

# Fatty acid composition of resynthesized *Brassica napus* L., *B. campestris* L. and *B. alboglabra* Bailey with special reference to the inheritance of erucic acid content

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The fatty acid composition of the oil of four resynthesized rapeseed (*Brassica napus* L.) lines resulting from crosses between *B. campestris* L. and *B. alboglabra* Bailey was compared with that of the mid-parent value. Low palmitic acid content was partially epistatic over high. High oleic acid content could be either partially hypostatic to or transgressively epistatic over low content of this fatty acid, depending on the erucic acid contents of the parental species. Epistasis was observed for low linoleic acid content in two crosses whereas additive gene action was shown for this fatty acid in the other two crosses. Partial or transgressive epistasis was observed for low linolenic acid content. High eicosenoic acid content was generally epistatic over low. Partial epistasis was observed for high erucic acid content in three crosses but hypostasis was also observed in one cross. Oleic acid content played a key role in the change of fatty acid composition. Regarding the inheritance of erucic acid content, the hypothesis was substantiated that *B. napus* contained two genes for this fatty acid residing in the genomes from *B. campestris* and *B. oleracea*. Caution should be taken in accepting the proposed hypothesis (Krzymanski and Downey, 1969) that there is a series of erucic alleles based on the phenotypic value of erucic acid content, because the influence of different genetic backgrounds and/or ploidy level on the allelic performance is not taken into consideration.

## INTRODUCTION

The fatty acid composition of the oil of *Brassica* species is characterized by the high content of erucic acid. Since erucic acid is nutritionally undesirable, its removal has been one of the most important breeding objectives for rapeseed. The genetic control of erucic acid content has been carefully investigated in *Brassica* crops. It was shown that the erucic acid in the oil is under the control of embryonic genotype and is governed by one gene in diploid species such as *B. campestris* (AA) (Dorrell and Downey, 1964) and two genes in amphidiploid species such as *B. napus* (AACC) (Harvey and Downey, 1964; Kondra and Stefansson, 1965; Siebel and Pauls, 1989). Of the two genes in the amphidiploid *Brassica* species, one occurs in each genome (Fernandez-Escobar *et al.*, 1988). While the genes for erucic acid content generally acted in an additive manner (Dorrell and

Downey, 1964; Harvey and Downey, 1964; Kondra and Stefansson, 1965; Chen *et al.*, 1988a), partial dominance for high erucic content was also observed (Jönsson, 1977). Krzymanski and Downey (1969) assumed that there are five alleles symbolized as  $e$ ,  $E^a$ ,  $E^b$ ,  $E^c$  and  $E^d$  which control the synthesis of 0, 10, 15, 30 and 3.5 per cent erucic acid in *Brassica* seed oils, respectively. However, no solid evidence is available to confirm whether these are truly alleles. An exception is the demonstration that  $E^a$  and  $e^d$  are true alleles that reside in the C-genome of *B. napus* (Anand and Downey, 1981). Furthermore, Krzymanski and Downey (1969) ignored the impact of differences in ploidy level when implying the control of erucic acid content to an allelic effect, because  $E^b$  and  $E^c$  were established in *B. campestris* whereas  $E^a$  and  $E^d$  were established in *B. napus*. In addition, it is suggested that a number of modifying genes (Dorrell and Downey, 1964) and environmental factors such as drought also influence the erucic acid content. Thus, the possibility cannot be completely excluded that  $E^a$  and  $E^c$  (as an example)

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may be the same allele of one locus. In the present paper, we compare the fatty acid composition of resynthesized *B. napus* with that of the parental species *B. alboglabra* (a form of *B. oleracea*) and *B. campestris*, with special emphasis on the inheritance of erucic acid content.

