Temperature Effects on Fatty Acid Composition During Development of Low-Linolenic Oilseed Rape (*Brassica napus* L.)

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ABSTRACT: The influence of temperature during seed development on the fatty acid composition of oilseed rape (*Brassica napus* L.) was studied in one low-linolenic and one conventional canola cultivar. The cultivar Regent produces seed oil with ~20% linoleic acid (C18:2) and ~8% linolenic acid (C18:3), whereas Stellar is relatively high in C18:2 (~25%) and low in C18:3 (~2.5%). Both cultivars were grown in the field, and the fatty acid compositions of the seed oils were monitored throughout the period of seed development. In the field, the content of saturated (C16:0 + C18:0) and monounsaturated (C18:1) fatty acids in the seed oil increased when seed developed under high temperatures. C18:3 levels were higher in seed harvested at sites with lower average daily temperatures. The low C18:3 trait of the cultivar Stellar was relatively stable over environments. Both temperature and duration of exposure to the temperature during seed development affected the fatty acid composition of the seed in a controlled environment study. Plants subjected to a high-temperature treatment (30/25°C day/night) for 40 d produced seed with the lowest C18:3 content and the highest levels of C16:0 + C18:0 and C18:1. This was observed in both cultivars.
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KEY WORDS: Canola, fatty acid composition, low-linolenic, oilseed rape, saturated, seed development, stability, temperature.

Conventional canola oil contains a high level (8 to 10%) of polyunsaturated linolenic acid (C18:3). High levels of C18:3 in the seed oil can lead to oxidative rancidity, a reduced shelf life, and the development of off-flavors and odors after prolonged storage or repeated frying use (1,2). One solution is to hydrogenate the oil to reduce the degree of unsaturation. The alternative is the development of cultivars with low levels of C18:3 in the seed oil.

Conventional canola oil contains approximately 6% saturated fatty acids (C16:0 + C18:0), 55 to 60% oleic acid (C18:1), 20 to 26% linoleic acid (C18:2), and 8 to 10% C18:3. The first low-C18:3 oilseed rape cultivar was released in 1987 (3). The low-C18:3 trait was produced by seed mutagenesis of the *Brassica napus* cultivar Oro, which led to the isolation of a mutation line, M11, with an altered C18:2/C18:3 ratio (4). A program of backcrossing to the adapted cultivar Regent, combined with selection, led to the release of the cultivar Stellar with approximately 3% C18:3 in the seed oil (3). Compared to conventional canola oil, oil from the low C18:3 cultivar Stellar had significantly better odor scores when heated (1), improved odor during frying (2), and greater stability under accelerated storage conditions (5).

The fatty acid composition of oilseed rape is influenced by aerial temperature during seed development (6). Many plants respond to lower temperatures by increasing the level of unsaturation in the fatty acids of membrane glycerolipids and to higher temperatures by reducing the level of unsaturation of their membrane fatty acids (7). The effect of temperature on the fatty acid composition of the seed oil has been studied in a number of oilseed crops, including sunflower (8), flax (9,10), and soybean (11). In general, these studies showed negative correlations between the levels of C18:1 and C18:2 (as well as C18:3 if present in the seed oil), with the degree of unsaturation decreasing when the crops were grown at higher temperatures.

The period of seed development for spring oilseed rape in western Canada can coincide with high daily temperatures (12). If specialty canola oil is to be marketed on the basis of a specific fatty acid composition, this trait must be stable when the crop is grown across a range of environments. The question of stability of the low-C18:3 trait (under 3%) over environments led to this investigation. Two oilseed rape cultivars, one with the conventional canola fatty acid composition and the other with the low-C18:3 trait, were evaluated at several locations throughout western Canada for 2 yr to determine the effect of environment on the fatty acid composition in mature seed. These two cultivars also were planted at one location in early and late seeding dates for 2 yr, to examine the pattern of fatty acid accumulation during seed development. A controlled-environment study was conducted with different lengths of exposure to high or low temperatures during seed development. The general objective was to determine the effect of ambient temperature during seed development on the fatty acid composition of low-C18:3 oilseed rape.

EXPERIMENTAL PROCEDURES

Effect of environment on fatty acid composition in oilseed rape. Two oilseed rape cultivars, Regent and Stellar, were grown at several locations throughout western Canada in 1990 and 1991.

