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Genetic study of some agronomic characters in winter oilseed rape (*Brassica napus* L.)

I. - Heterosis

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SUMMARY

*Heterosis,
Homeostasis,
Rapeseed,
Brassica napus,
Vegetative characters,
Yield characters,
Phenotypic correlations.*

140 F_1 hybrids of winter oilseed rape (reciprocal and direct combinations) have been studied for several agronomic characters in a two replication randomized block design, at the Rennes Plant Breeding Station. For seed yield, hybrid vigour averages 23.5 % on the basis of the mid parent and for a few combinations it reaches 50 % on the basis of the best parent which emphasizes the interest of hybrid varieties for improving yield.

Several growth period characters are analysed : it is concluded that the expression of heterosis changes according to time and space. Occurrence of reciprocal effects requires the involvement of nucleocytoplasmic interactions in any biological explanation of heterosis. Some phenomena are compared in hybrid and inbred plants and it is suggested that the two types are not really different.

RÉSUMÉ

*Hétérosis,
Homéostasie,
Colza,
Brassica napus,
Caractères végétatifs,
Rendement,
Corrélations phénotypiques.*

Etude génétique de quelques caractères agronomiques chez le colza oléagineux d'hiver (Brassica napus L.). I - Hétérosis

140 hybrides F_1 de colza (croisements directs et réciproques) et leurs parents ont été testés pour différents caractères agronomiques selon un dispositif bloc à deux répétitions, à la Station d'Amélioration des Plantes de Rennes.

Pour le rendement en grains, la vigueur hybride moyenne est de 23,5 p. 100 ou 12 p. 100 selon qu'elle est rapportée au parent moyen ou au meilleur parent. Dans les deux cas, la dispersion de la vigueur pour l'ensemble des hybrides est importante, et sa valeur peut atteindre 50 p. 100 du meilleur parent pour quelques combinaisons. Ces résultats soulignent donc l'intérêt des variétés hybrides dans l'amélioration de la productivité du colza ; la création de telles variétés est cependant liée à l'existence d'un système efficace de contrôle de la pollinisation, système non encore opérationnel chez le colza.

Des problèmes liés à l'échantillonnage n'ont pas permis d'estimer correctement la vigueur hybride pour les composantes du rendement.

L'hétérosis se manifeste globalement sur toute la plante ; son expression est variable selon les organes et selon les stades de développement de la plante. Différentes théories de l'hétérosis sont rappelées pour tenter d'expliquer les résultats observés ; les seules théories nucléaires semblent insuffisantes du fait de l'existence d'effets réciproques notamment pour le rendement en grains.

L'analyse des corrélations entre caractères chez les hybrides et chez les lignées suggère que ces deux types d'individus ne sont pas très différents et expriment une variabilité de même nature ; en particulier, l'élaboration du rendement en grains semble se faire de manière identique pour les uns et les autres. Les hybrides auraient en fait de plus grandes capacités d'adaptation aux variations du milieu du fait de leur diversité chromosomique et cytoplasmique ainsi que de nouvelles relations géno-cytoplasmiques se traduisant notamment par une absence temporaire de répression du génome.

I. INTRODUCTION

Rape (*Brassica napus* L., $2n = 38$) is a spontaneous amphiploid between *Brassica oleracea* L. ($2n = 18$) and *Brassica campestris* L. ($2n = 20$). Both are self-sterile and suffer from inbreeding depression following artificial self pollination. Rape is self-pollinated (about 2/3) and cross-pollinated (about 1/3).

Different breeding methods were therefore used following either a self-pollination scheme (pedigree method) or a cross-pollination scheme (population varieties were constituted by open pollination of the selected families). Using either method, yield was improved by 20 % over 10 years.

