Effect of Female and Male Genotypes and Environment on Wax Composition in Jojoba

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ABSTRACT: The objective of this study was to determine the effects of genotype and environment on wax composition in jojoba seed, and thus be able to control it. Production of waxes with different compositions—and hence changed wax properties such as viscosity, boiling point, and thermal stability—may be of importance for future requirements of the jojoba industry. Wax composition of 23 female clones was determined for two growing seasons. The ratio of FA elongated to the sum of those reduced and esterified differed among genotypes, resulting in differences in the percentage of wax esters longer than 40 or 42 carbons. The clones 'Yarden,' 'Gvati,' 'Hazerim,' 'BGU,' and 'Negev' had higher percentages of long-chain wax moieties than the clones '879-154,' 'MS 55-4,' and 'Forti.' The contribution of the male genotype to wax composition was tested by pollinating bagged female flowers of four female clones with pollen from three male plants. Both male and female genotypes additively influenced the composition of the wax esters. Wax composition varied between growing seasons and locations, but differences between genotypes were consistent. Salinity of the irrigation water did affect wax composition in some clones. Under high salinity, the salt-sensitive clone '64' produced a smaller percentage of long-chain wax esters, whereas in clone 'Q-106' wax composition did not change. In clone '874-154' the chain lengths of the wax moieties in the seeds increased under medium salinity. We conclude that jojoba wax composition is influenced by both female and male genotypes and by environmental factors such as climate and salinity.

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KEY WORDS: Jojoba, salinity, *Simmondsia chinensis*, wax composition, wax moieties.

Jojoba [*Simmondsia chinensis* (Link) Schneider] is a dioecious wind-pollinated shrub native to the Sonoran desert (1). It accumulates a unique storage-lipid wax in its seeds consisting of long-chain esters of monounsaturated FA and alcohols (mostly 20-, 22-, and 24-carbon chain length). This wax, commonly known as jojoba oil (2), is synthesized during seed development (3–5). Its final composition is a result of activities and affinities of the following three main enzymes: a fatty acyl-CoA elongase (β-ketoacyl-CoA synthase), which produces 20:1, 22:1, and 24:1 acyl CoA as precursors to the wax; fatty alcohol reductases (acyl CoA reductases); and acyl:alcohol transacylase (6).

The liquid wax, the most valuable of the products obtained from jojoba, is mainly used in the cosmetics industry. The wax content of the seed can affect profitability, whereas the composition of the wax affects its quality and suitability for different applications. Chain length influences properties such as viscosity and melting point, and it is predicted that in the future a range of waxes having different chain lengths, and hence a range of properties suitable for different applications, needs to be available to industry.

The content of wax in the mature seed is about 48–58% (7–9). Wax content may fluctuate for the same clones in response to climatic conditions (10). Clarke and Yermanos (11) showed considerable variability in wax content and composition in a collection of more than a thousand jojoba plants from the wild. Yermanos and Duncan (7) found variability in wax composition with time, and Dunstone *et al.* (10) demonstrated that temperatures prevailing at the time of wax synthesis affect the chain lengths of the FA and fatty alcohols. High temperatures during seed filling lowered the specificity for elongation of 20:1 and 22:1 acyl-CoA and increased their specificity for reduction to fatty alcohols.

Wax composition in jojoba is highly variable, as in other species such as almond (*Prunus amygdalus*) and walnut (*Juglans regia* L.) (12). Because there is extensive genotypic variation in jojoba and because wax is produced in the developing cotyledons of the embryo, it is expected that in addition to environmental effects, both female and male genes may contribute to the final wax composition. The objective of this study was to evaluate genotype and environmental effects on seed wax composition in jojoba.

EXPERIMENTAL PROCEDURES

Plant material. Seeds for the different experiments were harvested from three experimental plots: (i) A clonal test plot (containing 30 clones) was planted in May 1992 at Kibbutz Hazerim (Northern Negev, Israel) (8). (ii) Three commercial clones, '64,' 'Q-106,' and '879-154,' were planted in June 1991 at Ramat Negev (RN) Experimental Station (Negev Highlands, Israel). Plants at this plantation were subjected to

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salinity of 1.1, 3.2, or 6.2 dS/m in the irrigation water (13). (iii) A plot at Ramat Negev was planted in 1995.