#### MATERIALS AND METHODS

Resynthesized *B. napus* lines No2305, No3401, No7406 and No7407 (Chen *et al.*, 1988b) were derived from crosses between the *B. alboglabra* line No4003 and the *B. campestris* lines Sv85-38301, Sv741008, K-151 and K-88. The resynthesized *B. napus* lines can be divided into two categories according to the erucic acid contents of their parents, namely high-erucic × zero-erucic (No2305 and No3401) and high-erucic × high-erucic (No7406 and No7407) (table 1). In addition, a *B. napus* breeding line No7477 with no erucic acid was used in crosses with resynthesized *B. napus* for studying the inheritance of erucic acid content.

Crosses were made in the greenhouse to produce F<sub>1</sub> and F<sub>2</sub> progeny. It should, however, be mentioned that the seeds of the parental species, with the exception of K-151 and K-88, were not harvested from the greenhouse. Environmental factors might have had some influence on the fatty acid composition. The fatty acid composition was determined with a gas chromatograph according to a method described by Jönsson (1973).

#### RESULTS AND DISCUSSION

##### Fatty acid composition

Since resynthesized *B. napus* lines are homozygous, a change in their fatty acid composition, compared with that of the parents, would be attributed to the interaction between the homoeologous genes of the A and C genomes. Thus, intergenomic gene interactions in the resynthesized *B. napus* lines are expressed in terms of epistasis rather than dominance.

**Palmitic.** The three resynthesized *B. napus* lines No2305, No7406 and No7407 had a significantly lower content of palmitic acid than the mid-parent value whereas No3401 had a non-significantly higher content of this fatty acid (table 1). Therefore, low palmitic acid content is, intergenomically, partially epistatic over high.

**Oleic.** The four resynthesized *B. napus* lines showed either of two inheritance patterns of oleic acid content. No2305 and No3401 showed one pattern exhibiting significantly lower oleic acid content than the mid-parent value (table 1). The other pattern observed in No7406 and No7407 indicated an intergenomic interaction for a transgressively higher oleic acid content. This differential performance of oleic acid content is correlated with the parental erucic acid content. Parental high oleic lines had zero or low erucic acid content whereas low oleic lines had high erucic acid content. Thus, a high content of oleic acid can be

**Table 1** Fatty acid composition of parental *Brassica alboglabra* and *B. campestris*, the mid-parent value and the resynthesized *B. napus*

Accession	No. of seeds	Fatty acid composition as percent of total fatty acids (M ± SE)					
		Palmitic	Oleic	Linoleic	Linolenic	Eicosenoic	Erucic
No4003	25	3.7 ± 0.1	15.2 ± 0.5	15.2 ± 0.2	10.7 ± 0.3	7.1 ± 0.2	47.1 ± 0.4
Sv85-38301	20	12.6 ± 0.3	46.4 ± 0.7	23.2 ± 0.4	17.0 ± 0.4	0.5 ± 0.1	0.1 ± 0.1
Mid-parent		8.2	30.8	19.2	13.9	3.8	23.6
No2305	10	5.3 ± 0.1}***	26.3 ± 0.8}***	18.9 ± 0.5}ns	12.1 ± 0.3}**	12.9 ± 0.2}***	24.4 ± 0.4}***
No4003	25	3.7 ± 0.1	15.2 ± 0.5	15.2 ± 0.2	10.7 ± 0.3	7.1 ± 0.2	47.1 ± 0.4
Sv741008	11	3.5 ± 0.1	53.3 ± 0.7	26.8 ± 0.3	15.5 ± 0.4	0.8 ± 0.1	0.0
Mid-parent		3.6	34.3	21.0	13.1	4.0	23.6
No3401	20	3.7 ± 0.1}ns	27.5 ± 0.8}***	19.0 ± 0.3}***	10.5 ± 0.3}***	11.9 ± 0.1}***	27.4 ± 0.7}***
No4003	25	3.7 ± 0.1	15.2 ± 0.5	15.2 ± 0.2	10.7 ± 0.3	7.1 ± 0.2	47.1 ± 0.4
K-151	15	2.4 ± 0.1	11.5 ± 0.4	13.4 ± 0.2	10.0 ± 0.2	4.3 ± 0.2	56.5 ± 0.5
Mid-parent		3.1	13.4	14.3	10.4	5.7	51.8
No7406	20	2.7 ± 0.1}**	19.6 ± 0.7}***	12.6 ± 0.5}***	5.3 ± 0.3}***	6.0 ± 0.3}ns	53.5 ± 0.6}***
No4003	25	3.7 ± 0.1	15.2 ± 0.5	15.2 ± 0.2	10.7 ± 0.3	7.1 ± 0.2	47.1 ± 0.4
K-88	15	2.2 ± 0.1	13.0 ± 0.6	15.3 ± 0.2	6.5 ± 0.4	4.7 ± 0.2	56.8 ± 0.5
Mid-parent		3.0	14.1	15.3	8.6	5.9	52.0
No7407	20	2.6 ± 0.1}***	19.6 ± 0.6}***	14.6 ± 0.4}ns	4.5 ± 0.2}***	7.5 ± 0.2}***	50.8 ± 0.4}*

