
Volume 52, Part B, January 2014 ISSN 1161-0301
ELSEVIER
EUROPEAN JOURNAL OF
AGRONOMY
A Global Agronomy Journal
The Official Journal of the European Society for Agronomy
ESA

Europ. J. Agronomy 52 (2014) 237–246

Contents lists available at ScienceDirect

European Journal of Agronomy

journal homepage: www.elsevier.com/locate/eja

Contrasting patterns of fatty acid composition and oil accumulation during fruit growth in several olive varieties and locations in a non-Mediterranean region

Déborah P. Rondanini*, Diego N. Castro, Peter S. Searles, M. Cecilia Rousseaux

Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja (CRILAR-CONICET), Entre Ríos y Mendoza s/n, Anillaco 5301, La Rioja, Argentina[1]

ARTICLE INFO

Article history:
Received 31 January 2013
Received in revised form 22 August 2013
Accepted 4 September 2013

Keywords:
Fatty acid
Fruit growth
Olea europaea L.
Oil concentration
Temperature
Virgin olive oil

ABSTRACT

Olive growing has expanded considerably in the last few decades outside of the Mediterranean Basin to non-traditional regions in the Southern Hemisphere. When growing olive genotypes (i.e., varieties) outside of their area of origin, the importance of environmental factors such as temperature and genotype × environment interactions in determining olive oil production and oil quality has been suggested. In several Mediterranean varieties and one South American variety, we assessed the dynamics of fruit growth and oil accumulation along with the evolution of fatty acid composition at multiple locations over two growing seasons. Oleic acid content (%), the principal fatty acid present in olive oil, showed four contrasting patterns during fruit growth when modeled against thermal time from flowering using linear and bilinear regressions: (1) a sharp linear decrease for the varieties 'Arauco' and 'Arbequina'; (2) a plateau followed by a late linear decrease of moderate slope for 'Barnea' and 'Manzanilla Fina'; (3) a slow linear decrease for 'Frantoio'; and (4) no decrease in 'Coratina'. Linoleic acid (%) showed linear increases in 'Arauco' and 'Arbequina' that appear to be inversely related to the decreases in oleic acid, while bilinear patterns were found for many other varieties. Both the rates of fruit growth and of oil accumulation were more important in determining maximum fruit dry weight and oil concentration (%), respectively, than duration when expressed on a thermal time basis. Temperature during oil synthesis was negatively related to final oil concentration. Experiments under controlled conditions would greatly contribute to our understanding of how fruit growth as well as oil quantity and quality are influenced by environmental factors.

1. Introduction

Olive oil production in modern, intensively managed orchards is becoming increasingly important in the Southern Hemisphere (Grigg, 2001; Vossen, 2007). Non-traditional growing regions around the world use varieties from the Mediterranean Basin, but the olive oil quality obtained can be quite different from that of the Mediterranean (Mailer, 2005; Ceci and Carelli, 2010). Thus, a possible interaction between genotype and environment that modifies olive oil composition has been suggested for many of these regions (e.g., Mannina et al., 2001; Torres et al., 2009).

One of the aspects of olive oil quality that seems to be most affected by the environment is fatty acid composition. Low percentages of oleic acid (<55%) along with high palmitic acid (>16%) and linoleic acid (>21%) are common characteristics of the fatty acid profiles of some Mediterranean Basin varieties when grown in the northern regions of Argentina or Australia (Ravetti, 1999; Mailer et al., 2010; Rondanini et al., 2011). However, low values of oleic acid, the dominant unsaturated fatty acid in olive oil, do not allow for the potential human health benefits of olive oil to be fully achieved (Covas et al., 2006). The decrease in oleic acid along the south-to-north latitudinal gradient is somewhat surprising given that temperature is increasing along this gradient in the Southern Hemisphere, and given that annual oilseed crops such as sunflower show an increase in oleic acid with temperature (Lajara et al., 1990; Izquierdo et al., 2002; Sobrino et al., 2003; Rondanini et al., 2003). In addition, seasonal temperature during the oil accumulation period in olive can negatively correlate with oleic acid (%) at harvest (Rondanini et al., 2011).

Several studies from the Mediterranean Basin have observed that oleic acid remains fairly constant or shows a slight increase during fruit ripening, while saturated fatty acids such as palmitic may decrease (Poiana and Mincione, 2004; Anastasopoulos et al.,

---

* Corresponding author at: Cátedra de Cerealicultura, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, 1417 DSE, Buenos Aires, Argentina. Tel.: +54 11 4524 8053; fax: +54 11 4524 8053.
E-mail address: rondanin@agro.uba.ar (D.P. Rondanini).

[1] Tel.: +54 3827 494251; fax: +54 3827 494231.

1161-0301/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.eja.2013.09.002

2011). Such a pattern occurs in many Spanish genotypes (Uceda and Hermoso, 2001) although alternative patterns including a "V shape" for oleic acid have been reported for traditional Spanish varieties (Gómez-González et al., 2011). In contrast, an early study from central-western Argentina observed a drop in oleic acid and a rise in linoleic acid during olive fruit maturation in the variety 'Arbequina' (Cattaneo and Karman de Sutton, 1959). A similar pattern has been found for the variety 'Souri' in Israel (Dag et al., 2011).

In addition to oil quality, an indicator of oil quantity should be considered for non-traditional growing regions. Final oil concentration in olive fruit (principally in the fleshy mesocarp) is a direct consequence of the rate of oil synthesis and the duration of the oil accumulation period (Trentacoste et al., 2012). Similarly to fatty acid composition, both rate and duration of oil synthesis are controlled by several factors including genotype, environment, and their interaction. Genotypic differences in fruit growth and oil synthesis capacity have been identified at different levels of organization from crop to fruit tissue (Lavee and Wodner, 2004; Trentacoste et al., 2010; Hammami et al., 2011). During fruit ripening, there are changes in skin and flesh colors that serve as visual indicators of changes in chemical composition as oil accumulates and water is lost in the fruit (Beltrán et al., 2004). Alternatively to ripening index, thermal time (i.e., calendar time weighted by temperature) is a useful developmental index in fruit trees, as in other crops, that allows locations and seasons differing in temperatures to be compared (DeJong and Goudriaan, 1989; Pérez-López et al., 2008; Trentacoste et al., 2012).

Combining an analysis of both oil concentration and fatty acid composition for several well-known olive varieties grown in multiple locations would help to better understand the dynamics of oil accumulation and composition in a perennial oil fruit crop that ostensibly differs from oilseed crops in some environmental responses. Thus, the specific objectives of this study were to: (1) evaluate the dynamics of fruit growth and oil concentration and (2) determine the evolution of fatty acid composition in six olive varieties growing at three locations over two consecutive growing seasons. Variety, location, and growing season were considered as main factors, and the developmental time needed to maximize oil concentration and maintain fatty acid composition within industry standards was also taken into account.

2. Materials and methods

2.1. Experimental sites

Six varieties ('Arauco', 'Arbequina', 'Barnea', 'Coratina', 'Frantoio', and 'Manzanilla Fina') were evaluated in the valleys of Aimogasta (800 m above sea level, masl) and La Rioja (420 masl) during the 2006–2007 and 2007–2008 growing seasons in northwestern Argentina (Table 1). All of these varieties are frequently grown in the Mediterranean Basin with the exception of 'Arauco', which is considered to be unique to Argentina. The Aimogasta and La Rioja Valleys are separated by the Sierras de Velasco mountain range (4000 masl) and a distance of 100 km. In the second growing season, the valley of Chilecito (850 masl), lying 80 km to the west of the other two valleys at the base of the Sierra de Famatina (6000 masl) was incorporated into the study. Two to three commercial farms in each valley were employed (eight in total) with many varieties being sampled in multiple farms per valley. Within a farm, three orchards (i.e., experimental plots, $n = 3$) of a given variety were selected, and 6 trees were sampled per plot. The plots were monovarietal except for a farm in Chilecito that had rows of three different varieties within the same plot. The trees were 8–11 years-old with planting densities of 300–500 trees per hectare. Annual rainfall is scarce in the three locations (Table 1) so drip irrigation (1000–1200 mm per year) was applied to supplement rainfall. Potential evapotranspiration for this region has been estimated to be 1600 mm per year with a crop coefficient of about 0.7 (Correa-Tedesco et al., 2010). Adequate fertilization via the irrigation system or as solid-organic compost was applied. Chemical control of pests and diseases was also common.