Wax composition. About 20 seeds were crushed, and a sample was pressed with a manual screw press directly onto a stock of four disks of filter paper (2 cm in diameter). The upper and lower disks were discarded. One disk was subjected to ethanolysis, as described by Tonnet *et al.* (14), and the other was placed in petroleum ether and used for direct determination of wax components. The compositions of the ethanolysis products and of the intact wax esters were determined by GC [FID detector, CP9001 (Chrompack, Middleburg, The Netherlands) with a 10 m × 0.25 mm CP-Sil-5-CB (OVI) column].

Calculation of specificities. Calculation of composite specificity for the monounsaturated acyls was performed as described by Pollard *et al.* (15) and by Dunstone *et al.* (10). The method assumes that any acyl may be subjected to one of three competing reactions: chain elongation, reduction, or esterification.

Pollen collection and storage. Pollen grains were collected from three males at the Hazerim plantation by removing male inflorescences with dehiscent anthers and transferring them to a pollen room (23–25°C and 35–45% RH), where they were spread over white paper. Pollen shed overnight was cleaned from flower parts by passing it through a 100-µm mesh sieve. The pollen was stored in a desiccator at –18°C until further use.

Pollen germinability. Pollen attached to the tip of a glass rod was inoculated into each of six micro-wells, each containing 0.2 mL of germinating medium [containing 15% (w/w) sucrose, 160 mg/L boric acid, and 240 mg/L calcium nitrate tetrahydrate], and incubated for 20–24 h under room conditions (23–25°C and 35–45% RH). Germination was determined under a light microscope for 100 grains in each of the six wells. Pollen grains were considered to have germinated when the pollen tube was at least as long as the diameter of the pollen grain.

The effect of female genotypes. Seeds from 23 female genotypes on the Hazerim plantation and seven genotypes on the Ramat Negev plantation (wind-pollinated by the local population) were analyzed during several seasons.

The effect of male and female genotypes. Four female clones ('879-154,' 'Q-106,' 'Forti', and 'Hazerim') growing in the clonal test plot in Hazerim were used. Four branches (each with 5–15 closed flower buds) on five females of each clone were bagged in paper bags fitted with a transparent plastic window. Each of three bagged branches was pollinated with pollen from a different male. The fourth branch was not pollinated and was kept as a control. The latter step was performed twice to ensure that all pollinated flowers reached anthesis. Pollen was injected into the bags with a syringe without opening them.

RESULTS AND DISCUSSION

Effect of female genotype. Female genotypes differed in the proportion of long-chain wax moieties and of FA and alcohols longer than 20 carbons (Fig. 1, Table 1). The clones 'MS 82-18,' 'Yarden,' 'BGU,' 'Q-104,' and 'Rev XX' had a high percentage of long-chain wax moieties (70–76%), whereas the clones '879-154,' 'MS 55-4,' and 'Forti' had a smaller proportion of long-chain wax moieties (~58%). These differences in wax composition between genotypes resulted from differences in the ratio of elongated to reduced or esterified fatty acyl CoA (Fig. 2). A linear correlation was found between specificity (the ratio of 20:1 acyl CoA elongated chains to reduced or esterified chains) and the proportion of long-chain wax moieties in the wax esters (Fig. 2). The crucial role played by the condensing enzyme in the elongation of FA has previously been shown for *Arabidopsis* (16,17). In the latter, expression of the enzyme controls the amount of very long