\*, \*\* and \*\*\*: significant at 5, 1 and 0.1 per cent, respectively; ns: non-significant.

intergenomically either partially hypostatic to or transgressively epistatic over a low content, depending on the erucic acid levels of the parental species. Kondra and Thomas (1975) observed both additiveness and partial dominance for high oleic acid content in *B. napus*.

**Linoleic.** The linoleic acid content of No2305 and No7407 was not significantly different from the mid-parent value (table 1), which indicated an additive gene action for this fatty acid. However, No3401 and No7406 contained significantly lower content of linoleic acid than the mid-parent value (table 1), indicating intergenomic epistasis for low content of this fatty acid. Additive gene action and partial dominance for low linoleic acid content were observed in *B. napus* crosses (Kondra and Thomas 1975).

**Linolenic.** All four resynthesized *B. napus* lines contained a lower content of linolenic acid than the mid-parent value (table 1). In No7406 and No7407, the linolenic acid is lower than in the parental species K-151 and K-88. Intergenomically, low linolenic acid content is thus partially or transgressively epistatic over high. In their experiment, Kondra and Thomas (1975) observed dominance of low content of this fatty acid.

**Eicosenoic.** In two resynthesized *B. napus* lines, No2305 and No3401, the content of eicosenoic acid content is transgressively higher than the mid-parent value (table 1). The other two lines, No7406 and No7407, also contained a higher content of eicosenoic acid than the mid-parent value. However, the difference in No7406 is not significant. Thus, in general a high content of this fatty acid is, intergenomically, transgressively epistatic over low. In *B. napus* crosses, a high eicosenoic acid content was dominant over low (Kondra and Stefansson 1965).

**Erucic.** The erucic acid content of No2305 and No3401 is significantly higher than the mid-parent value (table 1), which indicated partial epistasis for high content of this fatty acid. No7406 also contained higher erucic acid content whereas No7407 had lower content of this fatty acid than the mid-parent value. Intergenomically, both incomplete epistasis or hypostasis for high erucic acid content thus prevail.

#### *Relationships among fatty acids*

The two types of resynthesized *B. napus* lines (No2305 and No3401 as one type, No7406 and No7407 as the other) have different fatty acid

composition (table 1). Compared with the mid-parent value, the reduction of oleic acid content in No2305 and No3401 was accompanied with an increase in eicosenoic and erucic acid content. In No7406 and No7407, a dramatic increase in oleic acid content paralleled the decrease in the linolenic acid content. This is a logical result if the biosynthetic pathways to the main fatty acids in rapeseed truly follow two directions from oleic acid, one towards eicosenoic and erucic acids, and the other towards linoleic and linolenic acids (Jönsson and Uppström, 1986). The relationship between eicosenoic and erucic acids is similar to what was previously reported (Jönsson, 1977), *i.e.*, eicosenoic acid content is the highest when the erucic acid content is intermediate.