According to some recent previous data (SCHUSTER, 1969 ; SHELKUDENKO, 1968, 1972 ; SCHUSTER & MICHAEL, 1976 ; CAMPBELL & KONDRA, 1978), greater improvements

could be expected by the use of heterosis : for example, the reported hybrid vigour for seed yields averages from 15 % to 50 % of the mean parent.

Hybrid vigour was measured for yield and for several characters directly or indirectly related to yield, in order to appraise the economic interest of hybrid varieties. The occurrence of reciprocal effects for these characters was tested. Using simple statistical analysis, morphological differences between hybrids and inbred lines were investigated and their physiological basis discussed.

II. MATERIALS AND METHODS

A. Materials. Experimental designs

Results of two experiments performed at the Plant Breeding Station at Rennes in 1977/1978 and in 1978/1979 are analysed.

In 1977/1978, 9 inbred lines differently related to « Primor » were chosen according to either qualitative or quantitative considerations, and crossed with « Primor » (male). A 4-replication randomized complete block design with plots of 3 metre long and 0,30 metre wide rows was used.

In 1978/1979, 24 lines from a broad genetic origin were crossed according to an incomplete diallel design composed of 7 (5×5) diallels, i.e. 140 hybrid combinations. This design met the requirements of a study of genetic parameters and will be discussed in a second report (LEFORT-BUSON, 1982). Crosses were made between distantly related parents. Each 5×5 diallel was sown in a 2-replication randomized complete block design with plots of 3 metre long and 0,30 metre wide rows (there were about 20 plants along 1 metre).

B. Characters

In order to improve the understanding of the mechanisms of rape growth and the effect of heterosis, yield, its components, and several morphological characters were measured. Since we have previously demonstrated competition between border lines of two successive plots (BUSON, 1979), we measured plot yield exclusively on the two central lines in both experiments.

Yield components (number of pods, number of pods per branching, number of seeds per pod, 1 000-seeds weight) and morphological characters (height and leaf number at rosette stage, height and branching number at maturity), were taken on 4 plants per plot ; each chosen plant was sufficiently far from the other to avoid competition between chosen plants. In addition, in 1979, yield components were evaluated independently on primary and secondary branching (namely BI and BII).

In 1978, several vegetative development characters were measured on 20 plants collected at one end of the plot. The individual measures were not correlated because each plant collected was three plants away from the others.

In 1979, for each plot we evaluated earliness of flowering, leaf canopy at the beginning of flowering, lodging at the end of flowering, plant density at maturity.

C. Methods of investigation

The measure of hybrid vigour poses the problem of a basis of comparison. Hybrid vigour is more often assessed as the relative difference either from the mean parent value or from the best parent value.

Comparison with the mean parent emphasizes the divergence from additivity. The concept of hybrid vigour would then be partially confused with those of general and specific combining ability (GALLAIS, 1975). However several authors who believe that heterosis is a general phenomenon which includes inbreeding depression, homeostasis, combining abilities, and hybrid vigour *sensu stricto* advise its use (WILLIAMS, 1959 ; SCHNELL, 1961 ; SINHA & KHANNA, 1975).

Comparison with the best parent underlines overdominance effects. Heterosis is then considered to be an advantage of the heterozygote. In addition, economic interest of hybrid varieties is better evaluated.

In this paper, both measures of hybrid vigour are presented and the meaning of both are discussed.

Hybrid and inbred values result from a classical 2-way analysis of variance. For each character, hybrid vigour was tested by a Welch test or a Student test according to whether or not the error variances of hybrids and inbreds were heterogeneous.

Reciprocal effects were in some cases demonstrated from the comparison of two errors in the two elementary models with and without reciprocal effects. Two studies of yield and yield components were performed independently on hybrids and inbred lines in order to compare them :

- i) the correlations between errors of the variance analysis and the identification of the relation between characters for each type of plant ;
- ii) the discriminant analysis of families according to variables independently measured on primary and secondary branching, and the comparison of the variables with a high coefficient along the significant axis.

