INTRA- AND INTERPOPULATION IMPROVEMENT IN SPRING BRASSICA NAPUS

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INTRODUCTION

Recurrent selection describes a variety of population improvement processes whereby the frequencies of desirable alleles contributing to the expression of quantitative traits are increased through a cyclical process of selection and intercrossing. Recurrent selection has been applied successfully in both self- and cross-pollinated crops, but the greatest levels of improvement have been obtained in open pollinated species (Hallauer and Miranda, 1981). Population improvement is an important component of canola breeding programs aimed at commercial hybrid development. This is because the development of new hybrids through random inbreeding, followed by evaluation of the large number of possible hybrid combinations is extremely inefficient, especially if no provision is made within the breeding program to produce improved populations as a future source of parental lines.

Single populations can be improved using intrapopulation methods such as S_1 per se, S_2 per se, mass selection, or half-sib selection. In order to increase heterosis between two populations over time, however, interpopulation approaches such as full-sib (FS) or half-sib (HS) reciprocal recurrent selection (RRS) must be used. Thompson and Hughes (1986) described a few of the methods of population improvement which have been applied in winter \underline{B} . napus in Europe. Recurrent selection has also been reported in oilseed turnip rape, \underline{B} . campestris (Downey and Rakaow 1987).

The objectives of the current investigation were: (1) to apply S_1 per se selection to a single population, and (2) to apply full-sib RRS to two heterotic populations which were to be used as an ongoing source of inbreds in a commercial hybrid development program.

MATERIALS AND METHODS

Two heterotic populations, A and B (cycle zero = C_0), were each synthesized by intercrossing 15 Fls involving six different cultivars. The classification of the 12 cultivars into A or B blocks was carried out according to Hallauer and Miranda (1981). The information on yield heterosis needed for classification was obtained from a 16 x 16 diallel.

Approximately 150 plants from each of C_0 A and C_0 B were grown in the greenhouse during the winter of 1987. At flowering, 92 full-sibs were produced by hand-crossing plants reciprocally. At the same time, a raceme on each plant was selfed to produce S1 seed. The 92 full-sibs were divided into four sets of 23 families each, with three common checks. Each set was planted in a separate, two-replicate RCBD experiment at two locations in western Canada. Six row plots (18 cm row spacing, 3 m x 1.4 m), were used throughout, with a seeding rate of 4.5 kg/ha. Seed yield (kg/ha) and days to maturity were recorded on all plots at both locations. The S_1 families representing the 92 full-sibs were grown in an Ontario nursery for visual evaluation.

The genetic and phenotypic variances among full-sib families, and broad-sense heritabilities were calculated for each trait in each experiment, using standard formulae. All variances were pooled across experiments, then pooled estimates were calculated for all parameters. Twenty-two full-sibs were selected from the C_0 experiments. An attempt

was made to select equal numbers of full-sibs from the four experiments. The S_1s from populations A and B representing the selected full-sibs were planted in the greenhouse during the fall of 1987, then intercrossed to synthesize C_1 A and C_1 B.

By the end of 1990, three full cycles (C_1 , C_2 and C_3) of full-sib RRS had been completed. Each cycle followed the same three steps: (1) FS and S_1 production in winter, (2) FS and S_1 evaluation in summer, and (3) resynthesis in the fall. Details of population sampling and FS evaluation for all cycles are summarized in Table 1.

In the C_0 , C_2 , and C_3 , oil and protein analysis for each entry at each location was done on bulked seed samples obtained from both replicates. In these cases, genotype x location variances were used as error terms to test the significance of mean squares, and to estimate heritabilities.

Table 1: Summary of FS evaluation and selection from Co to Co.

Cycle	Yr	S ₀ * sample	Total # FSs		Checks @	Reps	No. of tests		No. of FSs sel.
co	1987	150	92	23	3	2	4	2	33
$c_0 \\ c_1$	1988	250	96	24	2	2	4	2	20
c_2^-	1989	300	96	24	2	2	4	2	24
c ₃	1990	350	96	24	2	2	4	2	23

 $[\]emptyset$ Checks for C_0 = Westar, Regent and BBSyn-1, C_1 = Westar (duplicate plots), C_2 and C_3 = Westar and Delta

Two other populations, C_0 C and C_0 D, were also synthesized in the fall of 1986. Pop. C was based on eight, high combining cultivars from the original diallel. Pop. D was based on the 14 earliest, high-yielding crosses, also from the original diallel. In each population, mild selection for yield, maturity, and blackleg resistance was practised, using S_1 per se selection. These two populations were merged by intercrossing selected S1 lines from populations C_1 C and C_1 D. The resulting population, C_0 E, was subjected to S_1 per se selection for seed oil and protein. One hundred and thirteen C_0 S_1 s from C_0 E were evaluated in 1989, using the modified augmented design (MAD II), 33 of which were intercrossed to synthesize C_1 E. In 1990, 150 S_1 s were evaluated, 35 of which were intercrossed to form C_2 E.