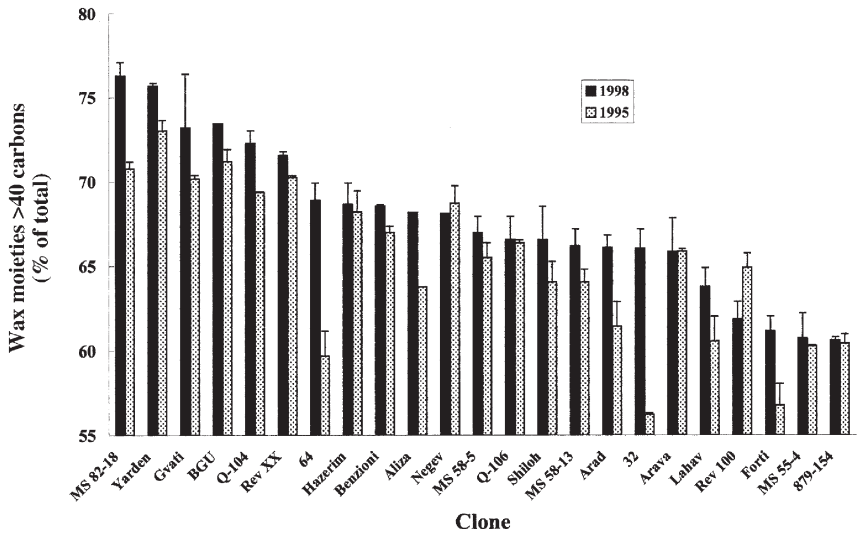

FIG. 1. Percentage of wax moieties >40 carbons in seeds from 23 jojoba female genotypes growing in the clonal test plot in Hazerim (Northern Negev, Israel). Wax composition of the seeds was determined in 1995 and 1998 (3 and 8 yr from planting, respectively). Values are means ± SEM of two extractions and two GC measurements each.

TABLE 1
Percentage of Wax Moieties with 38–46 Carbons in Jojoba Wax Obtained from the Seeds of Four Female Clones[a]

Female clone	Male clone	Wax moieties with 38–46 carbons (% of total)					
		38	40	42	44	46	>40
879-154	29	5.28^{b,*}	30.17^{b}	52.57^{b}	9.73^{b}	0.90^{a,b}	63.20^{b}
	25	6.75^{a}	33.20^{c}	49.82^{a}	8.47^{a}	0.71^{a}	59.01^{a}
	26	6.43^{a}	27.99^{a}	52.93^{b}	9.89^{b}	1.10^{b}	63.92^{b}
	Mean male	6.15^{b,**}	30.45^{c}	51.77^{a}	9.36^{b}	0.91^{a}	62.04^{a}
Forti	29	5.23^{b}	26.49^{a}	54.28^{b}	11.11^{b}	1.50^{a}	66.89^{b}
	25	7.35^{a}	29.86^{b}	50.70^{a}	9.09^{a}	1.08^{b}	60.87^{a}
	26	4.71^{b}	25.47^{a}	54.87^{b}	11.45^{b}	1.32^{a}	67.62^{b}
	Mean male	5.76^{a,b,**}	27.27^{b}	53.29^{b}	10.54^{b}	1.30^{b}	65.13^{b}
Hazerim	29	5.97^{a}	27.60^{b}	52.87^{a}	10.51^{a}	1.27^{a}	64.65^{a}
	25	5.67^{a}	27.48^{b}	51.93^{a}	11.14^{a}	1.81^{a}	65.00^{a}
	26	4.66^{b}	23.59^{a}	54.93^{b}	13.26^{b}	1.85^{a}	69.55^{b}
	Mean male	5.43^{a,**}	26.22^{a}	53.24^{b}	11.64^{c}	1.65^{b}	66.53^{b,c}
Q-106	29	5.99^{a}	26.63^{b}	53.97^{a}	10.93^{a}	1.22^{a}	66.12^{a}
	25	5.57^{a}	26.88^{b}	54.17^{a}	10.91^{a}	1.32^{a,b}	66.40^{a}
	26	4.85^{b}	22.79^{a}	56.59^{b}	12.90^{b}	1.59^{b}	71.07^{b}
	Mean male	5.47^{a,**}	25.44^{a}	54.91^{c}	11.58^{c}	1.38^{b}	67.86^{c}
	29	5.62	27.72	53.42	10.57	1.22	65.21^{b}
Mean female	25	6.34	29.36	51.66	9.90	1.23	62.94^{a}
	26	5.16	24.96	54.83	11.87	1.46	68.04^{c}