III. RESULTS

Only the mean results of each experiment are presented, this data being sufficient to obtain an idea of heterosis for all hybrids studied. Furthermore, experimental accuracy was not sufficient to differentiate between hybrids and consequently the analysis of their own values was not very significant ; (in each table of results, confidence intervals are only given if values are significantly different from 0 at 5 % limit).

A. Seed yield

Hybrid vigour averages 11 % of the mean parent in 1978, up to 23,5 % of the mean parent in 1979 (table 1). This discrepancy, not due to climatic conditions, could result from the use of highly related parents in 1978, since in this experiment the mean relationship coefficient between the parents of the 11 hybrids was 0,35. It appeared to be negatively related with the hybrid vigour ; the small number of results did not allow the measure of correlations (BUSON, 1979). Since, in 1979, the parents were chosen so as to be little related and since the number of hybrids studied was much higher, this experiment would appear more accurate. In 1979, 12 % of hybrids display 40 % more than the mean parent vigour. Despite the higher yields of these combinations, hybrid values are not significantly different one from another and the distribution of hybrid vigour about the mean is not different from a randomized distribution. Hybrid vigour based on the best parent averages a much lower value, 12 %, but remains significant.

These results are in agreement with those of SHELKUDENKO (1968), where vigour of 112 hybrid combinations

TABLE 1

Estimations of yield of inbreds and hybrids and of hybrid vigour from results of 1978 and 1979 trials.
Estimation des rendements des lignées, des hybrides et de la vigueur hybride à partir des essais de 1978 et 1979.

	Average yield in Qls/hectare		Hybrid vigour in Qls/hectare when referred	
	Inbreds	Hybrids	to the mean parent	to the best parent
1978	38,5	42,8	4,3 ^(a) ± 2,98 or 11 %	2,7 or 6,7 %
1979	31,7	38,9	7,11 ^(a) ± 0,78 or 23,5 %	3,52 ^(a) ± 0,90 or 12 %

^(a) Significant at 5 % level.

^(a) Significatif avec un risque de 5 p. 100.

was in average 25 % of the mean parent ; they are also consistent with the results of SCHUSTER & MICHAEL (1976) and CAMPBELL & KONDRA (1978).

B. Yield components

In 1978, hybrid vigour based on the mean parent was low but significant for the numbers of pods and seeds per pod (table 2), and not significant for 1 000 seed weight : here, each family is composed of 16 plants.

TABLE 2

Hybrid vigour for yield components in a 1978 trial.
Vigueur hybride pour les composantes du rendement dans l'essai de 1978.

Character	Hybrid vigour expressed in percentage of	
	mean parent	best parent
Number of pods	14,1	- 0,8
Number of seeds per pod	12,3 ^(a) ± 7	7,4
Thousand seed weight	0,4	- 3,6

^(a) Significant at 5 % level.

^(a) Significatif avec un risque de 5 p. 100.

In 1979, heterosis did not occur for yield components (table 3), though it was higher for plot yield in this experiment than in 1978. This implies that sampling is not acceptable as might have been expected since only 2 replications, namely 8 plants, were used to represent one family.

C. Vegetative characters

Heterosis affected plant height during the whole of plant development (table 4) ; in addition hybrid vigour decreased as the plant was growing.

Although not significant, the hybrid vigour observed for root characters (stem base diameter, top-root length, root weight) was always positive and 19 % over the mean parent for root weight.

From all above-ground characters, highest heterosis were obtained for dry matter weights at the rosette stage (18 % over the mean parent) and at the beginning of flowering (27 % over the mean parent) ; these data are consistent with

TABLE 3

Hybrid vigour for yield components in a 1979 trial.
Vigueur hybride pour les composantes du rendement dans l'essai de 1979.