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TABLE 1
Fatty Acid Content (%) of Cultivars Regent and Stellar over Locations in 1990 and 1991

		C16:0 + C18:0		C18:1		C18:2		C18:3	
Location	Mean temp. (°C)	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Regent 1990:									
Canora	10–20	5.20	0.10	61.57	0.73	20.07	0.52	10.03	0.18
Paddockwood	10–20	5.27	0.09	61.43	0.22	19.33	0.20	10.63	0.27
Tisdale	10–20	5.13	0.07	61.67	0.26	19.70	0.21	10.23	0.33
N. Batt.[a]	10–20	5.10	0.06	62.30	0.21	20.83	0.23	9.07	0.09
Winnipeg	15–25	6.00	0.20	64.40	0.21	19.96	0.27	7.40	0.30
Stellar 1990:									
Canora	10–20	5.80	0.02	60.13	0.18	27.03	0.23	3.70	0.10
Paddockwood	10–20	5.43	0.09	61.53	0.15	25.90	0.15	3.73	0.09
Tisdale	10–20	5.07	0.19	62.20	0.28	25.93	0.19	3.00	0.58
N. Batt.[a]	10–20	5.37	0.15	62.87	0.88	25.70	0.19	2.83	0.03
Winnipeg	15–25	5.76	0.08	63.10	0.64	26.30	0.55	2.40	0.58
Regent 1991:									
Winnipeg	15–25	5.05	0.03	63.50	0.19	19.83	0.10	9.33	0.11
Portage	10–20	5.45	0.03	64.53	0.17	18.93	0.06	8.08	0.23
Denholm	15–25	6.30	0.07	67.83	0.09	16.93	0.05	6.15	0.12
Beatty	15–25	6.85	0.10	61.50	0.17	21.43	0.21	6.75	0.10
Stellar 1991:									
Winnipeg	15–25	5.40	0.04	61.19	0.09	27.50	0.15	2.48	0.05
Portage	10–20	5.25	0.13	65.43	0.51	24.35	0.65	2.68	0.08
Denholm	15–25	6.28	0.03	65.55	0.29	23.05	0.25	2.50	0.04
Beatty	15–25	6.95	0.13	61.88	0.40	24.80	0.51	3.08	0.19

[a]N. Batt. = North Battleford

Regent has the typical fatty acid composition for canola rapeseed, including 8 to 10% C18:3, whereas Stellar is a low-C18:3 cultivar with less than 3% C18:3 in its seed oil. In 1990, the cultivars Regent and Stellar were planted at Canora, Paddockwood, Tisdale, and North Battleford in Saskatchewan and at the University of Manitoba campus in Winnipeg, Manitoba. In 1991, the trials were grown at Denholm and Beatty in Saskatchewan and at Portage la Prairie and Winnipeg in Manitoba. Three and four replicates of each cultivar were planted at each location in 1990 and in 1991, respectively.

A recommended seeding rate of 6 kg ha^{-1} was used, and each plot consisted of six rows, 5 m long with 0.3-m row spacings. The two cultivars were grown in isolation to prevent cross-pollination. Maximal and minimal daily aerial temperatures during seed development were obtained from the Environment Canada weather station closest to each site. Plots were swathed and machine-combined at maturity, determined as Harper-Berkenkamp growth stage 5.5 (HB 5.5) (13), and seed samples were obtained. Oil content was determined by nuclear magnetic resonance (NMR) (14), and fatty acid composition was analyzed by gas chromatography (GC) (15).

Effect of planting date on the fatty acid composition of oilseed rape during seed development. The study was conducted at Winnipeg, Manitoba, for 2 yr with early and late seeding dates each year; 7 May and 27 May in 1990, and 7 May and 21 May in 1991. Within each cultivar, the data were analyzed as a split-plot method with year as main effect, seeding date as subeffect, and harvest date as the sub-subplot. The plots of Regent and Stellar were laid out randomly with six replicates within each cultivar. Each cultivar was grown in isolation to prevent cross-pollination. A recommended seeding rate of 6 kg ha^{-1} was used. Each plot consisted of six rows, 5 m long with 0.3-m row spacings. Maximal, minimal, and average daily aerial temperatures were recorded during the period of seed development (from flowering, HB 4.1, to full maturity, HB 5.5).

Plants in the inner four rows of each plot were tagged at first flower to identify plants at the same physiological stage of development. At 20, 30, 40, and 50 (full maturity) days after flowering (DAF), ~30 plants were harvested from each plot. Seeds were removed from the siliques on the main stems, frozen, and dried. Oilseed content was determined by NMR (14), and fatty acid analysis by GC (15). Fatty acid composition of seed oils was expressed both on a percentage and an absolute basis (16,17).