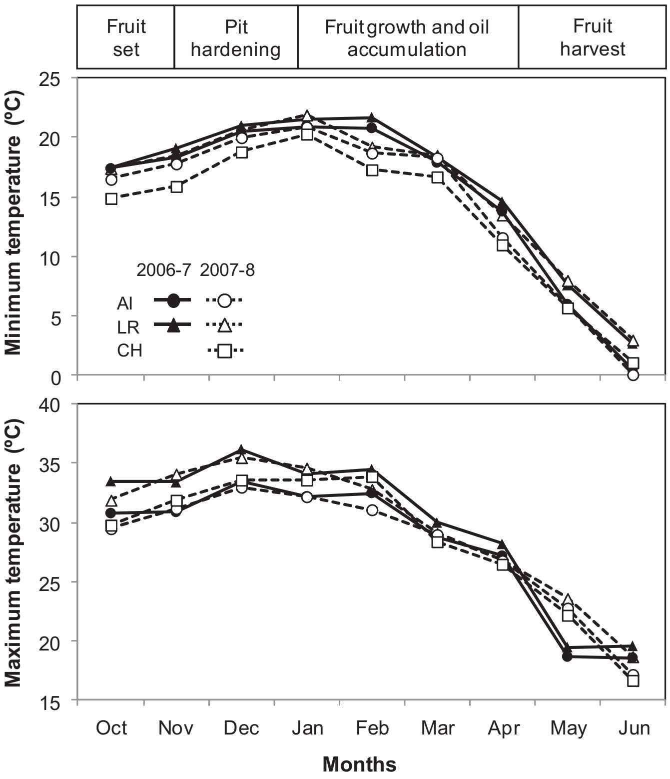

Fig. 1. Dynamics of minimum and maximum monthly temperatures during olive fruit growth in the valleys of Aimogasta (AI), La Rioja (LR), and Chilecito (CH) for two growing seasons (2006–2007 and 2007–2008). The phenological stages shown are representative for most of the olive oil varieties in the region.

2.2. Temperature conditions

Minimum and maximum monthly temperatures showed a slight increase from October to December during fruit set and pit hardening, and an acute decrease (3.5 °C per month) from February to June during the principal fruit growth and oil accumulation phase and fruit harvest (Fig. 1). In the 2006–2007 and 2007–2008 growing seasons, overall minimum values were similar with the exception of February and April when the 2007–2008 temperatures were somewhat lower than 2006–2007. The minimum temperature values varied among locations with the highest elevation location (Chilecito, 850 masl) exhibiting the lowest values (average of 13.5 °C between October and June) and the lowest elevation location (La Rioja, 420 masl) the highest values (average of 16 °C). La Rioja exhibited higher maximum temperatures than the other locations, especially from October to December during flowering, fruit set and pit hardening. From January to April (fruit growth and oil accumulation), La Rioja was only slightly warmer (average of 31.3 °C) than Chilecito (30.6 °C) and Aimogasta (30.2 °C).

2.3. Fruit growth

A total of 1 kg of fresh fruit was collected monthly from 6 trees per plot from November to June to evaluate fruit growth dynamics over the entire growing season. Each sample included fruit from all

Table 1
Characteristics of the locations in La Rioja (Northwest Argentina) included in this study.

Location	Latitude (South)	Longitude (West)	Elevation (m)	Soil texture	Climate	Annual rainfall (mm)	Historical temperature[a] (°C)	
							January	June
Aimogasta (AI)	28° 34′	66° 46′	800	Fine sand	Desert	104	27.1	11.9
La Rioja (LR)	29° 33′	66° 49′	420	Sandy-silt	Arid Chaco	415	28.0	12.9
Chilecito (CH)	29° 38′	67° 24′	850	Coarse sand	Desert	164	25.8	10.0

[a] Average mean temperature and total annual rainfall from the last 20 years.

four cardinal directions of each tree at a height of 1.5 m and both internally and externally positioned fruit were collected. The fresh weight of 100 sampled fruit was determined using an analytical balance and the fruit were dried at 60 °C in an oven until reaching a constant weight before re-weighing to obtain individual fruit dry weight. The fruit maturity index (MI) was calculated for each sample based on a color evaluation of the skin and flesh (Uceda and Hermoso, 2001).

In order to compare different years and locations, fruit growth was expressed as a function of thermal time (°Cd) from the respective date of flowering of each variety, location and year. Flowering occurred about two weeks later in 2007–2008 (October 12–25) than in 2006–2007 (September 29–October 13) in all varieties, and was earlier in La Rioja (the warmest location), than in Aimogasta and Chilecito. Daily average temperature was calculated for the thermal time estimations using daily maximum and minimum temperature records [$(T_{\min} + T_{\max})/2$] from meteorological stations at individual farms or from the National Meteorological Service of Argentina. Since little information is available for the temperature responses of olive fruits to temperature (Pérez-López et al., 2008), different base (5–8 °C) and upper limit (30 and 35 °C) temperatures were compared preliminarily to obtain the best relationships with fruit growth and other variables. These comparisons indicated that a lower base temperature limit of 5 °C was most appropriate, similar to Trentacoste et al. (2012). Thus, thermal time was not accumulated for days with average daily temperature below 5 °C. An upper temperature limit of 35 °C was also set.

Crop load (g fresh fruit per cm^2 trunk cross-sectional area) was approximated at final harvest using the entire orchard production divided by the number of trees in the orchard and approximate trunk diameter values. However, specific yield data for the six sampled trees used for fruit growth and other parameters was not determined. Crop load was generally intermediate or high in all varieties with the exception of 'Frantoio'. The values by variety ranged from: 'Arauco' (50–79 g cm^{-2}), 'Arbequina' (55–169), 'Frantoio' (4–26), 'Manzanilla fina' (37–219), 'Coratina' (134–215), 'Barnea' (58–264 g cm^{-2}).

2.4. Oil concentration and fatty acid composition

Whole fruit (50 g) were ground in a hammer mill and the resulting paste was dried overnight in an oven at 60 °C until reaching constant weight. The dried samples were cooled for 30 min in a desiccator and then re-weighed. Fruit oil concentration was determined by grinding the dry fruit samples to a fine meal and extracting 10 g of the meal with 150 ml hexane for 6 h in a Soxhlet apparatus (IUPAC Method 1.122). Oil concentration was then expressed as the percentage of fruit dry weight (i.e., % oil on a dry basis). The fatty acid composition of the oils was determined by gas–liquid chromatography. Fatty acid methyl esters were prepared by cold transmethylation in a basic medium (IOOC, 2001) and were separated in a HP 5890 II gas chromatograph (Hewlett-Packard, Sacramento, CA) fitted with a 25-m capillary column (CP-Wax 52 CB, Chrompack, Holland) that had a 0.32 mm I.D. and 0.25 μm film thickness. The chromatograph was equipped with split injection and a FID detector. Hydrogen was the carrier gas, and injector and detector temperatures were set to 250 and 300 °C, respectively. Oven temperature was programmed at 180 °C for 5 min, increased from 180 to 240 °C at 4 °C min^{-1}, and then was set at 240 °C for 10 min. Individual fatty acids (myristic, palmitic, palmitoleic, heptadecanoic, heptadecenoic, stearic, oleic, linoleic, linolenic, arachidic, arachidonic, behenic and lignoceric acids) were determined by comparison with retention times of known standards (AOCS-1, Sigma–Aldrich, St. Louis, MO) and expressed as percentage of the total.

2.5. Statistical analysis

For the individual varieties, the nonlinear routine of GraphPad Prism (GraphPad Inc., California) was used to fit bilinear broken stick functions with an unknown break point to obtain relationships between thermal time and fruit dry weight or oil parameters. The conditional model fitted was $y = a + bx$ for $x \leq c$ and $y = a + bc$ for $x > c$; where y was the fruit weight or oil concentration, x was thermal time from flowering, a was the intercept, b the slope of the linear section (rate of oil accumulation), and c was the unknown break point (i.e., the timing of maximum oil concentration). The significance of these parameters was determined by t-tests ($P < 0.05$). When a plateau could not be fitted ($P > 0.05$), simple linear regression was fitted to the data with the slope as the growth rate. The determination of bilinear functions for fatty acids was performed only during the period of linear fruit growth when the metabolism of fatty acid synthesis was active.