Character	Hybrid vigour expressed in percentage	
	mean parent	best parent
Number of pods on BI ^(b)	3,5 ^(a) ± 2,3	- 4
Number of pods on BII ^(b)	6,0	- 12,8
Number of seeds per pod on BI ^(b)	2,7	- 6,6
Number of seeds per pod on BII ^(b)	0,04	- 14,1
Weight of thousand seeds on BI ^(b)	1,4	- 6,2
Weight of thousand seeds on BII ^(b)	2,3 ^(a) ± 1,8	- 7,8

^(a) Significant at 5 % level.

^(b) BI is for primary branching ; BII is for secondary branching.

^(a) Significatif avec un risque de 5 p. 100.

^(b) BI correspond à la ramification principale ; BII correspond aux ramifications secondaires.

SHELKUDENKO's results (1972) who even suggested an early selection of hybrids based upon leaf development at the rosette stage. Hybrid vigour for leaf number at rosette stage and for branching at maturity was low and not significant, but always negative. At the rosette stage vigour would consist in increasing leaf number ; at maturity observed heterosis for seed yield would be more related to the vigour of components (pod number, seed number per pod) than to the branching number.

D. Plot agronomic characters : flowering earliness, lodging, canopy, density

On average, hybrids were significantly earlier than the mean parent but a little less early than the best parent (table 5). In most species this character is considered additive.

Hybrids were more susceptible to lodging than the mean parent and *a fortiori* than the best parent ; however at the beginning of flowering the leaf canopy of hybrids was better developed than that of either mean or best parents, which is consistent with the observed vigour of leaf weight and stem weight in the 1978 experiment.

TABLE 4

*Hybrid vigour for some vegetative characters.
Vigueur hybride pour quelques caractères liés au développement végétatif.*

Stage	Character	1978		1979	
		Hybrid vigour expressed in percentage of : mean parent best parent ^(b)		Hybrid vigour expressed in percentage of : mean parent best parent ^(b)	
Rosette	Height	6,7		28 ^(a) ± 4,4	11,9 ^(a) ± 5,6
	Number of leaves	- 0,7		- 12	
	Weight (leaves and stems)	17,9 ^(a) ± 15	10,4	—	—
	Neck diameter	5		—	—
Beginning of flowering	Height	7,1 ^(a) ± 3	1,8	11,5 ^(a) ± 2,0	6,6 ^(a) ± 2,2
	Number of leaves	2,3		—	—
	Weight (leaves and stems)	26,7 ^(a) ± 23	19,6	—	—
	Stem base diameter	6,9		2,5	
	Tap-root length	8,7		—	—
	Root weight	18,9		—	—
Maturity	Height	5,2 ^(a) ± 3,2	0,9	2,6 ^(a) ± 2,1	1,8
	Number of branching	2,3		- 3,4	

^(a) Significant at 5 % level (confidence intervals are given only in case of significant values).

^(b) Hybrid vigour expressed in percentage of the best parent is given only when vigour referred to the mean parent is significant.

^(a) Significatif avec un risque de 5 p. 100 (les intervalles de confiance sont donnés uniquement dans le cas où les valeurs sont significatives).

^(b) La vigueur hybride est donnée en se référant au meilleur parent uniquement dans le cas où la référence au parent moyen est significative.

TABLE 5

*Hybrid vigour for some agronomic characters in a 1979 trial.
Vigueur hybride pour quelques caractères agronomiques dans l'essai de 1979.*

Character	Hybrid vigour expressed in percentage of : mean parent best parent (P _{max})	
Earliness ^(b) of flowering	6 ^(a) ± 1,5	P _{max} = the earliest parent - 3 ^(a) ± 1,7
Lodging susceptibility	7 ^(a) ± 6,3	P _{max} = parent which is not susceptible 45 ^(a) ± 10
Canopy	55 ^(a) ± 7	P _{max} = parent having the greatest canopy 20 ^(a) ± 6,4
Density at maturity	9 ^(a) ± 3,6	P _{max} = parent having the greatest density 3

^(a) significant at 5 % level.

