Chances and Limitations for the Use of Heterosis in Synthetic Cultivars of Rapeseed*

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In rapeseed, the natural system of propagation is composed of self- and cross fertilization (for review see Becker 1987). Consequently, different types of cultivars are possible (Becker 1989). At present, cultivars on the market are line cultivars which to the utmost may originate from one doubled haploid plant, or population cultivars which preferably have the form of synthetics. During the recent years, rapeseed breeders also have paid increasing attention to hybrid cultivars. Table 1 demonstrates that all these cultivar types have their advantages and disadvantages as well (see also Becker 1987, Becker et al. 1998).

Table 1: Advantages (+) and disadvantages (-) of different cultivar types in rapeseed

Scope	Line cultivars	Population cultivars	Hybrid cultivars
High performance	-	±	+
Defined quality	+	-	±
Yield stability	-	± (+)	±
Rel. low breeding expense	+	±	-
Easy seed multiplication	+	±	-

As a partially cross-fertilizing species, rapeseed exhibits a considerable degree of heterosis for grain yield. But today the actual discussions about breeding of hybrid cultivars often disregard that heterosis can be exploited not only with hybrid cultivars. Plants are heterozygotic in synthetic cultivars and heterosis contributes to their performance, too. But for the practical utilization of heterosis high outcrossing rate is an essential factor. The following contribution summarizes results of experiments run over many years, measuring cross fertilization rate and yield performance of synthetic cultivars of spring and winter rapeseed.

Materials and Methods

Materials: Doubled haploid (DH) lines were used which represent the Swedish breeding materials of the mid eighties; however, these were not preselected for particular yield performance. The spring rape materials consisted of 20 DH lines received from W.Weibull AB; the 9 lines of winter rape were contributed by Hilleshög AB. In spring rape, 6 synthetic populations were composed as described in the chapter Results. In winter rape, 3 synthetic populations were set up:

Population A with 3 DH lines derived from the cultivar 'Jupiter',
Population B with 3 DH lines derived from the breeding line 'WW 933',
Population C with 3 DH lines derived from different populations.

Yield tests were performed with the immediate mixtures of the DH lines (SYN-0) as well as with the progenies raised from one or several cycles of random fertilization within them (SYN-1, SYN-2 etc).

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Methods: The rate of cross fertilization was determined by isozyme analysis (Becker et al. 1992). Yield tests were conducted with usual plot sizes and common agronomical treatments. For the spring rape materials, test sites were located in Sweden and Denmark, for the winter rape in Sweden, Denmark, Germany, Belgium and France. All experiments were continued over several years, as is indicated with the presented results.

Results

The rate of cross fertilization was highly variable for the 20 DH lines of spring rape (Fig. 1); differences were largely genetic and rather similar in both experimental years. But in other experiments (Becker et al. 1991, 1992), also significant environmental effects were observed..

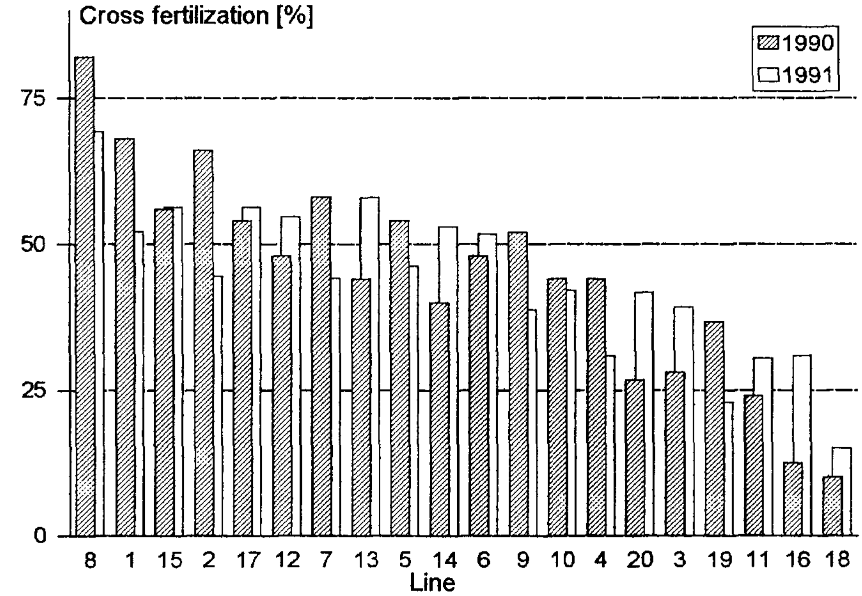

Figure 1: Cross fertilization rate of DH lines of spring rape (2 years, Landskrona/Sweden, Svensk, Karlsson and Becker unpublished)