Differences between varieties, locations, and growing seasons in fruit dry weight and oil concentration were assessed using an ANOVA factorial arrangement of 4 varieties ('Arauco', 'Arbequina', 'Frantoio', and 'Manzanilla Fina') by 2 locations (Aimogasta, and La Rioja) for both growing seasons (2006–2007 and 2007–2008). Separate analyses were also employed for each growing season because one variety ('Coratina') and one location (Chilecito) was added in the second growing season. A sixth variety 'Barnea' was only evaluated in La Rioja and Chilecito. Means were separated by Tukey's tests ($P < 0.05$).

Linear regression models were fitted to the relationships between oil concentration and several variables such as rate and duration of oil accumulation, fruit dry weight, and temperature during oil synthesis (minimum, maximum and mean).

3. Results

3.1. Olive fruit growth and maturity index

The dynamics of individual fruit growth were described as a function of thermal time from flowering using linear or bilinear regressions (Fig. 2), which allowed for the identification of growth rate (slope) and the timing of physiological maturity (breaking point) at which maximum fruit dry weight was achieved. All varieties exhibited linear rates, ranging from 0.01 to 0.10 g per 100 °Cd. until fruit growth ceased at breaking points ranging from 2600 to 4500 °Cd from flowering. These two parameters varied among olive

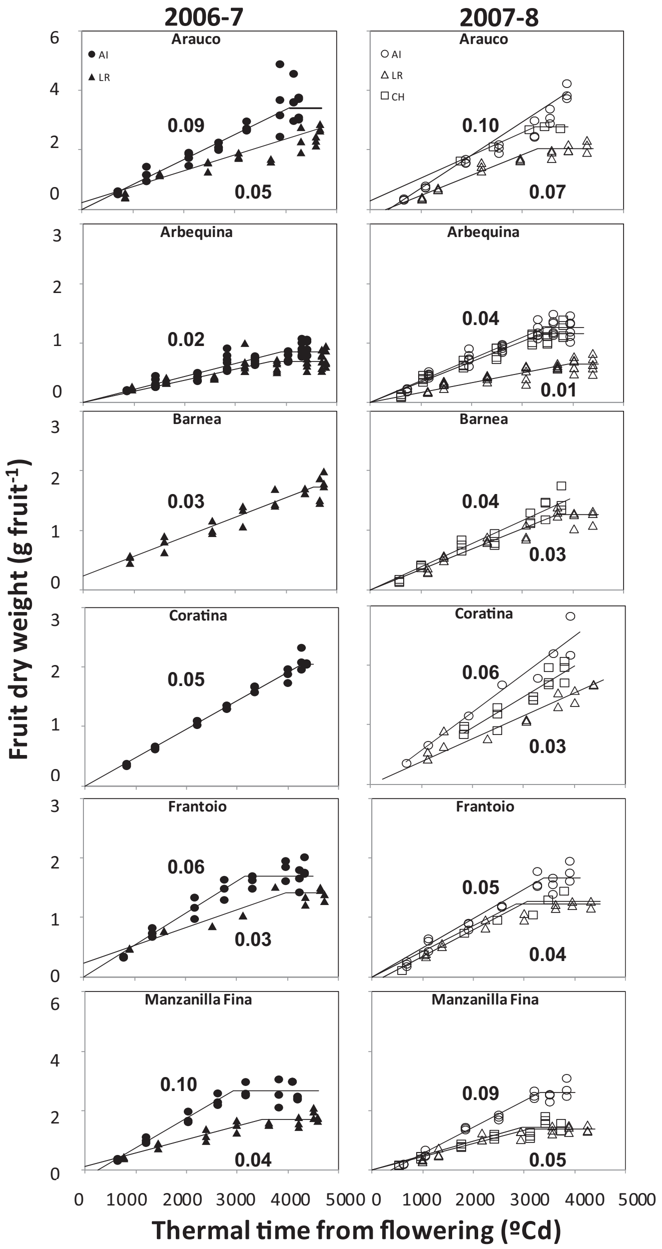

Fig. 2. Dynamics of individual fruit dry weight as a function of thermal time (°Cd from flowering) in six olive varieties during two growing seasons (2006–2007 and 2007–2008) in Aimogasta (AI), La Rioja (LR), and Chilecito (CH). Note the different scales on the fruit weight axis. Fitted linear or bilinear regressions are shown with numbers near the regression lines indicating maximum and minimum slopes (g per 100 °Cd) for the different locations.

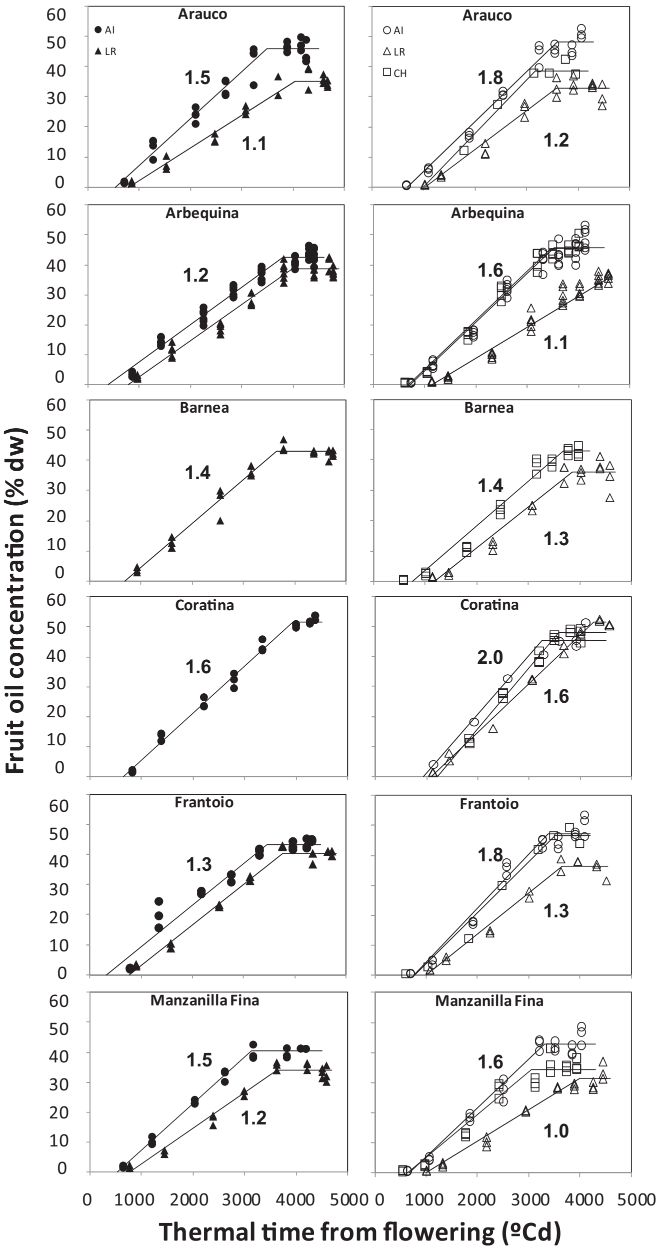

Fig. 3. Dynamics of fruit oil concentration (% dry weight basis) as a function of thermal time (°Cd from flowering) in six olive varieties during two growing seasons (2006–2007 and 2007–2008) in Aimogasta (AI), La Rioja (LR), and Chilecito (CH). Fitted bilinear regressions are shown with numbers near the regression lines indicating maximum and minimum slopes (oil% per 100 °Cd) for the different locations.

varieties, locations, and growing seasons with a coefficient of variation of 47% for fruit growth rate and 15% for growth duration. No significant relationship was found between rate and duration of fruit growth ($R^2 = 0.10$, $P = 0.10$).