Controlled environment study of temperature and duration of exposure on fatty acid composition. Seed of the two cultivars, Regent and Stellar, was planted in a controlled-environment growth room. Plants were maintained under growth conditions of 20/15°C day/night ambient temperature with a 16/8 h day/night photoperiod. The level of photosynthetically active radiation, provided by 1/3 Gro-lux wide spectrum VHO

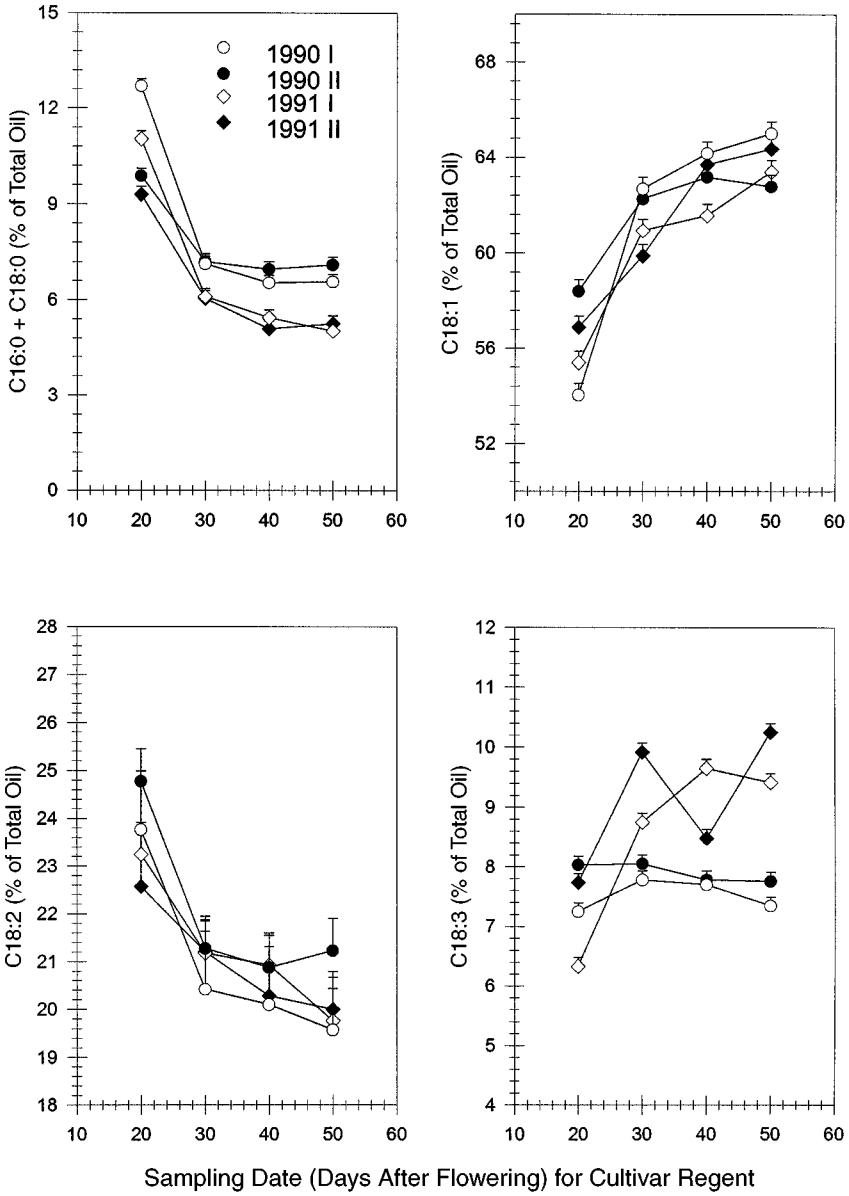

FIG. 1. Patterns of accumulation (%) of the major fatty acids (C16:0 + C18:0, C18:1, C18:2, and C18:3) in the seed oil of the oilseed rape cultivar, Regent, in two seeding dates in both 1990 and 1991.