[a]Each clone was pollinated with pollen from one of three male clones. The differences were calculated separately for each female clone. *Values within a female clone or column followed by different letters are different at the 0.05 level according to the Scheffé LSD test. **Values of averages for a female clone in the same column followed by different letters are different at the 0.05 level according to the Scheffé LSD test.

chain FA. In jojoba, acyl CoA serve as substrates for three different reactions; thus, the affinity of the acyl moiety for the condensing enzyme will eventually affect the wax composition (10).

Effect of male and female genotype. Pollen from each of three male plants was used to fertilize flowers of four female genotypes. The resulting seeds differed significantly in wax composition (Table 1). Female flowers pollinated with male '25' pollen produced seeds that had a higher proportion of short-chain fatty acids and alcohols compared with the two other pollen sources used (Table 2). Seeds resulting from pollination with the pollen from male '26' had the highest proportion of long-chain fatty acids and alcohols, and those produced after pollination with pollen from male '29' had intermediate values (Table 2). The effect of the male and female parents on wax composition seems to be additive. The highest proportion of long-chain wax moieties, 71%, occurred in seeds obtained by fertilization of the female clone 'Q-106' by male clone '26' (Table 1). Those seeds also had the highest specificity ratio of elongation vs. reduction plus esterification, ~0.77 (Fig. 3). The smallest proportion, ~59%, and the lowest specificity ratio, 0.52, were found in clone '879-154' pollinated with pollen from clone '25' (Table 1, Fig. 3). The effect of both female and male clones on wax composition was highly significant. The interaction between them was less significant (Table 3). Female and male clones also had a significant effect on the percentage of long alcohol and acid moieties. No interaction between female and male clones in this respect was found (Table 4).

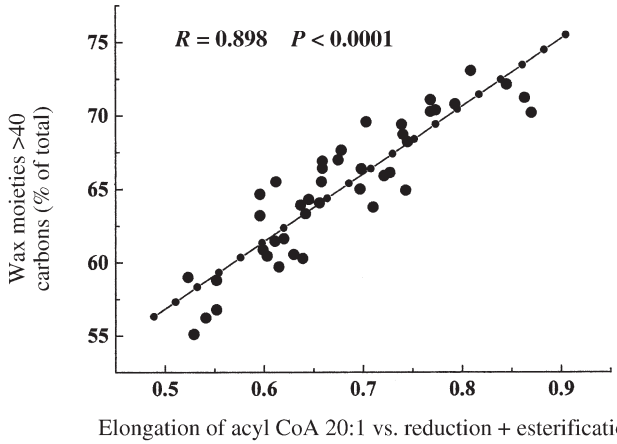

FIG. 2. Relationship between the percentage of wax moieties >40 carbons and the ratio of elongation to reduction plus esterification (specificity). All data are from wax determinations in the Hazerim clonal test plot.

TABLE 2
Percentage of Monounsaturated Alcohols and Acids with Lengths of 18–24 Carbons in Jojoba Wax from Seeds of Four Female Clones[a]