^(b) the flowering earliness is measured in number of days before the flowering date of the mean and the best parents.

^(a) significatif avec un risque de 5 p. 100.

^(b) la précocité de floraison est mesurée en nombre de jours précédent la floraison des parents moyen et maximum.

The density at maturity displayed significant heterosis on the basis of the mean parent (9 %), but not significant heterosis on the basis of the best parent.

E. Occurrence of reciprocal effects

Significant reciprocal effects were demonstrated for several characters : flowering date, height and leaf canopy at the

beginning of flowering, density at maturity. The range of variation for these effects is not very important except for height and density ; anyway, for these two characters, no further study of reciprocal effects has been made because of the bad accuracy of the experiment.

Although nonsignificant, differences between reciprocal crosses were high for height at rosette stage and for seed yield per plot. Thus, reciprocal effects were expressed at vegetative and maturity stages.

F. First interpretation of differences between the yield and yield components of hybrids and inbreds

In this study, the sampling method is not very important because we are interested in plant characters and not plot characters. So, the correlations have a real meaning, even if they are not representative of a plot phenomenon. The estimations of correlation coefficients between errors of variance analysis are given in table 6. When they were significant, estimates separately obtained for hybrids and inbreds were close. Correlations different from 0 were roughly compared in bulk : a total 5 % confidence limit, namely a 5 % confidence limit divided by the number of comparisons to be made, was used. Correlations between characters were assumed to be equal in hybrids and inbreds. Linear relations between yield and its components could therefore have the same origin in both types of plants ; however, estimates would be always slightly higher for hybrids than for inbred lines.

The following characters are highly correlated : total yield, and yield of secondary branches, BII yield and mean number of pods per secondary branch. On both types of branching, 1 000 seed weight was negatively correlated to the number of seeds per pod (compensatory effect) and was not correlated to the number of pods.

TABLE 6

*Correlations between errors of variance analysis on yield and yield components in populations of hybrids and inbreds.
Corrélations entre les résidus de l'analyse de variance du rendement et des composantes chez les lignées et les hybrides.*

Hybrids	Inbreds	Number of pods on BI	Number of pods on BII	Number of seeds per pod on BI	Number of seeds per pod on BII	Weight of 1 000 seeds on BI	Weight of 1 000 seeds on BII	Total Yield	BI Yield	BII Yield	Mean number of pods on BII
Number of pods on BI			0,511*	- 0,311	- 0,082	- 0,029	- 0,008	0,484*	0,632*	0,443*	0,384
Number of pods on BII		0,584 *		- 0,307	- 0,046	0,076	- 0,007	0,864 *	0,157	0,905 *	0,875 *
Number of seeds per pod on BI		- 0,094	- 0,152		0,512 *	- 0,312	0,092	0,095	0,585 *	- 0,009	- 0,119
Number of seeds per pod on BII		- 0,050	0,159	0,307		- 0,029	- 0,262	0,351	0,387	0,235	- 0,065
Weight of 1 000 seeds on BI		0,262	0,197	- 0,400 *	- 0,100		0,290	0,129	0,140	0,113	0,084
Weight of 1 000 seeds on BII		0,082	- 0,052	- 0,129	- 0,438 *	0,394 *		0,093	0,267	0,050	0,093
Total Yield		0,588 *	0,899 *	0,075	0,431 *	0,246	0,109		0,505 *	0,986 *	0,768 *
BI Yield		0,648 *	0,339 *	0,530 *	0,314	0,271	0,120	0,558 *		0,356	0,176
BII Yield		0,501 *	0,919 *	0,076	0,443 *	0,209	- 0,055	0,981 *	0,384 *		0,775 *
Mean number of pods per BII		0,478 *	0,876 *	- 0,107	0,208	0,147	- 0,063	0,779 *	0,218	0,775 *	

* Significant at level 5 %.

* Significatif avec un risque de 5 p. 100.