The cross fertilization rates presented in Figure 1 were determined with single plants of the respective genotypes inserted in a field stand of the tester genotype 'Korall'. Seeds of such plants were investigated by isozyme electrophoresis to identify the origin from self- and cross fertilization, respectively. In this way, the frequency of fertilization effected by foreign pollen was measured. This is not necessarily identical to the disposition of a genotype for outcrossing, i.e. the dispersion of pollen for the fertilization of neighbouring plants. Fertilization from introgression and outcrossing, respectively, does not always coincide for one and the same genotype. Genetic variation in cross fertilization may simply depend on the different quantity of produced pollen; a genotype with poor pollen production is more "sensitive" to foreign pollination, but less capable of outcrossing.

In order to test this hypothesis, the DH lines used in the above experiments were raised under controlled conditions in a growth room and the weight of their anthers was determined. Since no significant difference had been observed in pollen size (Damgaard, unpublished), anther weight is a good estimate for the amount of pollen produced. For determining the outcrossing rate, the respective DH lines were sown in plots and single plants of the test genotype 'Korall' were insown into these plots. From the progeny of the 'Korall' plants harvested from the different plots, rates of outcrossing from the surrounding DH line were measured via electrophoresis. As shown in Figure 2, lines in the order of increasing anther weights exhibited increasing outcrossing rates, but inversely were less fertilized by foreign pollen.

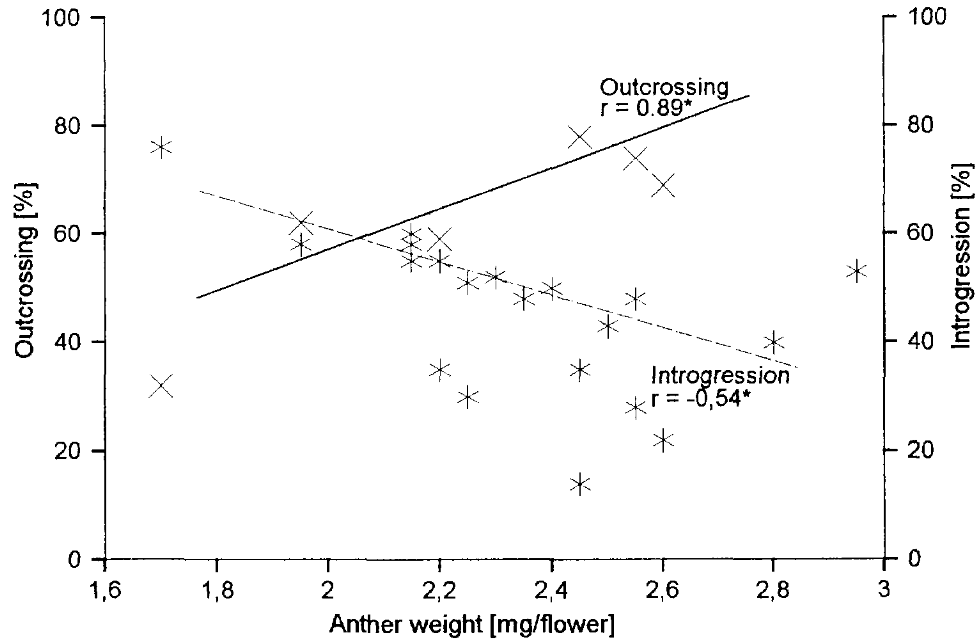

Figure 2: Relationship between rates of introgressive and of dispersive fertilization and anther weight (Becker and Karlsson unpublished)

Yield performance of synthetic populations

Theoretically, heterosis should be the better exploitable the higher the rate of cross fertilization is. This, however, because of the negative relationship between introgressive and dispersive pollination, is less obvious than one might assume at first sight. To experimentally verify the relationship of outcrossing and hybrid yield, synthetics were produced from line components differing in their degree of introgressive fertilization. As was expected, heterotic yield increase of the SYN-1 over the SYN-0 was particularly obvious after high rates of introgressive cross fertilization (Table 2).