2/3 cool white VHO, at the top of the plants was 300 $\mu Em^{-2}S^{-1}$ (18). At first flower, 40 plants of each cultivar were selected at the same growth stage; eight plants of each cultivar were designated as controls and were maintained in the 20/15°C growth room until maturity. The remaining 32 plants were moved into growth chambers (1/4 Gro-lux wide spectrum VHO, 3/4 cool white VHO) maintained at one of three temperature treatments (30/25, 25/20, or 15/10°C) with a 16/8 h day/night temperature cycle and photoperiod. After 10, 20, 30, and 40 d duration at each temperature, eight plants of each cultivar were returned to the original growth room (20/15°C) and maintained until maturity. Seeds were harvested from each single plant at maturity (HB 5.5) and analyzed for fatty acid composition by GC. Two runs of each treatment were conducted, and each run was treated as a replicate.

RESULTS AND DISCUSSION

Effect of location on fatty acid composition in oilseed rape. The levels of all major fatty acids (C16:0 + C18:0, C18:1, C18:2, and C18:3) in both cultivars were affected by the location of the trial, with the exception of the level of C18:2 in the seed oil of the cultivar Stellar in 1990 (Table 1).

In 1990, the Winnipeg location had the highest daily mean temperatures during the period of late seed development and yielded seed oil that contained the lowest levels of C18:3 and

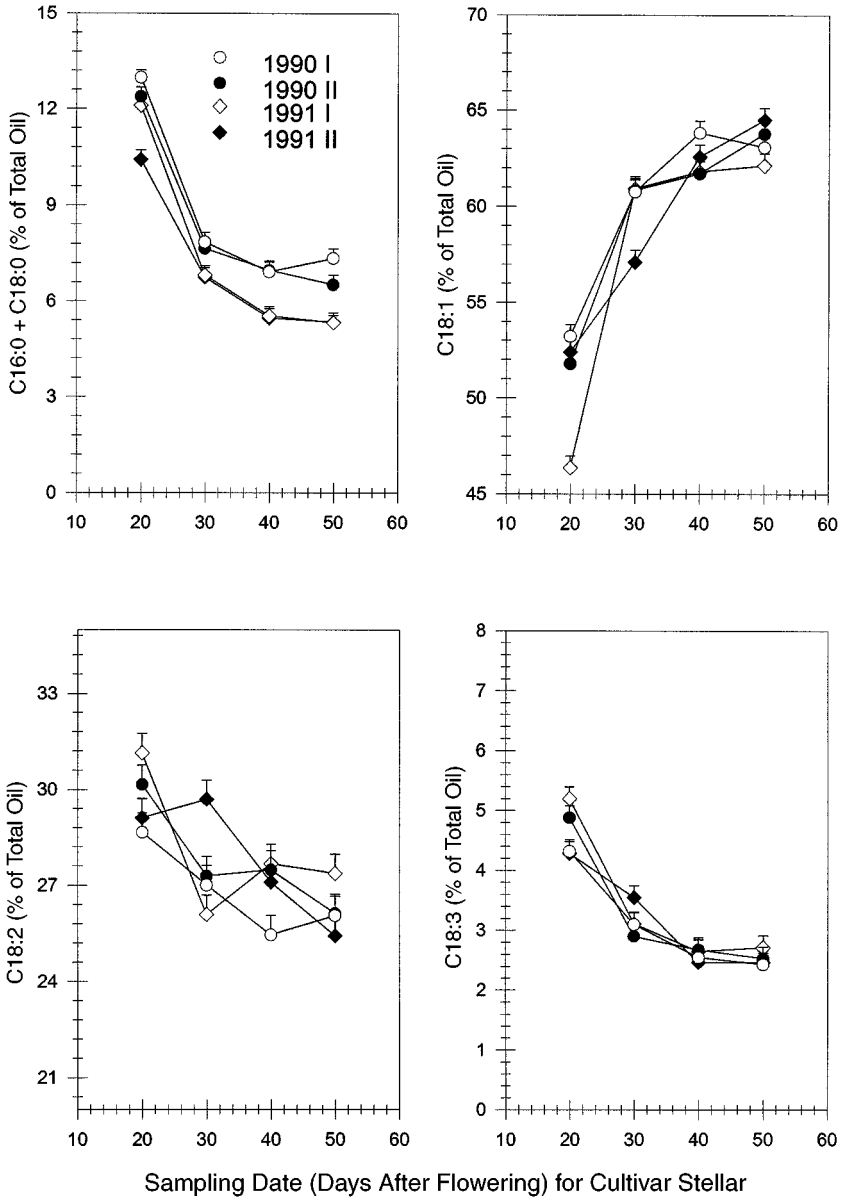

FIG. 2. Patterns of accumulation (%) of the major fatty acids (C16:0 + C18:0, C18:1, C18:2, and C18:3) in the seed oil of the low-linolenic oilseed rape cultivar, Stellar, in two seeding dates in both 1990 and 1991.

the highest levels of C16:0 + C18:0 (Table 1). The same trend was evident in 1991 at Denholm and Beatty, although not at Winnipeg. Levels of C18:1 and C18:2 were more variable; C18:1 levels were higher, and C18:2 levels were lower when the crop was grown at higher temperatures.