The table olive varieties 'Arauco' (>3 g) and 'Manzanilla Fina' (>2.5 g) reached the highest fruit dry weights, while 'Arbequina', an oil variety, had the lowest values (≤1 g) (Table 2). In addition to varietal differences, a location effect was observed for fruit weight over the two growing seasons with their being larger fruits in the higher elevation valley of Aimogasta (800 masl) than in the lower elevation valley of La Rioja (420 masl). Location explained 58 and 89% of fruit weight in 2006–2007 and 2007–2008, respectively, in four varieties ('Arauco', 'Arbequina', 'Frantoio', 'Manzanilla Fina') for these two valleys. A location × growing season interaction was also significant for 'Arauco' and 'Arbequina', explaining 17 and 20% of total variation, respectively. Differences between growing seasons in the fruit weight were generally significant, but only explained 2–13% of total variation. In the second growing season (2007–2008) when all three locations including Chilecito were evaluated, significant effects of variety, location, and variety × location were observed, which explained 61, 24 and 10% of total variation in fruit weight, respectively.

In some instances, the maturity index (MI) at maximum fruit dry weight was significantly different between varieties, locations, and years (Table 2). For example, the MI was lower at the La Rioja and Chilecito locations than in Aimogasta for some varieties during the second growing season (Table 2). Maturity index and final fruit dry weight were not significantly related under our growing

Table 2
Maximum fruit dry weight and maturity index in six olive varieties during two growing seasons (2006–2007 and 2007–2008) in Aimogasta (AI), La Rioja (LR) and Chilecito (CH).

Variety	Year	Location	Maximum fruit dry weight (g fruit^{-1})[a]	Maturity index at maximum fruit dry weight[a]
Arauco	2006–2007	AI	3.41 ± 0.22 a	4.7 ± 0.12 a
		LR	2.75 ± 0.06 b	3.4 ± 0.22 a
	2007–2008	AI	3.95 ± 0.15 a	3.4 ± 0.12 a
		LR	2.04 ± 0.07 c	1.6 ± 0.10 b
		CH	2.77 ± 0.02 b	2.4 ± 0.88 ab
Arbequina	2006–2007	AI	0.85 ± 0.05 a	2.7 ± 0.16 a
		LR	0.69 ± 0.05 a	3.9 ± 0.16 a
	2007–2008	AI	1.26 ± 0.06 a	4.2 ± 0.27 a
		LR	0.65 ± 0.04 b	2.6 ± 0.12 b
		CH	1.16 ± 0.05 ab	3.9 ± 0.01 ab
Frantoio	2006–2007	AI	1.84 ± 0.06 a	3.8 ± 0.06 a
		LR	1.41 ± 0.04 a	3.3 ± 0.11 a
	2007–2008	AI	1.66 ± 0.07 a	3.8 ± 0.01 a
		LR	1.22 ± 0.02 a	2.8 ± 0.01 a
		CH	1.27 ± 0.10 a	2.6 ± 0.06 a
Manzanilla Fina	2006–2007	AI	2.66 ± 0.12 a	4.4 ± 0.15 a
		LR	1.70 ± 0.07 b	3.7 ± 0.11 a
	2007–2008	AI	2.61 ± 0.11 a	4.7 ± 0.05 a
		LR	1.39 ± 0.11 b	1.8 ± 0.50 b
		CH	1.43 ± 0.10 b	1.4 ± 0.31 b
Coratina	2006–2007	AI	2.05 ± 0.01 –	2.9 ± 0.10 –
	2007–2008	AI	2.51 ± 0.26 a	4.2 ± 0.01 a
		LR	1.68 ± 0.05 b	3.6 ± 0.01 a
		CH	1.92 ± 0.10 b	2.2 ± 0.01 b
Barnea	2006–2007	LR	1.73 ± 0.08 –	5.0 ± 0.08 –
	2007–2008	LR	1.26 ± 0.04 a	2.0 ± 0.01 a
		CH	1.52 ± 0.08 a	2.9 ± 0.01 a

[a] Values are mean ± SE and different letters indicate significant differences ($P < 0.05$) between locations within the same year.

conditions ($P = 0.13$). Crop load may have had some modest effect on fruit weight and maturity although crop load values were generally intermediate to high. Approximate analyses indicated low R^2 values (0.1–0.2) between crop load and these variables under our conditions.

3.2. *Oil concentration*

The course of fruit oil concentration (% dry weight basis) may be described as a function of thermal time from flowering using bilinear regressions (Fig. 3). Oil synthesis began 300–1200 °Cd after flowering (late spring), and oil accumulation rate (slope) ranged 1–2 oil percentage points per 100 °Cd. The maximum oil concentration was reached at 2900–4600 °Cd (break point). A significant negative association was observed between oil accumulation rate and duration ($R^2 = 0.41$, $P < 0.0003$; data not shown). In 2006–2007, all the varieties showed higher final concentrations in Aimogasta (800 masl) than in the warmer La Rioja valley (420 masl) with the greatest difference occurring in the variety ‘Arauco’ (46 versus 35% oil) and the lowest in ‘Frantoio’ (43 versus 40% oil). In 2007–2008, La Rioja also had the lowest oil concentrations in most varieties, Chilecito was often intermediate, and Aimogasta had the highest values (Fig. 3). The variety ‘Coratina’ was an exception with similar oil concentration being found for all three locations.

Over both growing seasons, analysis of variance for oil concentration at the most contrasting locations, Aimogasta and La Rioja, showed a significant three-way interaction between variety, location, and growing season ($P < 0.0001$). A separate analysis for 2006–2007 indicated that location and variety accounted for 60 and 20% of the variability, respectively, although a location × variety interaction (15%) did occur. In 2007–2008 when all three locations were evaluated, the interaction between location × variety was also significant ($P < 0.0001$) and accounted for 28% of the variation.

When combining all of the data, maximum individual fruit dry weight was strongly related to fruit growth rate ($R^2 = 0.79$; $P < 0.0001$) but not to fruit growth duration ($P = 0.54$; data not shown). Similarly, maximum oil concentration was linearly related to oil accumulation rate ($R^2 = 0.43$, $P = 0.0002$) but not to oil accumulation duration ($P = 0.69$; Fig. 4). Final oil concentration was negatively associated with the mean daily temperature averaged over the entire oil accumulation period, so that oil concentration dropped 3% per each °C increase (Fig. 4). The negative effects of temperature were also evident when using minimum ($R^2 = 0.26$; $P = 0.0056$) or maximum ($R^2 = 0.50$; $P < 0.0001$) daily temperature.

3.3. *Main fatty acids*

Oleic acid was the most important unsaturated fatty acid in the oil of all varieties. All varieties began with a similar initial value of ca. 70% oleic acid, but ended with different final oleic values (Fig. 5). Linear or bilinear models were fitted to each variety, and four contrasting patterns of oleic acid dynamics during ripening were observed: (1) a sharp linear decrease for ‘Arauco’ and ‘Arbequina’; (2) a long plateau followed by a late linear decrease of moderate slope for ‘Barnea’ and ‘Manzanilla Fina’; (3) a slow linear decrease for ‘Frantoio’; and (4) no decrease in ‘Coratina’ (Fig. 5). The main difference among these varietal patterns was the thermal time at which oleic acid started to fall ($P = 0.01$). Differences in slope between varieties were also of some importance ($P = 0.06$) with significant differences between locations being observed in ‘Arbequina’ in 2007–2008 and ‘Frantoio’ in 2006–2007 with Aimogasta having the highest negative slope, and La Rioja the lowest (Table 3). All varieties were well below the upper limit of 83% oleic acid proposed by the International Olive Oil Council (IOOC) as a measure of genuine olive oil, while ‘Arbequina’ and ‘Arauco’ fell below the lower limit of 55% due to the sharp linear decrease in oleic acid content.

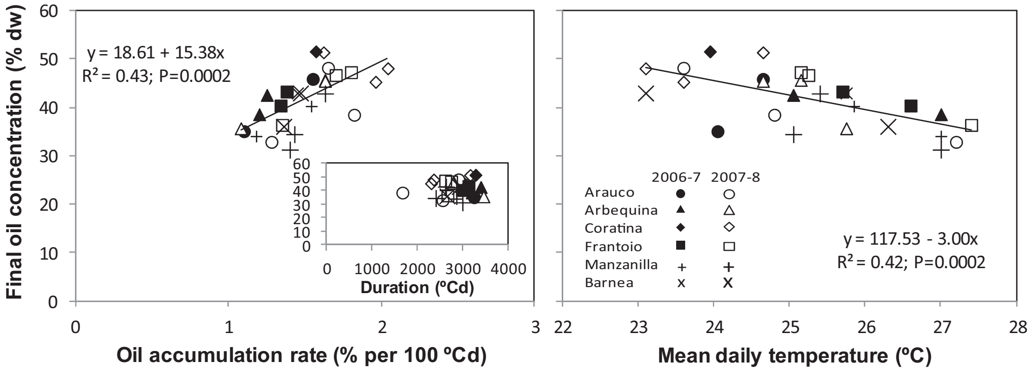

Fig. 4. Relationships between maximum fruit oil concentration and oil accumulation rate (left panel), and mean daily temperature during the period of oil accumulation (right panel) in six olive varieties during two growing seasons (2006–2007 and 2007–2008). Fitted linear regressions are included. The insert shows oil concentration duration.