RESULTS

The combined analysis of variance over two locations indicated that mean squares due to genotype were significant for all the traits under consideration. Genotype x environment mean squares, pooled over all four experiments were significant for yield in each cycle, indicating the presence of significant GXE for yield. The mean values of FSs, Westar, and selected FSs for seed yield, days to maturity, % oil, % protein, and blackleg ratings over four sets (trials) in different cycles are presented in Table 2. Westar was present as a check in each trial in each cycle. For each character recorded, the difference between the mean of all FSs and Westar, and the mean of selected FSs and Westar, expressed in phenotypic standard deviation units, were calculated. The differences over all four experiments for different traits in different cycles are summarized in Table 2.

The mean yield of C_0 FSs exceeded that of Westar by 11.6%; by C_3 , the difference had increased to 24.5%. The mean difference between the mean of all FSs and Westar increased from 0.9 standard deviations (sd) in

^{*} Number S₀ plants sampled per population prior to blackleg screening

		Yield (Kg/ha)	J/ha)		Dz	Days to mature	mature			oil %		Pro	Protein %		Blackleg	2
Parameter	CO	CI	62	C3	co	CI.	22	ឩ	C0	ຄ	ឧ	co	ន	ឩ	ឧ	a
MEANS																
FS Wester Vester	2820.4 2525.6 2941.8	1790.3 1544.1 1925.1	1465.7 1135.0	2481.5 1991.8 2634.9	92.5 88.8 91.6	85.4 84.8	88.1 88.1	85.5	44.9 44.9	44.5 43.7	44.8 44.8 45.2	25.0	33.5	25.0 25.4 24.8	1.87 4.25 1.37	1.60 3.90 1.20
DIFFERENCES	EXPRESSED	ED IN	STAN	STANDARD	DEVIATION	TION										
FS - Westar FS Sel - Westar Sel. differential	0.9 1.5 0.4	1.6 2.4 0.9	3.7 3.8 0.1	2.2 2.9 0.7	2.8 2.3 -0.7	-1:1 1:1	0.1	-0.6 -0.4 0.2	0.0 -0.1	0.8 0.6 -0.2	0.1 0.4 0.3	0.5	-0.8 -0.6	-0.5 -0.7 -0.2	-3.28 -3.98 -0.69	-3.62 -3.00 -0.62
COMPONENTS	OF VARIANCE	ANCE														
Genetic variance G x E variance	57940.7 22842.4	10958.9 10305.2	2040.7 15020.9	13384.4 46180.3	0.8 0.2	0.2	0.2	0.0	. 1.2	0.7	. 0.8	0,4	0.3	0.4		
Heritability CGV%	74.0 8.5	44.0 5.8	25.6 3.1	27.0 4.6	50.3 1.0	54.0 0.5	57.7 0.6	53.9 0.6	84.6 2.4	1.9	1.9	71.7 2.4	71.4 2.0	74.3 2.6		

 C_0 to 2.2 sd by C_3 . In C_0 , the average FS maturity was 2.8 days later than Westar. This improved to 1.0 day later than Westar in C_1 , equivalent to Westar in C_2 , and slightly earlier than Westar by C_3 (Table 2). From C_0 to C_2 , % seed oil increased by 0.82 sd, but % seed protein declined by 0.36 sd. Selection pressure for % protein was increased in C_2 , resulting in a 0.3 sd increase in C_3 ; this was accompanied, however, by a 0.41 sd reduction in % oil. For blackleg resistance, the mean difference between all FSs and Westar was -3.28 sd which increased to -3.62 in C_3 . The frequency distribution of FS means, expressed in phenotypic sd for C_0 vs. C_3 , is presented in Fig. 1 for seed yield and days to maturity.

Broad-sense heritability estimates varied from 25.6% to 75.8% for yield, and from 50.3% to 61.6% for maturity. For blackleg ratings, heritabilities were not calculated because observations were recorded on a 0 to 5 scale. Heritability estimates for % oil and % protein were higher than those for seed yield and days to maturity.

The estimates of genetic variance for seed yield varied from year to year. During 1989, drought affected trials at both locations, compressing the range for seed yield. The genetic variability, expressed as a percentage of the mean (GCV) for seed yield and days to maturity, reduced slightly from \mathbf{C}_0 to \mathbf{C}_1 , but changed very little thereafter.

The analysis of variance of unreplicated data from the modified augmented design (MAD II) showed no significant row, column, or row x column effects for either yield or maturity in C_0 and C_1 . The effects of one cycle of S_1 per se selection for % oil and % protein in Population E are summarized in Table 3. Oil content improved by 0.27 sd, and % protein by 1.64 sd; however, yield declined by 0.6 sd in the same cycle.