For each diallel, a discriminant analysis separately made for primary and secondary branching, gave most often one significant axis, but sometimes 2 and sometimes 0. For hybrids and for inbreds, 1 000 seed weight and yield (whatever the type of branching) mostly determined the first discriminant axis; these two variables were opposite along the axis. Thus, the same variables were useful to differentiate plant intra inbreds or intra hybrids.

IV. DISCUSSION

Heterosis affects the whole plant. Hybrid vigour was obvious for the vegetative characters (height, stem base diameter, leaf weight, stem weight, root weight) and for some yield characters (number of pods, number of pods per branch, number of seeds per pod, seed yield) of the individual plants. Vigour of families observed at plot level resulted in a profuse canopy, higher lodging susceptibility which could be partly related to plant height, and higher seed yield.

This confirms earlier results of CLARKE (1978) for spring rape; he pointed out that leaves, through their photosynthetic activity at the beginning of flowering, determine seed yield, since he found that defoliation at this stage causes a decrease of branches and pod numbers whereas defoliation at the end of flowering had no consequence. The vital energy (stocks) of leaves which die after flowering is saved in stems and pods and used to produce seeds (MAJOR

et al., 1980). Therefore any agricultural practice which increases leaf life would cause an increase of the stocks and so of yield. It would be interesting to check whether heterosis would also result in a longer life of leaves.

Vigour was not the same for all characters (height at the beginning of flowering 11,5 %, lodging susceptibility 7 %, canopy 55 %, plot yield 23,5 %). Different attempts to explain this variability were based on the complex nature of the characters involved: overdominance of complex characters such as seed yield would be caused by dominance effects of elementary characters such as yield components (GRAFFIUS, 1960; WILLIAMS, 1959; DUARTE & ADAMS, 1972). However, according to MOLL *et al.* (1962) overdominance for yield will never occur if it does not occur for at least one yield component. Our results show overdominance for seed yield, canopy at the beginning of flowering, and leaf, stem and root weights, and thus are consistent with the previous theories. These theories are nevertheless unlikely: first, it is difficult to define « elementary » and « complex » characters since each « elementary » components of yield results itself from several even more « elementary » characters; second, in the case of experiments at multiple localities overdominance may occur for yield but not for any components, as was shown by hybrids which were always superior to one or the other parent in different localities.

Hybrid vigour seems also to vary for single characters as the plant is growing: for plant height, it averages in the 1979

experiment 11,5 % at the beginning of flowering and 2,6 % at maturity. This emphasizes that heterosis is expressed differently according to organs and physiological stages of development. The environment is changing all through plant development: climatic conditions are modified, and competition between plants increases when the plant grows; the adaptation of the plant to these variations of environment may cause the different expressions of heterosis through its development.

DEMARLY (1972), who assigned a very broad sense to the term « environment » has also explained the dependence of heterosis on the physiological stage of development: repressive systems would come into force progressively in cells as soon as fertilization has occurred and would further develop with age; by hybridization new nucleocytoplasmic conditions would be established, offering new functional possibilities which would be even greater, the more different were the parents. In contrast, by self-pollination, the nucleocytoplasmic interactions would be hardly modified and the preexistent repressive system would already fit the new cell.

Hybrid vigour for plant height was, in 1978 and 1979, lowest at maturity which is consistent with the results of BUNISSET-BERGOUNIOUX (1978) on *Petunia* hybrids. She observed a regular decrease of heterosis during plant growth: the epigenetic environment was progressively modified and consequently the expression of heterosis was affected.

Reciprocal effects were demonstrated for several vegetative characters and for yield. Since these effects were measured at maturity, the hypothesis of only maternal effects such as initial seed quality is eliminated. According to CAMPBELL & KONDRA (1978) who also observed such effects on rape yield, nucleocytoplasmic interactions are more likely than maternal cytoplasmic effects since the direction of the effects observed was not constant in the following generations.