The percentage of linoleic acid, the second most abundant unsaturated acid, was also fit with thermal time from flowering using linear or bilinear regressions (Fig. 6). All of the varieties started the active fruit growth period with low values (<10%), but showed different patterns of accumulation with thermal time. In 'Arauco', 'Arbequina', and 'Frantoio', linoleic acid increased linearly over the entire period of oil synthesis. This increase appears to be inversely related to the linear decrease in oleic acid in these varieties. In contrast, linoleic acid was adjusted to a bilinear pattern with a pronounced late increase in 'Manzanilla Fina' and 'Barnea'. In 'Coratina', only slight increases in linolenic acid occurred with the exception of Aimogasta in 2007–2008. At the end of the season, linoleic acid in 'Arbequina' and 'Arauco' largely exceeded the upper limit recognized by the IOOC (21%) in most locations and growing seasons

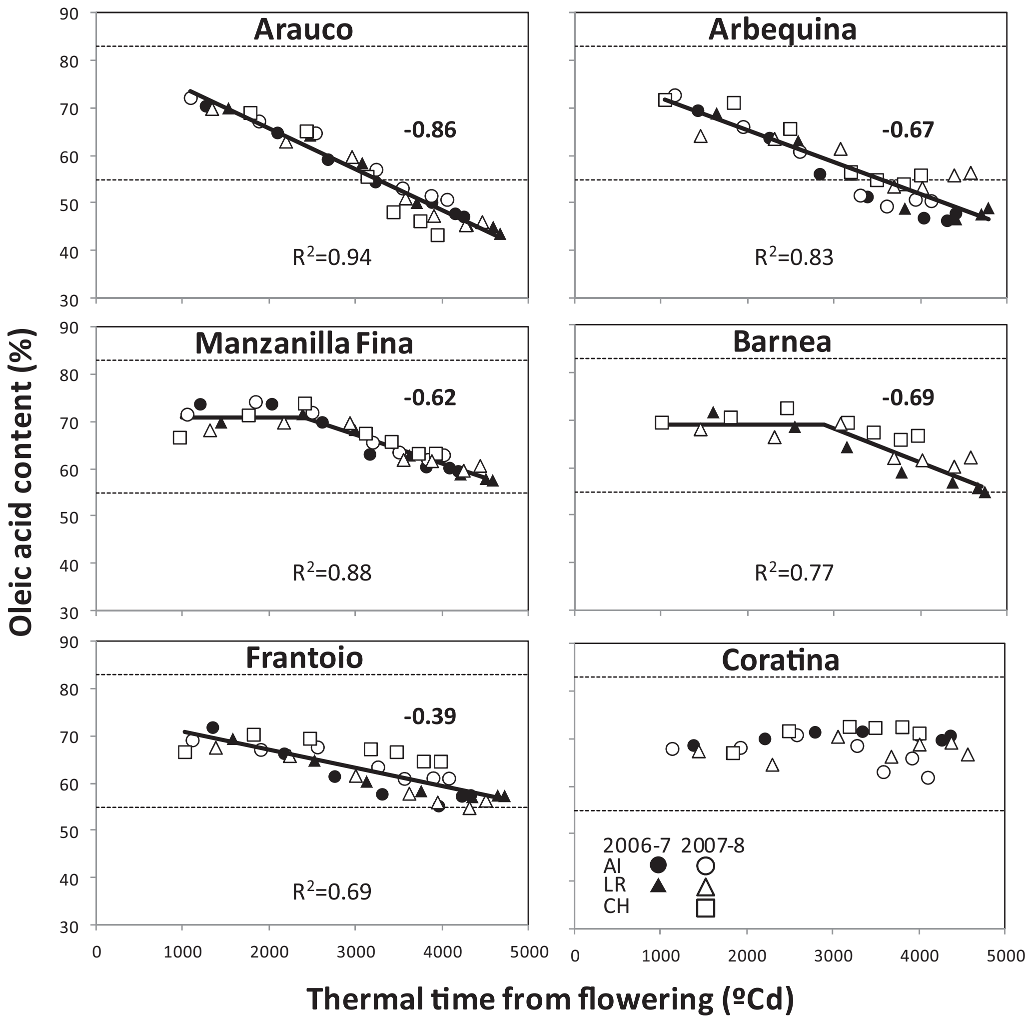

Fig. 5. Dynamics of oleic acid content in the oil (% of total fatty acids) of six olive varieties during two growing seasons (2006–2007 and 2007–2008) in Aimogasta (AI), La Rioja (LR) and Chilecito (CH). Solid lines are linear or bilinear regressions fitted to the data from all three locations. Numbers near the regression lines indicate the descending slopes (% oleic acid per 100 °Cd). Dotted horizontal lines are limits of oleic content (55–83%) for virgin olive oil according to the International Olive Oil Council (IOOC).

Table 3

The slope of oleic acid content versus thermal time for the linear and bilinear relationships in six olive varieties during two growing seasons (2006–2007 and 2007–2008) in Aimogasta (AI), La Rioja (LR) and Chilecito (CH). Coefficients of determination (R^2) for the fitted functions are also shown.

Variety	Growing season	Location	R^2	Slope[a] (% per 100 °Cd)
Arauco	2006–2007	AI	0.99	−0.79 ± 0.018 a
		LR	0.98	−0.93 ± 0.066 a
	2007–2008	AI	0.97	−0.77 ± 0.076 a
		LR	0.95	−0.86 ± 0.130 a
		CH	0.97	−0.82 ± 0.254 a
Arbequina	2006–2007	AI	0.98	−0.90 ± 0.059 a
		LR	0.97	−0.86 ± 0.116 a
	2007–2008	AI	0.99	−0.97 ± 0.064 a
		LR	0.83	−0.47 ± 0.130 b
		CH	0.97	−0.94 ± 0.150 a
Frantoio	2006–2007	AI	0.99	−0.73 ± 0.022 a
		LR	0.96	−0.46 ± 0.052 b
	2007–2008	AI	0.83	−0.31 ± 0.087 a
		LR	0.97	−0.47 ± 0.077 a
		CH	0.96	−0.35 ± 0.078 a
Manzanilla Fina	2006–2007	AI	0.96	−0.79 ± 0.080 a
		LR	0.99	−0.68 ± 0.067 a
	2007–2008	AI	0.96	−0.67 ± 0.140 a
		LR	0.87	−0.55 ± 0.170 a
		CH	0.99	−0.80 ± 0.154 a
Coratina	2006–2007	AI	na[b]	na
	2007–2008	AI	–	–
		LR	–	–
		CH	–	–
Barnea	2006–2007	LR	0.97	−0.56 ± 0.488 –
	2007–2008	LR	0.66	−0.37 ± 0.241 a
		CH	0.93	−0.43 ± 0.253 a

[a] Values are means ± SE and different letters are significantly different ($P < 0.05$) between locations within the same year.

[b] na = not applicable due to lack of significant linear or bilinear relationships.

(up to 27–28%), while other varieties were near or below the upper limit (Fig. 6).

Palmitic acid (the main saturated fatty acid) showed different patterns during fruit growth between varieties and also patterns were different from those observed for oleic and linoleic acid (Fig. 7). It increased during fruit growth from an initial value of 15% until reaching a breakpoint near 20% in ‘Arbequina’ and ‘Arauco’. The varieties ‘Manzanilla’, ‘Barnea’, and ‘Frantoio’ showed initial values of 15–17% palmitic acid, but remained stable or descended slightly. In contrast, ‘Coratina’ was fairly constant from 1000 to 1800 °Cd before steadily falling to the end of the season with final values of 11–12% (Fig. 7).