#### *Inheritance of erucic acid content*

The distribution of erucic acid content is shown in fig. 1 for both parents,  $F_1$  and  $F_2$  in the *B. campestris* cross Sv85-3801  $\times$  K-151. While the female parent of this cross was zero-erucic, the average content of erucic acid of  $F_1$  seeds (43 per cent) was higher than the mid-parent value (28.3 per cent), thereby indicating the embryonic control of this fatty acid and partial dominance for high content. The  $F_2$  seeds showed a segregation not significantly different from a 1:3 ratio (zero-erucic: erucic-containing seeds). It thus supports the conclusion that one gene controls the erucic acid content in *B. campestris*. However, the high content of erucic acid of K-151 is not recovered in the  $F_2$  seeds, which is probably due to the small sample size but more likely due to the divergence between the two types of *B. campestris* in the cross. The erucic-gene possibly functions more effectively in the genetic background of K-151 than in Sv85-38301. Dorrell and Downey (1964) pointed out that the divergence of *B. campestris*, *e.g.*, the yellow sarsons from India compared to the Polish types, could even lead to the failure of erucic acid segregation to fit the expected ratio.

According to the hypothesis proposed, amongst other researchers, *e.g.* by Fernandez-Escobar *et al.* (1988), the two types of resynthesized *B. napus* lines must have different genotypes. No2305 and No3401 must be of the genotype  $e_A e_A E_C E_C$  whereas No7406 and No7407 are of the genotype  $E_A E_A E_C E_C$ . Zero-erucic *B. napus* material is of the genotype  $e_A e_A e_C e_C$ .

When the genotype  $e_A e_A E_C E_C$  is crossed with  $e_A e_A e_C e_C$ , a monogenic segregation could be expected. The result obtained with this cross fits well with the prediction (Chen *et al.*, 1988a). If