A similar observation was made by Cherry *et al.* (19), who found that the fatty acid composition of mature soybean was significantly influenced by the production area. Two soybean lines, selected for low C18:3, produced significantly less C18:1 and more C18:2 when grown in the northern United States compared to further south, and all lines produced more C18:3 and less C16:0 when grown in the north. Our results are generally in agreement with these observations and with reports for other oilseed crops, such as flax (10) and sunflower (14). When seed development occurred during high temperatures, the fatty acid profile was higher in saturated and monounsaturated fatty acids and lower in polyunsaturated fatty acids, compared to seed development under lower temperatures.

There was a considerable range observed for levels of each fatty acid in the seed oil of each cultivar over all locations in both years of the study (Table 1). The C18:3 level of Stellar rose above 3% at two locations, Canora and Paddockwood, in 1990. The ranges of mean daily temperatures at these two locations (10 to 20°C) were not sufficiently lower than at the other locations in 1990 to support temperature during seed development as the cause of the higher C18:3 levels. Pollen

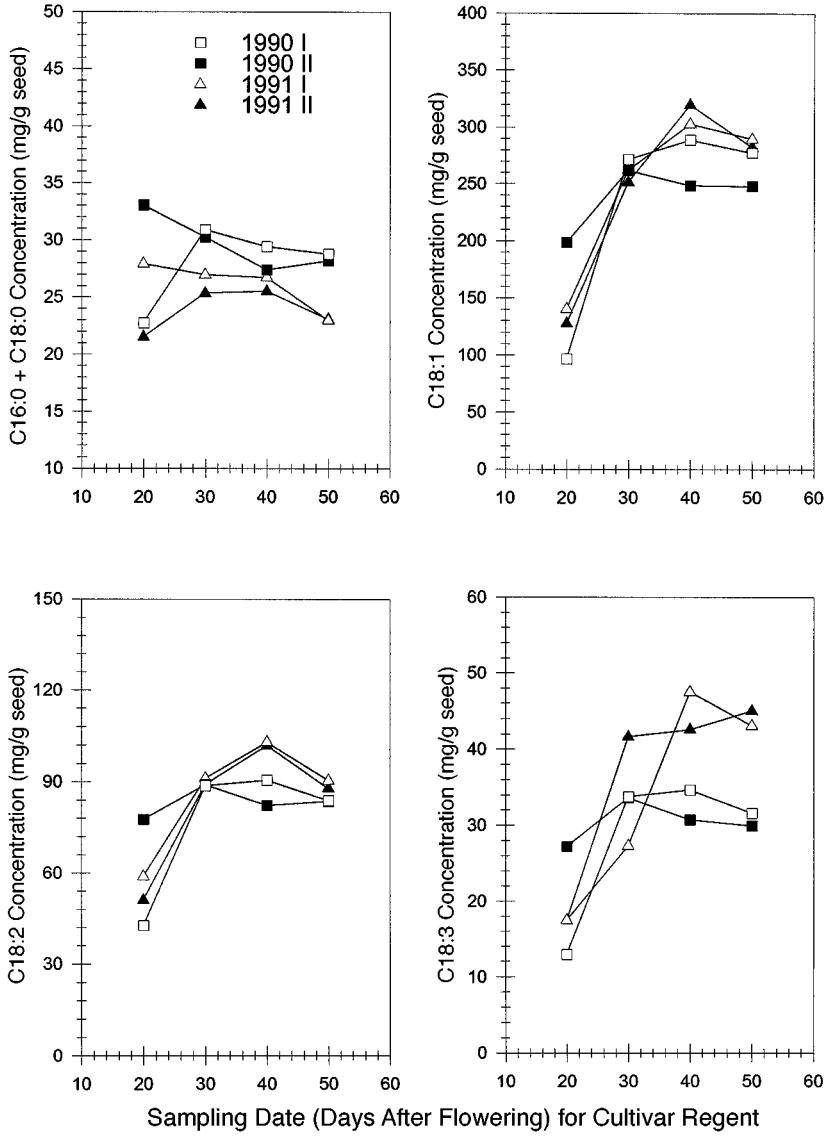

FIG. 3. Patterns of accumulation [mg (g seed)$^{-1}$] of the major fatty acids (C16:0 + C18:0, C18:1, C18:2, and C18:3) in the seed oil of the oilseed rape cultivar, Regent, in two seeding dates in both 1990 and 1991.

contamination from nearby plots of conventional (high-C18:3) canola cultivars may have contributed.