4. Discussion

Although the intraspecific variation in the dynamics of fruit growth and oil concentration have been modeled previously for a single location (Trentacoste et al., 2012), an increased understanding of such dynamics can potentially be obtained by including multiple locations that represent a range of environmental conditions. Additionally, little information exists in olive on how the dynamics of oil quality parameters including fatty acid composition respond quantitatively in different genotypes over multiple seasons and locations.

4.1. Dynamics of fruit growth

Fruit growth was described by linear and bilinear functions, which allow for quantifying the rate and duration of fruit growth, expressed in thermal time (i.e., calendar time weighted by the temperature) from flowering date. The final fruit weight was related more strongly to the fruit growth rate than to growth duration with rate explaining 47% of the variation and duration only 10%. Trentacoste et al. (2012) previously reported that fruit growth rate accounted for 91% of variation. Thus, maximizing olive fruit size requires maximizing fruit growth rate. This also coincides with annual grain crops such as wheat, corn, soybeans, and sorghum where the rate of grain filling is the attribute most associated with final grain weight (Egli, 1975; Brocklehurst, 1977; Bruckner and Frohberg, 1987; Gambín and Borrás, 2005; Ehdaie et al., 2008).

Location explained an important proportion of variability of final fruit weight in four varieties when comparing orchards from a fairly high elevation valley (Aimogasta; 800 masl) with a lower elevation valley (La Rioja; 420 masl). The larger fruit in Aimogasta than in La Rioja can be explained by greater fruit growth rate, although the controlling factors for this response are uncertain. If excessively high maximum temperatures have an important effect on fruit size, it might be expected that the coolest valley (Chilecito; 850 masl) would have the largest fruit, but this was not consistently found. On the other hand, the rate of oil accumulation described in more detail in the next section was modestly; but negatively, related to average mean and maximum temperature. A greater sensitivity of oil concentration (%) than fruit weight to temperature has also been observed under controlled, manipulative conditions by heating individual branches (García-Inza, unpublished results). Additionally, Trentacoste et al. (2012) has noted recently that temperature, vapor pressure deficit, and daily solar radiation likely play a role in these dynamics, although it is recognized that such factors are highly correlated.

4.2. Dynamics of oil concentration

Maximum fruit oil concentration (%) ranged from 30 to 53% of fruit dry weight among varieties, locations, and growing seasons with oil concentration being more related to the rate of oil accumulation than to its duration, similarly to fruit growth. Oil rates

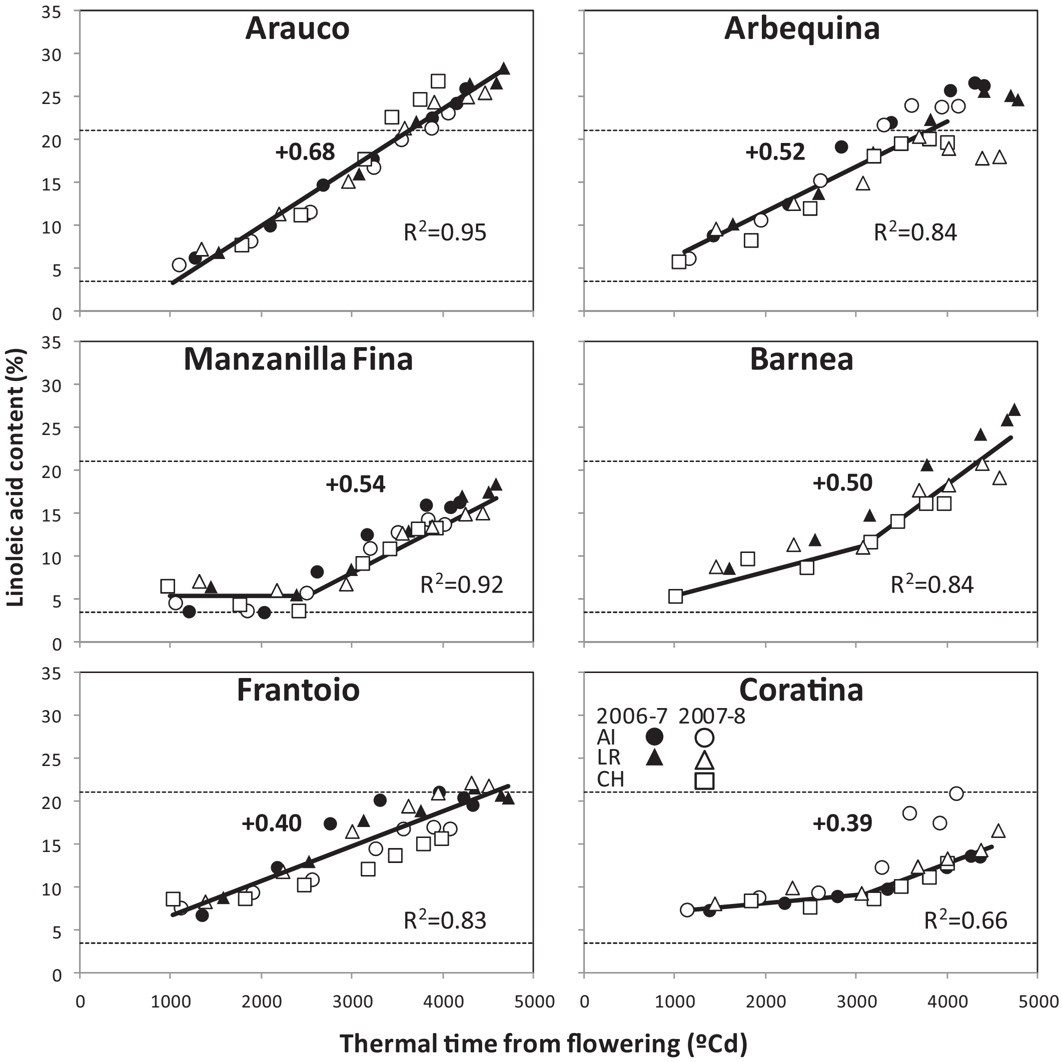

Fig. 6. Dynamics of linoleic acid content in the oil (% of total fatty acids) of six olive varieties during two growing seasons (2006–2007 and 2007–2008) in Aimogasta (AI), La Rioja (LR), and Chilecito (CH). Solid lines are linear or bilinear regressions fitted to the data from all three locations. Numbers near the regression lines indicate the ascending slopes (% linoleic acid per 100 °Cd). Dotted horizontal lines are limits of linoleic content (3.5–21%) for virgin olive oil according to the IOOC.

were 1–2 percentage points per 100 °Cd, which corresponds to maximum values of about 0.3% per day. These rates for northwestern Argentina are within the range reported for Italian, Spanish and North African (e.g., Orlandi et al., 2012; Piravi-Vanak et al., 2012; Sakouhi et al., 2011) varieties growing in Mediterranean countries. The importance of rate for explaining the final oil concentration has previously been reported by Lavee and Wodner (1991), although little variability among varieties in oil accumulation rate was detected in ten olive varieties grown at a single location in central western Argentina (Trentacoste et al., 2012). Reasons for the differences between our study and Trentacoste et al. (2012) cannot be attributed to different methodology in the thermal calculations because very similar approaches were employed. In the only variety (i.e., 'Frantoio') assessed by both studies, oil rate was lower (1.3–1.8 versus 2.6% per 100 °Cd) and duration from the date of flowering was longer (3400–3800 versus 2760 °Cd) in our warmer, northwestern region (La Rioja) than in cooler, central western Argentina (Mendoza). Further investigation across a latitudinal gradient could be used to better interpret these differences.

In terms of the three locations evaluated in northwestern Argentina, many varieties showed consistently lower fruit oil accumulation rates and final oil concentrations in La Rioja valley (420 masl) relative to the higher valleys of Aimogasta (800 masl) and Chilecito (850 masl). Significant effects of variety, location, and variety × location interaction were all observed. A simplified example of a variety × location interaction would be to compare the varieties 'Frantoio' and 'Coratina' during the second growing season when 'Frantoio' had a much higher oil concentration in Aimogasta and Chilecito (47%) than in La Rioja (38%), while the oil concentration of 'Coratina' was not affected by location. If location can be partially assumed to be a proxy for environment, this suggests that final oil concentration showed a genotype (G) × environment (E) interaction. Padula et al. (2008) reported significant genotype and location effects on oil concentration for 134 olive selections grown at three locations in central and northern Italy, but a G × E interaction was not specifically observed. In oilseed crops such as sunflower, such interactions for oil related parameters have been reported across large latitudinal gradients (de la Vega and Chapman, 2001; Chapman and de la Vega, 2002).