Table 2: Yield performance of synthetic cultivars of spring rape depending on the rate of cross fertilization (mean over 5 environments, Svensk unpublished)

Synthetic population	Mean cross fertilization rate	Relative yield	
		SYN-0	SYN-1
11/16/18	20.5	100	103
3/4/11/14/16/18	29.8	100	103
1/5/9	51.9	100	102
2/7/8/13/15/19	53.1	100	123
7/8/14	57.7	100	126
2/8/15	62.3	100	119

In the experiment with winter rape, different from the spring rape approach, the synthetics were produced without knowing their cross fertilization rates. The comparison of the spring with the winter rape data reveals a considerably higher yield increase in the spring than in the winter rape experiment (Table 3). When the development of yield in the successive Syn-generations wass analyzed separately for the three synthetics of winter rape (Table 4), surprising variation became obvious, which because of the high number of test environments can not be explained simply by experimental error. For understanding the yield structure in the synthetic populations it is necessary to take into account that shifts in the composition of these populations may occur resulting from competition among their components.

Table 3: Relative yield in consecutive generations of synthetic populations (spring rape: 5 environments, Svensk unpublished; winter rape: 9 environments, Engqvist and Becker unpublished)

	Spring rape	Winter rape
DH lines	100	100
Mixture of the DH lines (=SYN-0)	105	103
SYN-1	117	107
SYN-2	117	109

Table 4: Relative yield of DH lines (=100) and synthetic populations in three sets of materials (A, B, C) in winter rape (means over 9 environments, Engqvist and Becker unpublished)

	A	B	C	Mean
DH lines	100	100	100	100
SYN-0	104	104	100	103
SYN-1	121	92	108	107
SYN-2	119	98	110	109
SYN-3	129	100	118	115

Competition in rapeseed populations

Rapeseed is a crop, in which genotypes can strongly influence each other within a heterogenic population by competition. This is demonstrated in Figure 3 by an experimental mixture of the two winter rapeseed cultivars 'Jupiter' and 'Jet Neuf'. In pure stands both cultivars produce very similar grain yields. In a 1:1 mixture of them, according to an enzyme electrophoretic analysis, 'Jupiter' contributes to the total performance much more than 'Jet Neuf'. Accordingly, the harvest of such miced plot (corresponding to a SYN-0) preponderantly consists of seeds which are grown on 'Jupiter' plants. Admittedly, 'Jupiter' and 'Jet Neuf' were taken for this experiment because they represent cultivars of a rather divergent growth habit. But synthetic cultivars may also consist of very different genotypes, since they are composed of a mixture of the parental homozygous components and the F_1, F_2, back crosses etc.from them.

Within the three synthetics of winter rape, the genotypic composition of the consecutive generations were analyzed by isozyme and RAPD markers (Table 5). Although in the synthetics A and B the components were derived from one initial population and thus were rather similar genetically, considerable differences were stated regarding the composition of the SYN-populations. In particular, the fraction of the hybrid plants was very small in the early generations. This result can be explained only by the fact that under the environmental conditions of southern Sweden the rate of cross fertilization is very low in winter rape. These rather severe shifts in composition of the synthetic populations may also provide an explanation of the unexpected changes in yield developments during the consecutive SYN-generations.