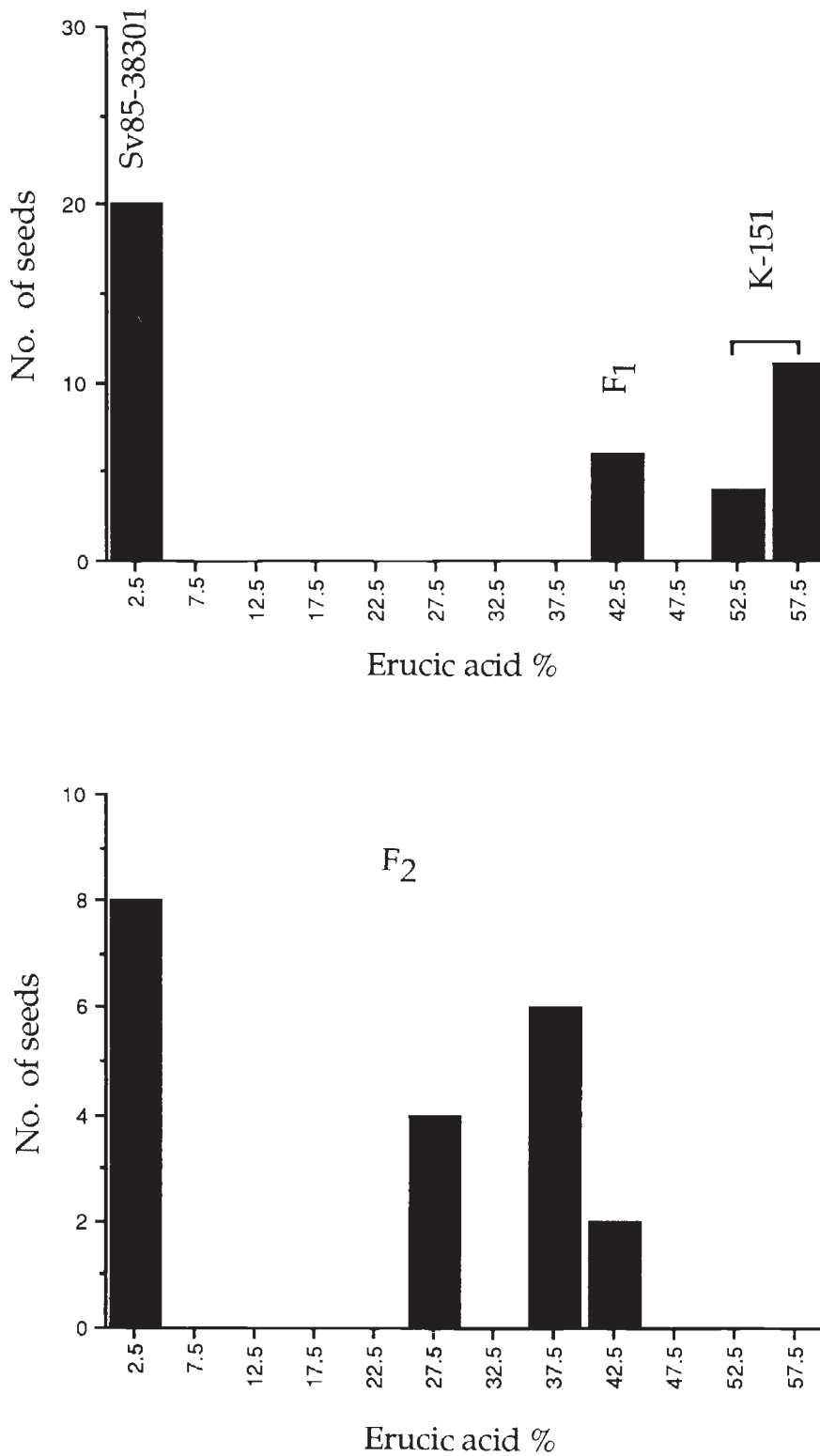
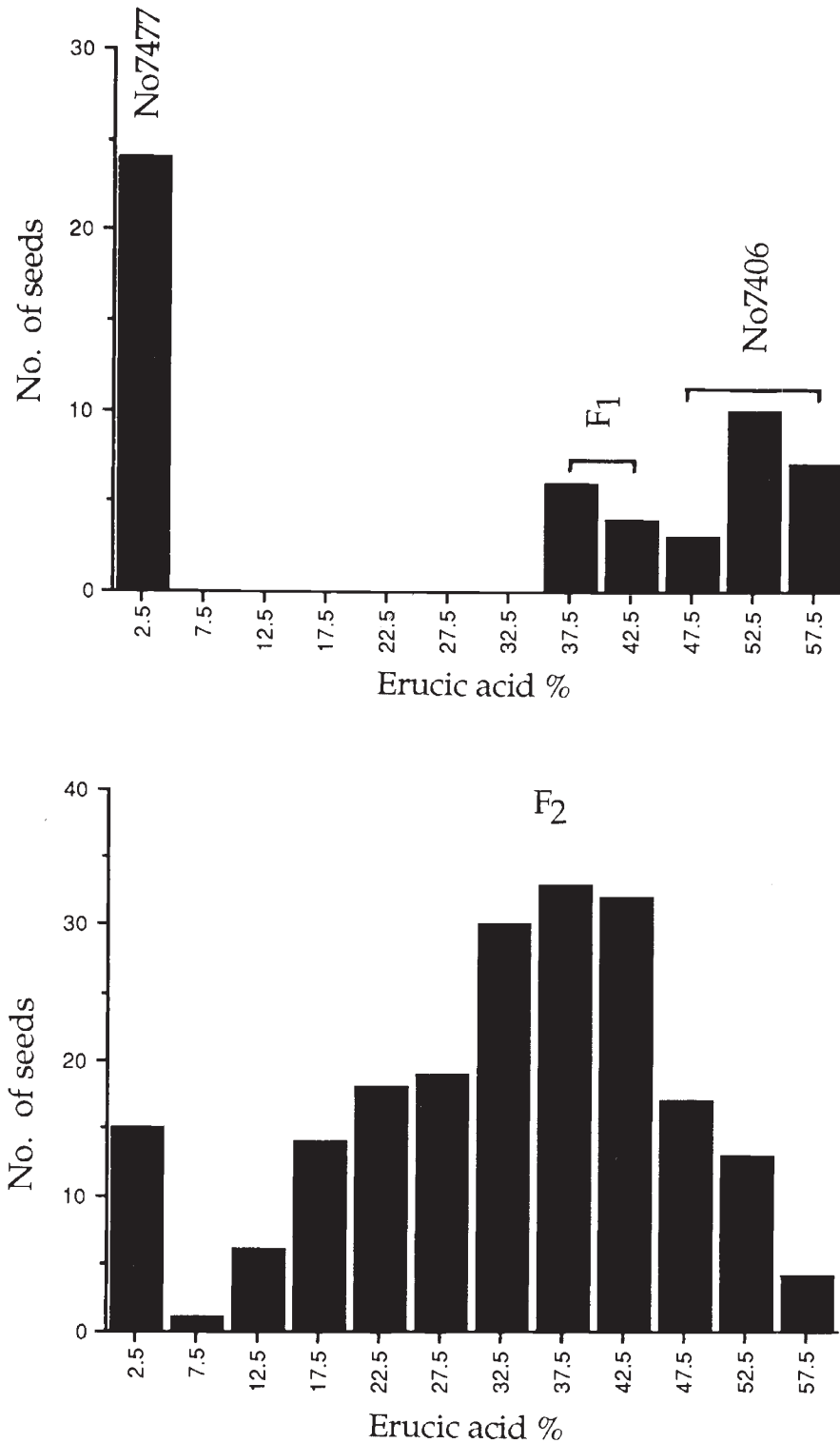