4.3. Dynamics of fatty acids

Fatty acid composition of virgin olive oils is often affected by variety and environmental factors. Uceda and Hermoso (2001) have suggested that genotype is the major source of variability for the major fatty acids based on an evaluation of the world

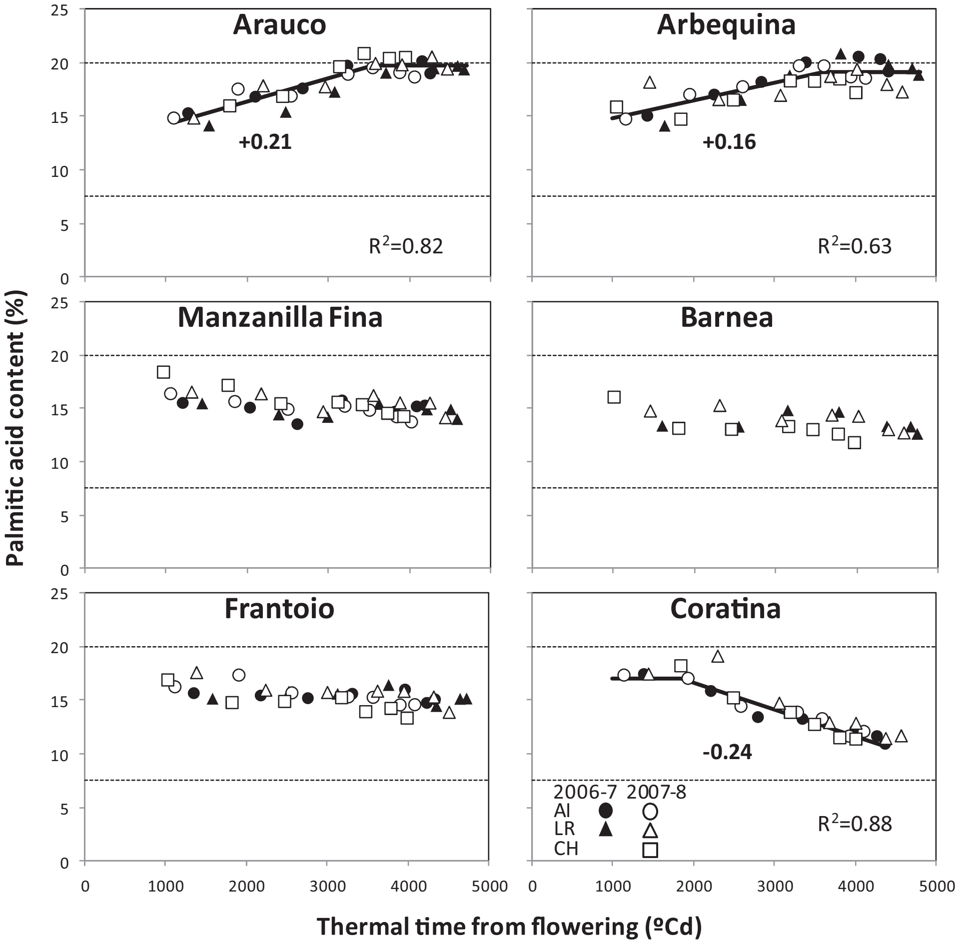

Fig. 7. Dynamics of palmitic acid content in the oil (% of total fatty acids) of six olive varieties during two growing seasons in Aimogasta (AI), La Rioja (LR), and Chilecito (CH). Solid lines are bilinear regressions fitted to the data from all three locations. Numbers near the regression lines indicate the slope (% palmitic acid per 100 °Cd). Dotted horizontal lines are limits of palmitic content (7.5–20%) for virgin olive oil according to the IOOC.

bank of olive germoplasm, while the environment and the G × E interaction are secondary. In our study, four different patterns of oleic acid evolution were observed for only 6 varieties. Linoleic and palmitic acid evolution also showed strong varietal responses. Although many authors have assessed such patterns (e.g., Poiana and Mincione, 2004; Dag et al., 2011), fatty acid dynamics have not been modeled in terms of thermal time and slope using linear and bilinear regressions. The Spanish variety ‘Arbequina’ and the South American variety ‘Arauco’ showed pronounced linear decreases in oleic acid (%) of approximately 0.8 percentage points per 100 °Cd. This resulted in oleic acid values of less than 50% by 3500° Cd. The dynamics of oleic acid over time gives a satisfactory explanation for the low oleic values observed in these highly planted varieties by the oil industry in northwestern Argentina (Ceci and Carelli, 2010; Rondanini et al., 2011). The variety ‘Coratina’ was the only variety that did not show reductions in oleic concentration during fruit ripening. The controlling mechanisms behind the varietal differences in oleic acid pattern could be related to different enzymatic capacities in the metabolism of fatty acid desaturation (Ramli et al., 2005), but this needs to be further examined. Potentially different responses among varieties to environmental factors such as temperature should also be assessed under controlled conditions.

In addition to oleic acid, varietal differences with thermal time were also important in fatty acids such as linoleic and palmitic acids. Decreasing oleic acid corresponded with increasing linoleic acid in the varieties ‘Arauco’ and ‘Arbequina’. Interestingly, the variety ‘Coratina’ did show some increase in linoleic acid after 3000° Cd, although it did not show changes in oleic acid. For palmitic acid, both increases and decreases were seen depending on variety. The relationships between different fatty acids may be important to modeling oil composition in olive oils as has been done in oilseed crops such as sunflower (Pereyra-Irujo and Aguirrezabal, 2007). Experiments under controlled conditions would greatly contribute to our understanding of how olive oil quality is influenced by environmental factors.

Acknowledgements

We thank the following farms: Agro Aceitunera, Olmedo Agropecuaria, Olivos Argentinos, Palas Atenea, Pepe Jiménez, CER, VG Agropecuaria, and Zait Shemen for providing access to their olive orchards. D. Del Carril, G. Mateos, E. Barbero, and E. Silva provided technical assistance; Vanesa Aybar provided some flowering data; Eduardo García and Orlando Barros also helped at various stages of the study. Grants from the Government of La Rioja and Cámara Olivícola Riojana (MICE-COR-CRILAR N° 130) and the Ministerio de Ciencia y Tecnología of Argentina (ANPCyT-PICT 32218 and COFECyT – PFIP 121) supported this study. During the experiments, D.R. held a post-doctoral fellowship co-supported by Agro Aceitunera SA and CONICET.

References

Anastasopoulos, E., Kalogeropoulos, N., Kaliora, A.C., Kountouri, A., 2011. The influence of ripening and crop year on quality indices, polyphenols, terpenic acids, squalene, fatty acid profile, and sterols in virgin olive oil (Koroneiki cv.) produced by organic versus non-organic cultivation method. Int. J. Food Sci. Technol. 46, 170–178.

Beltrán, G., del Río, C., Sánchez, S., Martínez, L., 2004. Seasonal changes in olive fruit characteristics and oil accumulation during ripening process. J. Sci. Food Agric. 84, 1783–1790.

Brocklehurst, P.A., 1977. Factors controlling grain weight in wheat. Nature 266, 348–349.

Bruckner, P.L., Frohberg, R.C., 1987. Rate and duration of grain fill in spring wheat. Crop Sci. 27, 451–455.

Cattaneo, P., Karman de Sutton, G., 1959. Composición química de aceites de oliva argentinos. Revista Argentina de Grasas y Aceites 1, 3–10 (in Spanish).

Ceci, L.N., Carelli, A.A., 2010. Compositional data review of monovarietal Argentinean olive oils. In: Tomas, M.B. (Ed.), Advances in Fats and Oil Research. Transworld Research Network, Kerala, India, pp. 71–97.