Female clone	Male clone	Monounsaturated acids and alcohols (% of total) 18:1 Alcohol	18:1 acid	20:1 Alcohol	20:1 acid	22:1 Alcohol	22:1 acid	24:1 Alcohol	24:1 acid	Alcohols + acids >20
879-154	29	0.15^{a,*}	3.94^{a}	20.51^{a}	38.63^{a}	23.05^{b}	7.82^{a}	4.78^{a,b}	0.69^{a}	36.35^{b}
	25	0.54^{b}	4.77^{b}	22.57^{b}	38.44^{a}	21.63^{a}	7.67^{a}	3.99^{a}	0.43^{a}	33.73^{a}
	26	0.53^{b}	4.35^{a,b}	19.71^{a}	37.25^{a}	23.18^{b}	8.74^{b}	6.05^{b}	0.42^{a}	38.39^{b}
	Mean male	0.41	4.35	20.93	38.11	22.62	8.08	4.94	0.51	36.15^{a,**}
Forti	29	0.58^{a}	4.69^{a,b}	19.05^{a}	36.80^{a}	23.90^{a}	8.68^{b}	5.05^{b}	0.62^{a}	38.25^{a}
	25	0.55^{a}	5.30^{b}	20.81^{b}	36.75^{a}	23.57^{a}	8.03^{a}	4.05^{a}	0.61^{a}	36.26^{b}
	26	0.55^{a}	4.14^{a}	18.45^{a}	37.24^{a}	24.51^{a}	8.39^{a,b}	5.48^{b}	0.76^{a}	39.15^{a,b}
	Mean male	0.56	4.71	19.43	36.92	24.0	8.37	4.86	0.66	37.88^{b}
Hazerim	29	0.52^{a}	5.07^{a}	20.1^{a,b}	37.83^{a}	23.2^{a,b}	8.37^{a}	4.82^{a,b}	0.72^{a}	37.13^{a}
	25	0.54^{a}	5.07^{a}	20.34^{b}	36.92^{a}	22.97^{a}	8.31^{a}	4.56^{a}	0.83^{a}	36.68^{b}
	26	0.59^{a}	4.41^{a}	17.96^{a}	36.64^{a}	24.11^{b}	9.06^{b}	5.92^{b}	0.91^{a}	40.00^{b}
	Mean male	0.55	4.85	19.45	37.13	23.43	8.58	5.10	0.82	37.94^{b}
Q-106	29	0.49^{a}	4.11^{a}	18.29^{b}	35.86^{a}	23.49^{a}	9.33^{b}	6.52^{a}	1.38^{a}	40.72^{a}
	25	0.52^{a}	5.03^{b}	19.82^{c}	35.81^{a}	22.97^{a}	8.21^{a}	6.04^{a}	0.75^{a}	37.98^{b}
	26	0.36^{a}	4.29^{a}	17.36^{a}	35.47^{a}	24.72^{a}	9.65^{b}	6.62^{a}	1.15^{a}	42.13^{b}
	Mean male	0.46	4.48	18.49	35.71	23.72	9.07	6.39	1.10	40.28^{c}
Average female	29	0.44	4.46	19.47	37.28	23.41	8.55	5.29	0.85	38.11^{b}
	25	0.54	5.04	20.89	37.00	22.79	8.06	4.66	0.66	36.16^{a}
	26	0.51	4.30	18.37	36.65	24.13	8.96	6.02	0.81	39.92^{c}

[a]Each clone was pollinated with pollen from three male clones. The differences were calculated separately for each female clone. *Values within a female clone and column followed by different letters are different at the 0.05 level according to the Scheffé LSD test. **Values of averages for a female clone in the same column followed by different letters are different at the 0.05 level according to the Scheffé LSD test.

An effect of genotype on oil composition has been observed in many genotypes, and long-chain FA varied between 22 and 35% (w/w) of the total seed FA content (18). *Crambe abyssinica* genotypes differ in the percentage of erucic acid (19). Almond genotypes differ in the concentration and in the composition of oil; the main difference found was in the ratio of oleic to linoleic acid (20,21). Walnut genotypes were found to differ in PUFA composition (12).

Differences between growing season. The wax composition of seeds changed from one growing season to another. In 1995 the proportion of long-chain wax esters was somewhat smaller than that in 1998 for most clones, with the difference being more marked for the clones '32,' '64,' and 'Forti' (Fig. 1). In 1998, during the main period of fruit filling (May and June), minimum temperatures were cooler compared to 1995 (Fig. 4). The cooler temperatures during this period may have enabled synthesis of longer wax moieties (10). Further studies are required to determine whether the differences in wax composition did indeed stem from the small differences in minimum temperature.