Since heterosis affected the quantitative expression of characters, we wondered whether relations between characters were different in hybrids and inbreds:

- i) the constitution of seed yield (namely correlations between yield residues and yield component residues) was similar for both hybrids and inbred lines considering primary and secondary branching respectively, where as it differed according to the branching type within the same plant;
- ii) relations between height or stem-base diameter at beginning of flowering and seed yield (phenotypic correlations in bulk) were the same for a hybrid or an inbred plant (BUSON, 1979);
- iii) variables which best differentiate families along an axis or a plan were identical for homozygotes and heterozygotes.

Thus, it is suggested that a hybrid and an inbred plant are not very different and that their physiological mechanisms are similar. However, because of cytoplasmic and chromosomal diversity, namely additional genes, new nucleocytoplasmic interactions and temporary lack of genome repression, a hybrid would have a greater ability to adapt to a changing environment (here considered in its widest interpretation) than an inbred.

This may be explained if we assume that any plant (hybrid or inbred) would have a higher yield ability (C) than it could use in normal field condition practices. If conditions were not limiting, hybrids and inbreds would have the same development since nothing would oppose the whole use of

C. If conditions are limiting, hybrids grow better than inbred lines because of their better ability to adapt to a challenging environment. One observation supports this hypothesis for rapeseed: in the field where competitive effects were demonstrated (BUSON, 1979), hybrids show a better ability to compete with the surrounding plots than inbred lines in the same environment (BUSON, 1979; no statistical measures of this phenomenon could be made because of the small number of data).

This theory agrees with the homeostasis theory developed by LERNER (1954) for hybrids and later by SCHWARTZ (1971) and OROZCO (1975). OROZCO emphasized the requisite involvement of environment in any explanation or use of heterosis and he suggested a model of gene effects: « some genes with strictly additional effects would determine the character *per se*; others with dominance effects would indirectly determine the expression of the character since they rule the adaptation ability of an animal to stressing conditions ».

This theory cannot be directly used with plants and must be carefully considered. Nevertheless it is interesting to extend the environment concept in order to better understand the variations of heterosis. The concept of environment covers here all external conditions to the plant but it can be extended to « internal » conditions according to the parameter under consideration: for — an allele — a gene — a cell — a tissue — an organ and — a plant, the environment is respectively — the gene — the cell — the tissue — the organ — the plant and — the population. This is related to DEMARLY's theory (1979) who symbolized the « genotype-environment system » by imbricated spaces, thus emphasizing the gap between genes and ecosystem.

The assumptions provide a first and rough explanation of the variations of the rate of heterosis within a given species according to locations and years (external conditions are different), and within a given plant according to development stage and to the organ under consideration (progressive modifications under epigenetic conditions, variations of internal correlations between organs).

V. CONCLUSIONS

F₁ hybrid rape varieties are of economic interest since some combinations yield up to 30 %, 40 % or 50 % more than the best parent. However, creation of hybrid varieties requires a usable male-sterility and satisfactory pollination. Male-sterile flowers are pollinated by bees despite a low nectar yield; two male sterility systems are presently under studies at the Rennes Plant Breeding Station; in the first one, « Bronowski » sterility, fertility is recovered at the end of flowering, and in the other, « Radish » sterility, sterility is complete but no restorer genes are known and it is closely related to chlorophyll deficiencies.

Heterosis affects the whole hybrid plant (both vegetative characters measured at different stages of development and yield characters), but its expression changes according to time and space.

Mechanisms which control the expression of a character such as seed yield are not different in inbred and hybrid plants, which emphasizes the physiological identity of both types of plants.

Because of the occurrence of reciprocal effects any explanation of heterosis must involve nucleo-cytoplasmic interactions. Heterosis would express itself most obviously in the most stressing environments. The superiority of

hybrids compared to inbred lines would be due to a better homeostasis.

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