Chapman, S.C., de la Vega, A.J., 2002. Spatial and seasonal effects confounding interpretation of sunflower yields in Argentina. Field Crops Res. 73, 107–120.

Correa-Tedesco, G., Rousseaux, M.C., Searles, P.S., 2010. Plant growth and yield responses in olive (*Olea europaea*) to different irrigation levels in an arid region of Argentina. Agric. Water Manage. 97, 1829–1837.

Covas, M.I., Ruiz-Gutierrez, V., de la Torre, R., Kafatos, A., Lamuela-Raventos, R.M., Osada, J., Owen, R.W., Visioli, F., 2006. Minor components of olive oil: evidence to date of health benefits in humans. Nutr. Rev. 64, 20–30.

Dag, A., Kerem, Z., Yogev, N., Zipori, I., Lavee, S., Ben-Dabid, E., 2011. Influence of time of harvest and maturity index on olive oil yield and quality. Sci. Hortic. 127, 358–366.

de la Vega, A.J., Chapman, S.C., 2001. Genotype by environment interaction and indirect selection for yield in sunflower: II. Three-mode principal component analysis of oil and biomass yield across environments in Argentina. Field Crops Res. 72, 39–50.

DeJong, T.M., Goudriaan, J., 1989. Modeling peach fruit growth and carbohydrate requirements: reevaluation of the double-sigmoid growth pattern. J. Am. Soc. Hortic. Sci. 114, 800–804.

Egli, D.B., 1975. Rate of accumulation of dry weight in seed of soybeans and its relationship to yield. Can. J. Plant Sci. 55, 215–219.

Ehdaie, B., Alloush, G.A., Waines, J.G., 2008. Genotypic variation in linear rate of grain growth and contribution of stem reserves to grain yield in wheat. Field Crops Res. 106, 34–43.

Gambín, B.L., Borrás, L., 2005. Sorghum grain weight: growth pattern from different positions within the panicle. Crop Sci. 45, 553–561.

Gómez-González, S., Ruiz-Jiménez, J., Luque de Castro, M.D., 2011. Oil content and fatty acid profile on Spanish cultivars during olive fruit ripening. J. Am. Oil Chem. Soc. 88, 1737–1745.

Grigg, D., 2001. Olive oil, the Mediterranean and the world. GeoJournal 53, 163–172.

Hammami, S.B.M., Manrique, T., Rapoport, H.F., 2011. Cultivar-based fruit size in olive depends on different tissue and cellular processes throughout growth. Sci. Hortic. 130, 445–451.

IOOC, 2001. Preparation of the Fatty Acid Methyl Esters from Olive Oil and Olive-Pomace Oil. International Olive Oil Council, Madrid, http://www.internationaloliveoil.org/estaticos/view/222-standards/ [on line date 1/3/13].

Izquierdo, N., Aguirrezabal, L., Andrade, F., Pereyra, V., 2002. Night temperature affects fatty acid composition in sunflower oil depending on the hybrid and the phenological stage. Field Crops Res. 77, 115–126.

Lajara, J., Díaz, U., Quidiello, R., 1990. Definite influence of location and climatic conditions on the fatty acid composition on sunflower seed oil. J. Am. Oil Chem. Soc. 67, 618–623.

Lavee, S., Wodner, M., 1991. Factors affecting the nature of oil accumulation in fruit of olive (*Olea europaea* L.) cultivars. J. Hortic. Sci. 66, 583–591.

Lavee, S., Wodner, M., 2004. The effect of yield harvest time and fruit size on the oil content in fruits of irrigated olive trees (*Olea europaea*), cvs. Barnea and Manzanillo. Sci. Hortic. 99, 267–277.

Mailer, R.J., 2005. Variation in oil quality and fatty acid composition in Australian olive oil. Aust. J. Exp. Agric. 45, 115–119.

Mailer, R.J., Ayton, J., Graham, K., 2010. The influence of growing region, cultivar and harvest timing on the diversity of Australian olive oil. J. Am. Oil Chem. Soc. 87, 877–884.

Mannina, L., Fontanazza, G., Patumi, M., Ansanelli, G., Segre, A., 2001. Italian and Argentine olive oils: a NMR and gas chromatographic study. Grasas y Aceites 52, 380–388.

Orlandi, F., Bonofiglio, T., Romano, B., Fornaciari, M., 2012. Qualitative and quantitative aspects of olive production in relation to climate in southern Italy. Sci. Hortic. 138, 151–158.

Padula, G., Giordani, E., Bellini, E., Rosati, A., Pandolfi, S., Paoletti, A., Pannelli, G., Ripa, V., De Rose, F., Perri, E., Buccoliero, A., Mennone, C., 2008. Field evaluation of new olive (*Olea europaea* L.) selections and effects of genotype and environment on productivity and fruit characteristics. Adv. Hort. Sci. 22, 87–94.

Pereyra-Irujo, G.A., Aguirrezabal, L.A.N., 2007. Sunflower yield and quality interactions and variability: analysis through a simple simulation model. Agric. Forest Meteorol. 143, 252–265.

Pérez-López, D., Ribas, F., Moriana, A., Rapoport, H.F., De Juan, A., 2008. Influence of temperature on the growth and development of olive (*Olea europaea* L.) trees. J. Hortic. Sci. Biotechnol. 83, 171–176.

Piravi-Vanak, Z., Ghasemi, J.B., Ghavami, M., Ezzatpanah, H., Zolfonoun, E., 2012. The influence of growing region on fatty acids and sterol composition of Iranian olive oils by unsupervised clustering methods. J. Am. Oil Chem. Soc. 89, 371–378.

Poiana, M., Mincione, A., 2004. Fatty acid evolution and composition of olive oils extracted from different olive cultivars grown in Calabrian area. Grasas y Aceites 55, 282–290.

Ramli, U.S., Salas, J.J., Quant, P.A., Harwood, J.L., 2005. Metabolic control analysis reveals an important role for diacylglycerol acyltransferase in olive but not in oil palm lipid accumulation. FEBS 272, 5764–5770.

Ravetti, L., 1999. Caracterización preliminar de variedades y aceites de oliva vírgenes de la provincia de Catamarca. Aceites y Grasas 36, 361–369.

Rondanini, D., Savin, R., Hall, A.J., 2003. Dynamics of fruit growth and oil quality of sunflower (*Helianthus annuus* L.) exposed to brief intervals of high temperature during grain filling. Field Crops Res. 83, 79–90.

Rondanini, D.P., Castro, D.N., Searles, P.S., Rousseaux, M.C., 2011. Fatty acid profiles of varietal virgin olive oils (*Olea europaea* L.) from mature orchards in warm arid valleys of Northwestern Argentina (La Rioja). Grasas y Aceites 62, 399–409.

Sakouhi, F., Herchi, W., Sebei, K., Absalon, C., Kallel, H., Boukhchina, S., 2011. Accumulation of total lipids, fatty acids and triacylglycerols in developing fruits of *Olea europaea* L. Sci. Hortic. 132, 7–11.

Sobrino, E., Tarquis, A.M., Díaz, M.C., 2003. Modeling the oleic acid content in sunflower oil. Agron. J. 95, 329–334.

Torres, M.M., Pierantozzi, P., Cáceres, M.E., Labombarda, P., Fontanazza, G., Maestri, D.M., 2009. Genetic and chemical assessment of Arbequina olive cultivar grown in Córdoba province, Argentina. J. Sci. Food Agric. 89, 523–530.

Trentacoste, E.R., Puertas, C.M., Sadras, V.O., 2010. Effect of fruit load on oil yield components and dynamics of fruit growth and oil accumulation in olive (*Olea europaea* L.). Eur. J. Agron. 32, 249–254.

Trentacoste, E.R., Puertas, C.M., Sadras, V.O., 2012. Modelling the intraspecific variation in the dynamics of fruit growth, oil and water concentration in olive (*Olea europaea* L.). Eur. J. Agron. 38, 83–93.

Uceda, M., Hermoso, M., 2001. La calidad del aceite de oliva. In: Barranco, D., Fernández-Escobar, R., Rallo, L. (Eds.), El cultivo del olivo. Junta de Andalucía-Ediciones Mundi-Prensa, Madrid, pp. 589–614.

Vossen, P., 2007. Olive oil: history, production, and characteristics of the world's classic oils. Hort. Sci. 42, 1093–1100.