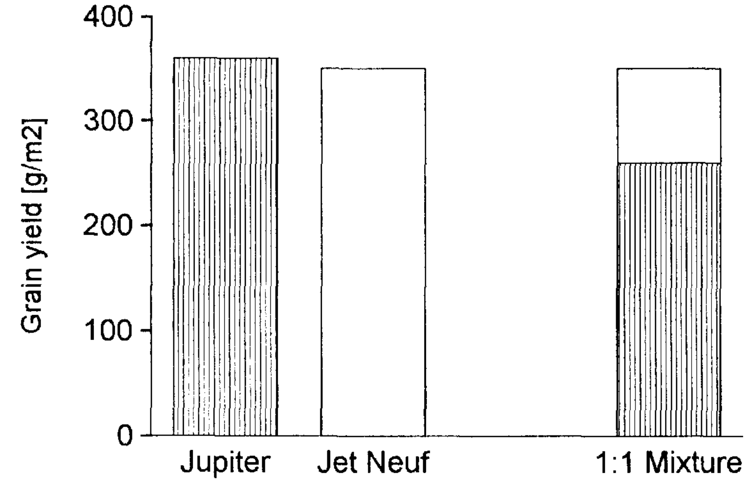

Figure 3: Grain yield of two rapeseed cultivars and their share in the yield of a 1:1 mixture (mean over 4 environments, Becker and Léon unpublished)

Table 5: Genotypic composition (5) of synthetic populations derived from three DH lines in winter rape (mean over 2 environments, Engqvist and Becker unpublished)

		DH 1	DH 2	DH 3	Crosses[a]
A	SYN-1	54	15	23	8
	SYN-2	58	4	20	18
B	SYN-1	44	44	5	6
	SYN-2	6	53	22	18
	SYN-3	9	47	20	24
C	SYN-1	39	46	13	3
	SYN-2	42	29	17	13
	SYN-3	27	33	22	18

[a] F_1 and all other possible types of crosses

The largest competition effects to be expected within a synthetic population are those between the homozygous lines as the parental components and their heterozygous F_1 progeny. To investigate the influence of this competition on yield, the three possible F_1 hybrids were each produced by hand crossing for the two populations A and B of winter rape. Field tests then were conducted to determine the yield of mixtures from DH lines and F_1 hybrids combined in diverse proportions. DH lines and F_1 hybrids of each population were represented as a mixture of the pertinent three lines and crossing products, respectively.

As expected, the heterosis value was clearly higher in population C made up of unrelated lines, than in population B (Fig. 4). But it is also noteworthy that a considerable amount of heterosis was observed in population B, too. Thus it can be concluded that in rapeseed heterosis can play a decisive role for yield increase even in genetically confined population cultivars. But it is particularly interesting to note that in both populations the relation between hybrid fraction and yield is not linear. Already with a portion of 50% to 75% hybrid plants the resulting yields equal those of a pure hybrid stand. Probably at usual plant densities the hybrids in such mixed stands suppress the plants of the inbred lines completely. Therefore the fact that allogamy is only partially expressed in rapeseed does not hinder the utilization of heterosis in synthetic cultivars of winter rape to be as efficient as in completely cross fertilizing crop species.