Figure 1 Distribution of per cent erucic acid in the parents, F<sub>1</sub> and F<sub>2</sub> of the *B. campestris* cross between lines Sv85-38301 and K-151.



**Figure 2** Distribution of per cent erucic acid in the parents, F<sub>1</sub> and F<sub>2</sub> of the *B. napus* cross between cultivated zero-erucic breeding line No7477 and resynthesized high-erucic line No7406.

the genotype  $E_A E_A E_C E_C$  is crossed with  $e_A e_A e_C e_C$ , a digenic segregation should be expected. The cross between No7406 and No7477 is of this type. The distribution of erucic acid content is shown in fig. 2 for both parents,  $F_1$  and  $F_2$  of this cross. The average erucic acid content (40.4 per cent) of  $F_1$  seeds is much higher than the mid-parent value (26.8 per cent), indicating the embryonic control of this fatty acid and partial dominance for high content. In the  $F_2$ , the seeds containing erucic acid exhibit a continuous variation but had a clear-cut boundary with the zero-erucic seeds. The zero-erucic seeds were recovered at the expected probability (1/16;  $\chi^2 = 0.53$ ,  $df = 1$ ,  $P_{\text{range}}: 0.50-0.30$ ), thereby confirming the digenic control of erucic acid in No7406. The hypothesis is thus substantiated that two genes govern the erucic acid in *B. napus*, one of which is from the *B. campestris* genome and the other from the *B. oleracea* genome.

Krzymski and Downey (1969) assumed a series of alleles for various erucic acid contents. From a genetic viewpoint, the effect of one allele for a specific erucic acid content can be greatly influenced by the genetic background and the level of ploidy. For example, the allele in the A-genome of cultivated *B. napus* contributes about 10 per cent erucic acid (Harvey and Downey, 1964) whereas the allele in the A-genome of *B. campestris* var. yellow sarson contributes about 30 per cent erucic acid. However, we have no allelic tests to show whether the two alleles are truly different in the A-genome locus or that they actually represent different quantitative expressions of the same allele. In the present study, the change of allelic effect for erucic acid content is implicated when comparing *B. campestris* K-151 with resynthesized *B. napus* No7406. Also, the impact of genetic background on erucic-allelic effect is observed in the *B. campestris* cross Sv85-38301  $\times$  K-151. Therefore, one should be cautious to assume different alleles exclusively based on the phenotypic value of erucic acid content.

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