Pattern of fatty acid accumulation of oilseed rape during seed development in the field environment. The pattern of accumulation of each major fatty acid was monitored based on both percentage of total fatty acids in the oil (Figs. 1 and 2) and absolute amounts [fatty acid, mg (g seed)$^{-1}$ = 1 g seed × oil content (%) × % fatty acid] (Figs. 3 and 4) within each cultivar in both early and late seeding dates in 1990 and 1991. Based on a comparison of the maximal, minimal, and mean daily aerial temperatures, the temperature regimes in the early and late seeding dates were similar during the period of seed development in both 1990 and 1991. Therefore, the two seeding dates in both 1990 and 1991 did not provide the desired distinct temperature environments during seed development.

For both cultivars, Regent and Stellar, the relative proportion (%) of C16:0 + C18:0 decreased throughout seed development until ~40 DAF, when the levels stabilized. On an absolute basis, the total amount of saturated fatty acids decreased slightly after an early increase prior to 30 DAF. The relative proportion of C18:1 in the seed oil of both cultivars continued to increase until full maturity at 50 DAF, whereas the absolute amount reached a maximum by 40 DAF and then stabilized. The percentage of C18:2 in the seed oil of both cultivars continued to decrease until full maturity, while the absolute amount reached a maximum at 30 to 40 DAF.

The pattern of C18:3 accumulation was distinct in the two cultivars. For the conventional canola cultivar, Regent, the relative proportion of C18:3 was constant over the period of seed development. For Stellar (the low-C18:3 cultivar), the