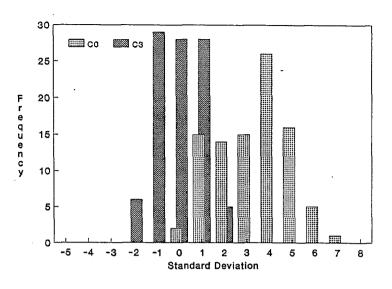
Table 3: Effects of one cycle of S₁ per se selection in Population E.

Parameter:	Seed Yield		Maturity		% Oil		% Protein	
	℃	c_1	c _o	c ₁	ු ද	c_1	c_0	c ₁
Means:								
s_1	1467	2200	91.9	86.8	46.0	44.8	23.6	24.3
Westar	1179	2078	91.0	85.8	45.6	43.8	24.6	24.8
Sel S _l s	1491	2452	91.8	85.9	46.2	45.4	23.7	24.0
Differences	expresse	ed in st	andard o	eviatio	on units	:		
S ₁ -Westar	0.9	0.3	0.4	0.5	0.6	0.8	-2.1	-0.4
Sēl-Westar	1.0	8.0	0.3	0.1	0.7	1.3	-1.9	-0.7

DISCUSSION

The presence of significant heterosis in rapeseed (Schuster and Michael, 1976; Sernyk and Stefansson, 1983; Grant and Beversdorf, 1985), and the existence of pollination control systems (cytoplasmic-genetic male sterility, CMS, and sporophytic self-incompatibility, SI), provide the elements necessary for commercial hybrid development. This has resulted in hybrid breeding activites in several centers, and B. napus hybrids based on CMS and on SI have recently been registered in Canada.

The original C_0 A and C_0 B populations exhibited heterosis for yield relative to a commercial check cultivar, Westar. Yield heterosis increased an average of 4.3% per cycle over three cycles of RRS. The majority of C_0 full-sibs were also later maturing than Westar. However, response to selection for earliness in the first cycle (C_0 to C_1) was very dramatic. This was expected, as maturity is simply inherited in B. napus, and earliness is partially dominant. By C_3 , most of the full-sibs were both earlier and higher yielding than Westar. The positive improvements in both traits indicate that these improved populations will



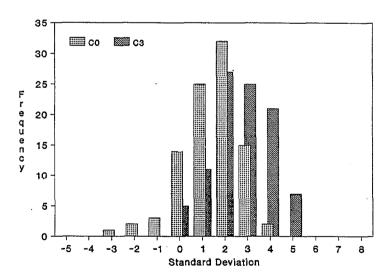


Fig. I. Phenotypic distributions of C_0 and C_3 full—sibs for days to maturity (top) and seed yield (bottom). Both traits expressed in standard deviation units.

be a good future source of high-yielding, early-maturing hybrids.

While improvements in yield and maturity are important, increasing \$ seed oil and \$ seed protein is also essential, since these are the constituents which are of economic importance to the crushing industry. Oil and protein are strongly negatively correlated, as the experiences in this study demonstrate: selection for oil in C_0 and C_1 increased \$ oil at the expense of protein, while in the C_2 , increased selection pressure for \$ protein improved protein content at the espense of oil.

During C_1 , C_2 and C_3 , single plant selection for blackleg resistance was carried out prior to pairing plants for full-sib production (Table 1). In C_2 and C_3 , disease ratings were recorded on FS families in a field disease nursery, and only those with moderate to good resistance were selected for recombination. This resulted in a general improvement in the

mean level of resistance of the populations from C_2 to C_3 .

When the breeder wishes to improve several traits, the overall response to selection is affected by correlations among the traits under consideration. It becomes extremely difficult to improve all traits in the same cycle. A better approach is to cull for different traits in different cycles. In this study, while progress for oil and protein was relatively low from C_0 to C_3 , a few FSs with high oil and protein, high yield, and blackleg tolerance were available for further breeding.

Intrapopulation improvement using S_1 per se selection resulted in increased oil and protein content in Pop. E. This population has not been selected rigorously for yield and maturity, but is viewed as a future source of improved lines with superior quality and disease resistance.

The main goal of this recurrent selection program is to develop germplasm sources for a hybrid program. Reciprocal full-sib selection is designed to capitalize on both general and specific combining ability (Hallauer, 1984), and is a one year cycle in spring rape when greenhouse facilities are used. In any cycle, selfing can be continued in selected S_1 s to produce finished inbred lines, or $S_1 \times S_1$ or $S_2 \times S_2$ full-sibs can be produced and evaluated for further selection of specific combinations.

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