ² ; 1- ψ	H	0.878*	0.322	0.841*
D ² ; 1- ψ ; 1/2 (P _i + P _j)	E	0.880*	0.793*	0.860*
Measured on both selfed-lines and F1 hybrids	I			
G ² ; 1- ψ	G	0.784	0.311	0.703
D ² ; 1- ψ ; G ²	H	0.884	0.320	0.869
D ² ; 1- ψ ; 1/2 (GCA _i + GCA _j)	T	0.908	0.784	0.890
G ² ; 1- ψ ; 1/2 (GCA _i + GCA _j)		0.756	0.347	0.794
Measured on selfed-lines				
D ² ; 1- ψ	Y	0.778*	0.565	0.444
D ² ; 1- ψ ; 1/2 (P _i + P _j)		0.833*	0.757*	0.586
Measured on both selfed-lines and F1 hybrids	I			
G ² ; 1- ψ	E	0.528	0.384	0.612
D ² ; 1- ψ ; G ²	L	0.805	0.588	0.655
D ² ; 1- ψ ; 1/2 (GCA _i + GCA _j)	D	0.910	0.836	0.847
G ² ; 1- ψ ; 1/2 (GCA _i + GCA _j)		0.757	0.440	0.856

N.B. : For parental predictors, the test of significant correlations was done with a 5 % risk ; no test was done as soon as predictors estimated from F1 hybrids were introduced, because of statistical dependance of correlated parameters.

correlations between F1 performance and R^2 distance were lower than above one ; with *Pennisetum* also, R^2 seemed particularly useful in F1 yield prediction.

IV. CONCLUSION

Results clearly showed the advantage of simultaneously using different types of genetic distances between lines when inbred and when crossed to predict heterosis or cross values more or less accurately. Moreover, in this particular example with rapeseed autogamous plants, good knowledge of selfed lines including pedigree has been useful for the predictions considered, even for the character "seed yield" with low heritability ; if possible, information should be supplemented with a biochemical distance between lines.

However, as suggested by ARUNACHALAM (1981), the efficiency of predictors depended on character : in this particular example, the prediction of a simple character such as height with medium heritability was better than the prediction of a rather complex charac-

ter such as seed yield with low heritability. Moreover, in height prediction parental information alone was very efficient, whereas for yield prediction preliminary progeny tests seemed necessary for establishment of "good" distances.

The limits of such a study, besides the repeatability of the experiment, lay in the use of the same results for predictors and variables to be predicted ; for example, F1 values gave access to estimates of hybrid vigour as well as to average GCA and G^2 distance. In the future, the estimation of predictors should be separated from that of predicted parameters. For example, the behaviour of lines in testcrosses (with 3 or 4 test varieties as done by GALLAIS (pers. comm.) in maize permits estimations of GCA and different types of distances ; it may be informative in prediction of both heterosis and cross values relative to F1 hybrids for the lines considered. For example, if good predictors are obtained, testing 50 lines with four testers (instead of crossing the 50 lines two by two) would save about 1000 out of 1200 crosses, and *a fortiori* improve genetic gain per unit of time or means.

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