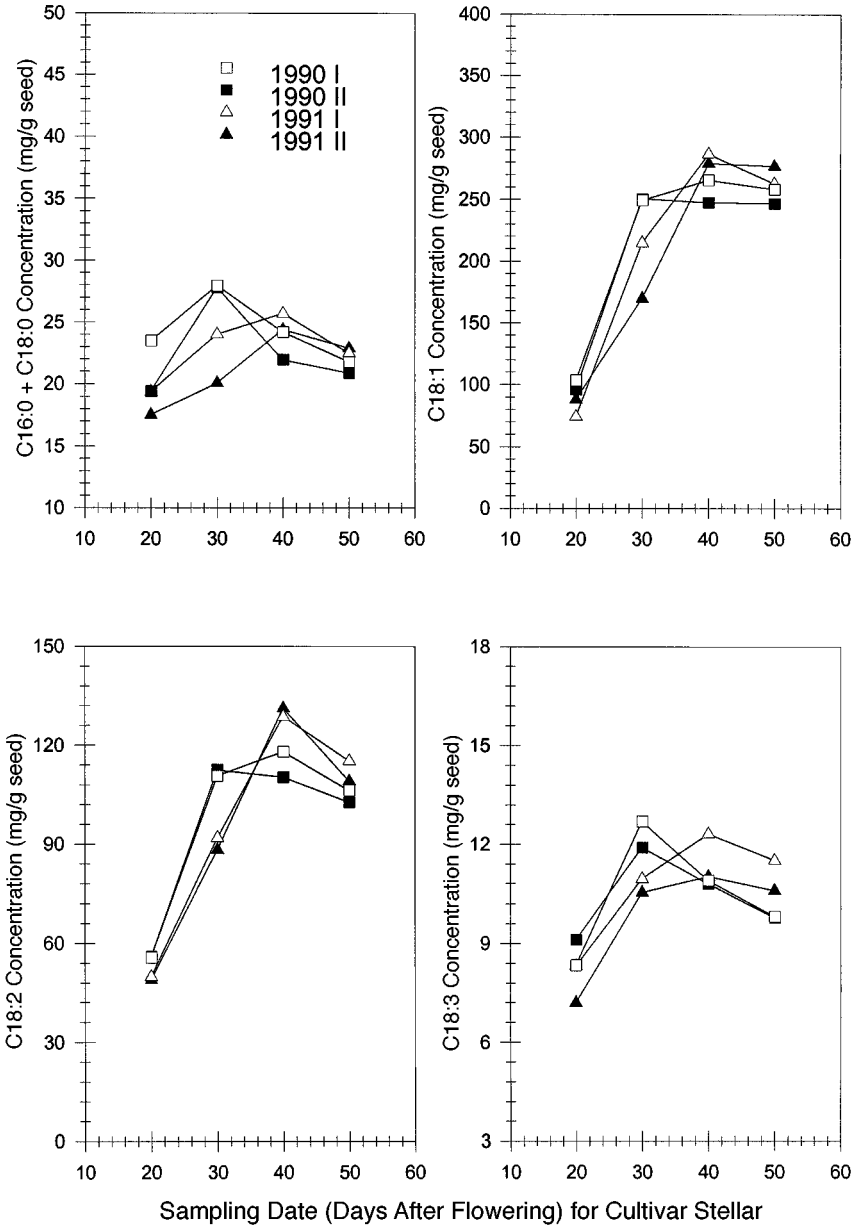

FIG. 4. Patterns of accumulation [mg (g seed)$^{-1}$] of the major fatty acids (C16:0 + C18:0, C18:1, C18:2, and C18:3) in the seed oil of the low-linolenic oilseed rape cultivar, Stellar, in two seeding dates in both 1990 and 1991.

relative proportion of C18:3 decreased until seed maturity at 50 DAF. The absolute amount of C18:3 reached a maximum by 30 to 40 DAF, and then declined until maturity.

In summary, the accumulation of saturated fatty acids C16:0 + C18:0 appeared to occur early in seed development of both cultivars. The apparent desaturation activity increased dramatically in the developing seed from 20 to 40 DAF. These results are in agreement with those of Rakow and McGregor (17), who examined changes in the fatty acid composition of M364, a high-C18:3 line (20%), and M57, a low-C18:3 line (5%), during seed development. The accumulation of the major fatty acids of Stellar is similar to that of M57, and Regent followed a similar pattern to M364. However, there was no decrease in the relative proportion of saturates during seed development in M364 (17).

Pattern of oil accumulation. Oil storage was similar for both cultivars in both seeding dates of each year. The oil concentration (mg g seed^{-1}) rapidly increased between 20 and 30 DAF, then remained relatively constant. The pattern of oil accumulation observed in this study is comparable to the results of Fowler and Downey (20). Their study showed that oil content (mg oil 100 seed^{-1}) increased rapidly between 14 and 21 d after pollination, and then continued to increase at a slower rate until full maturity.

TABLE 2
Comparison of the Final (40 DAF) Fatty Acid Composition of Cultivars Regent and Stellar Under Three Temperature Regimes

	CV Stellar		CV Regent	
Temperature (°C)	C16:0 + C18:0 mean (%)			
15/10	5.96	B[a]	5.92	A
25/20	5.94	B	6.08	A
30/25	6.59	A	5.81	A
	C18:1 mean (%)			
15/10	64.65	A	64.43	AB
25/20	60.98	B	62.52	B
30/25	65.34	A	66.06	A
	C18:2 mean (%)			
15/10	23.66	B	18.16	B
25/20	27.52	A	20.40	A
30/25	22.54	B	19.07	AB
	C18:3 mean (%)			
15/10	3.09	A	8.26	A
25/20	3.10	A	8.43	A
30/25	2.40	B	6.33	B

[a]Means within cultivar between different temperatures that are followed by the same letter are not significantly different at the level of 0.05 of significance, based on Duncan's test. DAF, days after flowering.

TABLE 3
Duncan's Mean Comparison Test Results of the Cultivar Regent and the C16:0 and C18:0 of the Cultivar Stellar Under Five Durations of 0, 10, 20, 30, and 40 DAF of Each Temperature Treatment

Duration (DAF)	30/25°C		25/20°C		15/10°C	
C18:3 for cultivar Regent						
00	8.70	A[a]	9.90	A	6.58	C
10	9.30	A	9.38	AB	7.25	C
20	5.52	BC	8.30	B	7.53	C
30	4.48	CD	7.46	B	9.13	B
40	3.68	D	7.10	B	10.82	A
C16:0 + C18:0 for cultivar Stellar						
00	5.41	C	5.59	A	5.95	A
10	5.77	C	5.79	A	5.68	A
20	6.94	B	6.05	A	5.85	A
30	7.45	A	6.17	A	6.06	A
40	7.39	AB	6.18	A	6.30	A

[a]Means between durations within each temperature treatment that are followed by the same letter are not significantly different at the level of 0.05 significance, based on Duncan's test. For abbreviation see Table 2.