Effect of location. Wax composition of identical genotypes growing in Hazerim and Ramat Negev, two locations having different climatic conditions, was different. For the seeds harvested from Ramat Negev, the proportion of long-chain wax esters was significantly smaller both in 1995 and in 1998 (Table 5). It has previously been shown that wax composition is related to mean maximum temperatures at the time of fruit filling (10), but for the period of our study the mean maximum temperatures were quite similar at the two sites (Fig. 4). Another factor that could account for the difference is the limited selection of male genotypes at Ramat Negev.

Effect of salinity. Salinity did not affect seed wax content (13), but it did influence wax composition in some genotypes

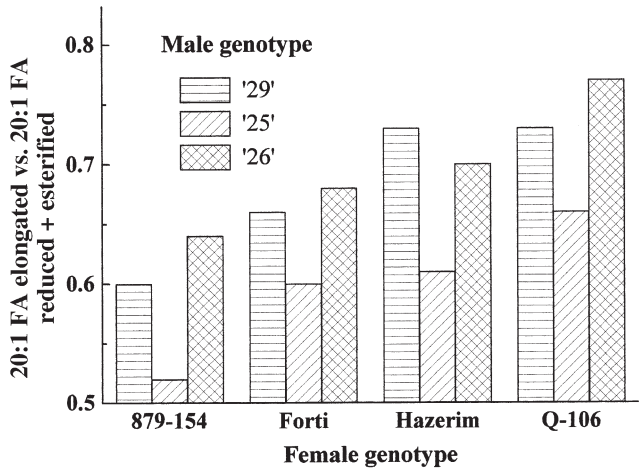

FIG. 3. Effects of male and female genotypes on the specificity of the wax elongation ratio. Values for calculating ratios were from two extractions and two GC determinations of each extraction. Between 15 and 20 dry seeds were used for each extraction.

TABLE 3
ANOVA for Wax Moieties[a]

		Wax <40		Wax 44		Wax 42		Wax 40	
	df	*F*-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Female clone	3	20.66	0.0001	24.20	0.0001	13.80	0.0001	60.73	0.0001
Male clone	2	28.73	0.0001	27.91	0.0001	25.12	0.0001	82.15	0.0001
Male·female	6	3.40	0.0142	3.47	0.0131	2.53	0.0486	3.62	0.0106

[a]See Table 1 for raw data.

TABLE 4
ANOVA for Monounsaturated Alcohols and Acids[a]

		<20:1 Alcohol + acid		24:1 Alcohol		22:1 Acid		22:1 Alcohol	
	df	*F*-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Female clone	3	25.79	0.0001	6.36	0.0025	7.75	0.0009	5.87	0.0037
Male clone	2	42.32	0.0001	7.52	0.0029	12.27	0.0002	10.08	0.0007
Male·female	6	0.83	0.5592	0.53	0.7792	1.81	0.1394	0.60	0.7274

[a]See Table 2 for raw data.

TABLE 5
Wax Composition in the Growing Areas of Hazerim (Northern Negev, Israel) and Ramat Negev (Negev Highland, Israel)[a]

	Wax esters of 42–46 carbons (% of total)			
	1995		1998	
Clone	Hazerim	Ramat Negev	Hazerim	Ramat Negev
64	59.69 ± 1.48	53.88 ± 0.78	63.88 ± 0.52	60.94 ± 2.23
Q-106	66.37 ± 0.20	61.74 ± 0.62	65.18 ± 1.88	62.73 ± 0.22
879-154	60.43 ± 0.54	47.22 ± 0.29	60.43 ± 0.05	55.77 ± 0.40
Forti	ND[b]	ND	60.61 ± 1.13	60.62 ± 1.32
Benzioni	ND	ND	68.37 ± 0.28	58.71 ± 0.96
BGU	ND	ND	70.63 ± 0.21	67.98 ± 0.10
Mean	62.16	57.46	66.55	61.13
P (*T* = *t*, one-tailed)	0.0086		0.0048	

[a]Pollination was by heterogenous male population in the plantation.
[b]ND, not determined.