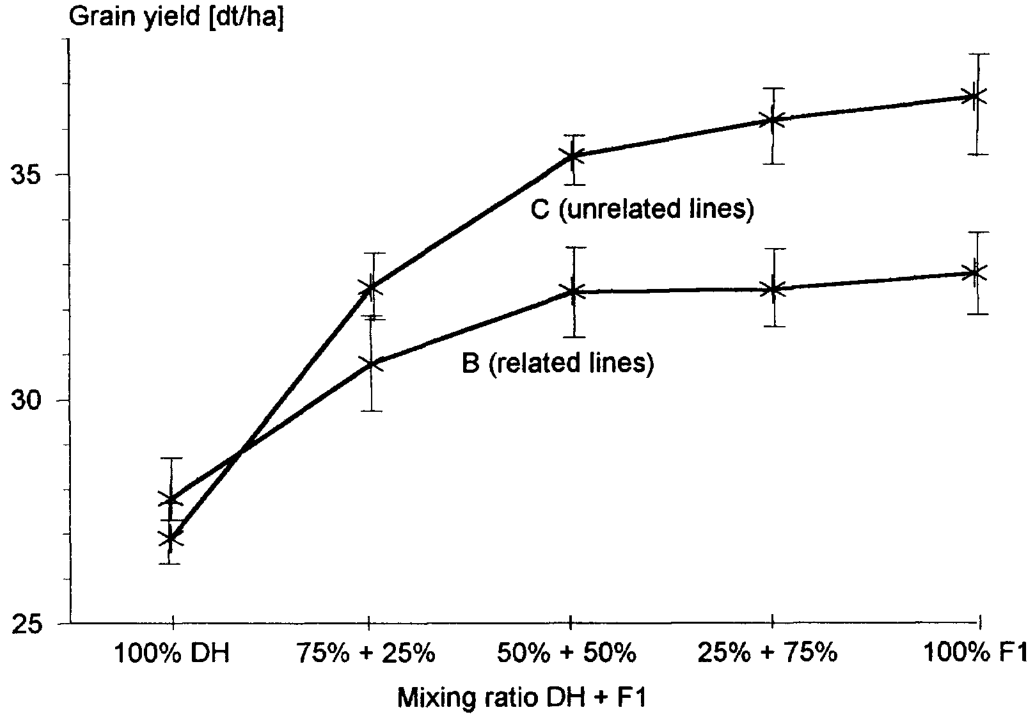

Figure 4: Grain yield of mixtures from DH lines and their F_1 hybrids (means over 7 environments, Engqvist and Becker unpublished)

The results presented in Figure 4 are also important for hybrid breeding. Evidently it is not required for the full exploitation of the yield potential of hybrid cultivars that the "hybridity" of the certified seed is 100%. A certain amount of parental lines in the seed does not necessarily reduce the final yields.

Conclusions and summary

It is not easy to form an opinion of the chances of synthetic populations as a practical cultivar type in rapeseed. Synthetic populations exhibit a yield superiority of 10 - 15% over the mean of DH lines. But for the farmer, the only relevant comparison is that to the available best DH line. It should also be considered that the breeding of synthetic cultivars like that of hybrids is much more expensive and takes more time than the development of DH lines.

A particular prerequisit of the breeding of synthetic populations is a high rate of cross fertilization. This is not so easy to secure, since outcrossing is also variable by environment. Yet at least in spring rape the cross fertilization rate was shown to be predominantly controlled by genetic variation.

A major difficulty for the breeding of synthetic cultivars are the competition effects between its components. At least in winter rape these can be considerable and may lead to unpredictable fluctuations in yield performance. Most favourable, however, is the finding that in consequence of this competition a mixture of 75% heterozygotic and 25% homozygotic plants already produces the same yield as a stand of 100% heterozygotic plants. Although fertilization in rapeseed is only partially allogamous, the yield potential of synthetic cultivars can well be exploited if a sufficiently high degree of cross fertilization is realized.

The chances of synthetic cultivars in rapeseed probably deserve specific valuations for different product uses. The vast majority of rapeseed oil is produced in Canola quality today, which provides an excellent salad oil. For this standard quality, hybrid cultivars will be the dominating ones in the main areas of production in the near future. Besides, however, other oil qualities are being developed at present for specialized uses, e.g. with a high content of oleic acid for frying, of palmitic acid for margarine production and of lauric acid for use in solid foodstuffs. As a raw material for the oleochemistry, high proportions of erucic acid, or of oleic acid, or medium chain fatty acids meet particular interests. It cannot be assumed that breeders will develop hybrid breeding programs for all these specialities. The first cultivars to be marketed for such uses certainly will be line cultivars. But for oil qualities which would meet greater demand in future markets, breeding of synthetic cultivars might be an interesting option.

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References

Becker, H.C., 1987: Quantitative Genetik und Zuchtmethodik bei Raps - Versuch einer Literaturübersicht. Ber.Arb.tagung 1987 A.G.Saatzuchtleiter, Gumpenstein:67-82.

Becker, H.C., 1989: Breeding synthetic varieties in partially allogamous crops. Vortr.Pflanzenzüchtg. 16:81-90.

Becker, H.C., Damgaard, C., and Karlsson, B., 1992: Environmental variation for outcrossing rate in rapeseed (*Brassica napus* L.). Theor.Appl.Genet. 84:303-306.

Becker, H.C., Karlsson, B., and Damgaard, C., 1991: Genotypic and environmental variation for outcrossing rate in rapeseed. GCIRC 8th Int.Rapeseed Congress 1991. Proceedings 5:1454-1459.

Becker, H.C., Löptien, H., and Röbbelen, G., 1998: Breeding. In: Gómez-Campo, C. (ed.): Biology of Brassica Cenospecies. In Print