Controlled environment study of temperature and duration of exposure on fatty acid composition. The C18:3 content, as well as the other major fatty acids in the seed oil of Regent and Stellar, showed a significant response to high and low temperatures and to different durations of exposure. For both cultivars, the higher C18:3 content occurred under the lower temperature treatment, whereas the lowest C18:3 content was under the highest temperature treatment (Table 2). This is consistent with results obtained by Tremolieres *et al.* (21). In their study, exposing oilseed rape plants to low temperatures (12 to 17°C) during seed maturation increased C18:1 and C18:2 desaturation, resulting in an increase in polyunsaturate content in the mature seed oil.

Saturated fatty acid levels were not affected by temperature in the conventional cultivar, Regent. However, in the seed oil of Stellar (low-C18:3 cultivar), the highest level of C16:0 + C18:0 occurred when the plants were exposed to the highest temperature (30/25°C) during seed development (Table 2).

Both C18:1 and C18:2 contents in the seed oil of both cultivars responded to temperature treatment. In the cultivar Stellar, the lowest level of C18:1 and the highest level of C18:2 were produced under the intermediate temperature (25/20°C) treatment (Table 2). In Regent, the same trend was apparent, but the magnitude of the differences between temperature treatments was smaller. Green (10) observed that high temperatures during flaxseed development decreased the level of desaturation through reduced levels of C18:2 and C18:3 in the seed oil, accompanied by an increase in saturated and monounsaturated fatty acids.

The only significant effects of the duration of exposure within each treatment were on the C18:3 content of the cultivar Regent and the saturated fat content of Stellar. When plants of the cultivar Regent were exposed to high (30/25°C) or intermediate (25/20°C) temperatures, longer durations of exposure (30 to 40 d) resulted in a lower C18:3 content in the mature seed (Table 3). The C18:3 levels rose with longer exposure to low temperatures (15/10°C).

Under the high-temperature treatment (30/25°C), the C16:0 + C18:0 levels in the seed oil of Stellar were highest with the longest duration of exposure (30 to 40 d) (Table 3). Duration of exposure to low (15/10°C) or intermediate (25/20°C) temperatures had no effect on the level of saturates (Table 3).

In summary, both high and low temperatures and duration of exposure influenced the fatty acid composition of the seed oil of the two cultivars in this study. Saturated and monounsaturated fatty acid levels were higher when seed developed under high temperatures. Intermediate temperatures during seed development resulted in a high C18:2 content. Low temperatures increased the level of polyunsaturates in the seed oil. The effect of temperature on the C18:3 content of Stellar was not so great as on the C18:3 content of Regent.

In the model of the fatty acid desaturation pathway (22), oleic acid (C18:1) is desaturated to linoleic acid (C18:2), which is desaturated to linolenic acid (C18:3). High temperature increased C18:1 and decreased C18:3 content, while hastening seed maturation by 10 to 15 d, compared to low temperatures. A similar pattern of increase in C18:1 and decrease in C18:3 was shown in soybean seed oil under high-temperature treatment of 35/30°C day/night (23). Cheesbrough (24) observed that high temperatures hastened seed maturation, stimulated the biosynthesis of C18:1, and inhibited its desaturation.

The highest level of C18:2 in both cultivars occurred under intermediate temperature, accompanied by high C18:3 and low C18:1. For the conventional cultivar, Regent, this may be due to higher activity of the 18:1 and 18:2 desaturases under intermediate temperatures. The low-C18:3 trait in Stellar may be the result of altered activity of the 18:2 desaturase, resulting in the lower desaturation rate of C18:2 to C18:3 under all temperature conditions. Rakow and McGregor (17) concluded

that the significant differences in C18:1 and C18:3 content in the oil of mature seed of M57 (5% C18:3) and M364 (20% C18:3) were not caused by differences in the length of time during which accumulation occurred but by different rates of accumulation. The shorter duration of seed development under high temperatures would accentuate the differences between cultivars with different rates of accumulation of C18:3.

The low-C18:3 trait in Stellar demonstrated good stability over locations and under the temperature conditions used in this study. This result provides quality assurance to the producers and processors of low-linolenic cultivars developed from this source of the low-linolenic trait.

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