TABLE 6
Effect of Salinity on the Percentage of FA and Alcohols >20:1 and on the Percentage of Wax Chains >40 Carbons (% of total) in Three Clones[a]

EC (dS/m) of irrigation water	FA and alcohols >20 carbons (% of total)				Waxes >40 carbons (% of total)			
	64	Q-106	879-154	Mean	64	Q-106	879-154	Mean
1.1	34.1 ± 1.5	35.6 ± 0.9	29.0 ± 0.7	32.9	58.0 ± 1.2	62.4 ± 0.5	53.4 ± 0.4	57.9
3.5	30.7 ± 0.6	35.7 ± 0.7	33.3 ± 0.6	33.2	54.7 ± 0.9	62.5 ± 1.2	58.2 ± 1.0	58.5
6.3	28.6 ± 1.0	35.5 ± 0.5	30.0 ± 0.4	31.4	54.2 ± 0.6	63.9 ± 0.9	55.3 ± 1.6	56.5

[a]Pollination was by the heterogenous male population on the plantation. Values are means of three repetitions per season and three seasons ± SEM.

(Table 6). In the salt-sensitive clone '64,' the percentages of long-chain wax moieties and long-chain fatty acids and alcohols fell in response to increased salinity, whereas no changes were recorded in wax from the clone 'Q-106' in response to salinity. In the medium-salinity treatment, the chain lengths of wax moieties increased in clone '874-154.' In another experiment with clones 'Forti,' 'BGU,' and 'Benzioni' over two seasons, no significant effect of salinity on wax content and composition was found (Benzioni, A., and Y. Vaknin, unpublished data).

In other oil-producing species, environmental conditions appear to exert their main effect on the degree of unsaturation (19). In the almond, for example, the oil content and composition were found to be both genotype and environment

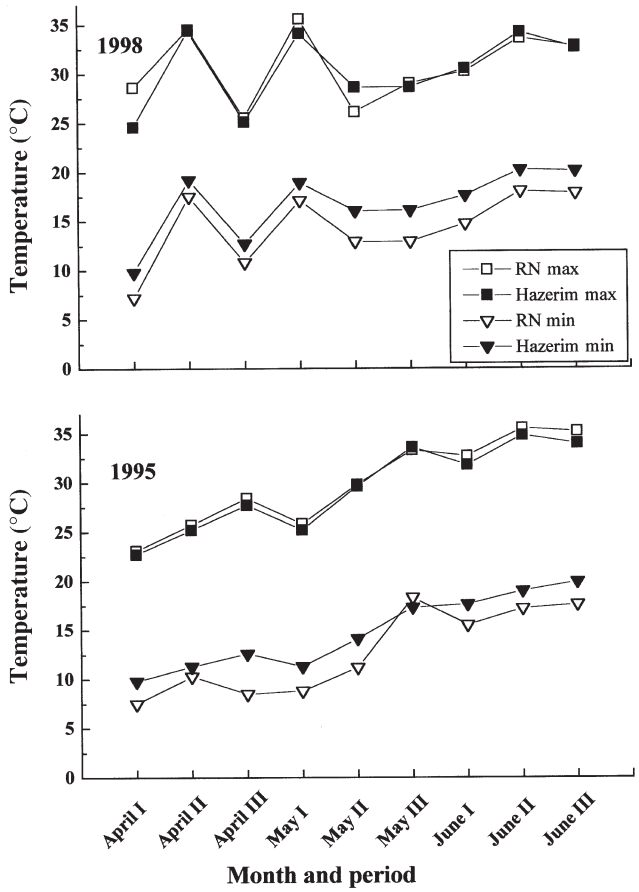

FIG. 4. Minimum and maximum temperatures in Hazerim (Northern Negev, Israel) and Ramat Negev (RN) (Negev Highlands, Israel) during the time of fruit filling in 1995 and 1998. (I, first 10 days, II, days 11–20; III, day 21 to the end of the month.)

dependent (20,21). The oil composition of almonds was reported to vary between seasons, as was found here. The differences in wax composition among various jojoba clones are dependent on genetic factors as well as on environmental conditions such as temperature and salinity. The differences in wax composition may affect wax properties such as viscosity, boiling point, and thermal stability, factors that may be of importance in meeting the future requirements of the jojoba wax industry.

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