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Opposite oleic acid responses to temperature in oils from the seed and mesocarp of the olive fruit

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ABSTRACT

Olive oil is mostly extracted from the mesocarp (~95%) of the fruit with the seed (endosperm and embryo, ~5%) containing little oil. There are correlative and manipulative evidence that temperature modulates fruit oil content and fatty acid composition of the oil from the whole fruit (i.e., with no distinction being made between oils derived from each oil-bearing structure) of olive. Notably, oleic acid concentration of olive oil decreases as fruit mean growth temperature increases. This response in the olive fruit is opposite to that documented in annual oil-seed crops such as sunflower and soybean. The objectives of the present study were: i) to compare temperature effects on fatty acid composition of oil derived from seed and from mesocarp; ii) to compare temperature effects on seed and mesocarp dry weights and oil concentrations. To do this, fruiting branches were enclosed in transparent plastic chambers with individualized temperature control. Temperature was manipulated during the seed growth (Period A) and during the second half of mesocarp growth (Period B) subphases. In both periods, the oleic acid proportion in mesocarp oil decreased as temperature increased, and was accompanied by increases of palmitic acid, linoleic and linolenic acids. Mesocarp dry weight did not respond significantly to temperature, but mesocarp oil concentration fell significantly as temperature increased. Seed dry weight, oil concentration and fatty acid composition exhibited responses to temperature during Period A only, with seed dry weight increasing between 20 and 25 °C with a sharp decrease at higher temperature, and oil concentration linearly falling 1.2% per °C. In contrast, seed oil oleic acid percentage increased between 20 and 28 °C, and fell slightly with higher temperature. Palmitic and stearic acids in seed oil increased sigmoidally with temperature, while linoleic acid decreased sigmoidally. Oleic acid percentage showed opposite responses in oil from the seed and the mesocarp. The response of the seed to temperature was similar to those observed in oil from embryos of annual oil-seed crops, although the abrupt fall in palmitic and stearic acid with temperature >25 °C seems to be distinctive for olive seed oil.

1. Introduction

Olive oil comes mostly from the mesocarp (epicarp and fleshy mesocarp, ~95%) with a small contribution from the seed of the fruit (endosperm and embryo, ~5%) (Conde et al., 2008). Within the seed, most of the oil is present in the embryo (Rapoport and Gómez del Campo, 2008). Fruit growth takes about 4–6 months, and seed and mesocarp growth are asynchronous, with seed growth being completed at the time the mesocarp has only achieved about half its final weight. Within the fruit growth phase, two sub-phases can be distinguished based on the intensity of cell division (Hammami et al., 2011). Period 1 (from bloom to 8 weeks after bloom) is characterized by active cell division. Approximately 66% of final cell number is generated during this period and 25% of cell size is achieved, with fruit transverse area reaching 34% of its final value. During Period 2 (from 8 to 32 weeks after bloom) cell division rate is lower and the remaining 75% of cell size increase takes place. Concomitantly, the endocarp cross-sectional area (which includes the endocarp and the enclosed seed) expands exponentially from soon after bloom to 8 weeks after bloom while the mesocarp cross-sectional area increases constantly and substantially from bloom to maturity (28 weeks after bloom).

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The parental origin of mesocarp and seed tissues is different. The pericarp (including epicarp, mesocarp and endocarp) is formed from ovary tissues of the flower (maternal tissues), while most of the seed tissues are generated after fertilization. With regard to oil storage some structural differences between these tissues have been reported. Seed oil contains oleosin, an oil-body protein that is typically present in oil from annual oil-seed crops (e.g., sunflower, safflower, maize, soybean, rapeseed, etc., Tzen et al., 1990) but this protein is not found in mesocarp oil (Ross et al., 1993). An early review (Hilditch and Williams, 1964) of fatty acid composition of oils from different species reported similar proportions of some fatty acids in both mesocarp and seed oils of olive. Palmitic was 7–15% in mesocarp and 6% in seed, while oleic was 70–85% and 83%, and linoleic was 4–12% and 7% in mesocarp and seed respectively. At a molecular level, some studies have revealed differences between these structures (i.e., mesocarp and seed) in the expression levels or in the timings of maximum expression of genes that encode fatty acid desaturase (FAD) enzymes during fruit growth (Poghosyan et al., 1999; Banilas et al., 2005;). In contrast to this considerable body of information on the adaptive, structural and enzymatic differences between these two oil-bearing fruit structures, there is a knowledge gap relating to the effects of temperature, a major environmental factor, on them. This gap is particularly marked in relation to the seed.

Correlative studies in olive, based on surveys of fruit produced in locations with different temperature regimes, have shown that whole-fruit dry weight is related more strongly to fruit growth rate than to fruit growth duration (Rondanini et al., 2014; Trentacoste et al., 2012), but the role of controlling factors, like temperature, behind this response are uncertain. A temperature manipulation study showed that final fruit dry weight is affected by temperatures higher than 25 °C, but no temperature effect was detected with average seasonal temperatures in the 16 and 25 °C range (García-Inza et al., 2014). In the oil-seed crop sunflower, temperature increases embryo growth rate up to a maximum (25 °C) while duration falls as temperature increases (Chimenti et al., 2001). In olive, fruit weight is important because of its relation with fruit caliber when the destination is Table olive, while oil accumulation is a key determinant for oil production. Correlative evidence using different varieties, years and locations showed a negative relationship between fruit oil concentration and seasonal mean daily temperature in the 23 − 27.5 °C range (Rondanini et al., 2014) and fruit oil concentration in the cultivar Arauco decreased 1.1% per °C of temperature increment in the 16 °C to 32 °C range in a temperature manipulation experiment (García-Inza et al., 2014).

Fatty acid proportion is an important attribute of edible oils and for olive oil its values for commercialization are regulated by the International Olive Oil Council (IOOC, 2013). To qualify as extra virgin olive oil, oleic acid levels in the oil must be within the limits of 55 and 83%, palmitic between 7.5 and 20%, linoleic between 3.5- and 21%, and linolenic must be ≤1%. Oil fatty acid composition is affected by the variety (Uceda and Hermoso, 2001), but the environment and genotype x environment interactions can also influence it (Rondanini et al., 2011). Temperature is one of the environmental factors that modulate fatty acid composition in olive oil and other oil-seed crops. There are correlative (Lombardo et al., 2008; Mailer et al., 2010; Orlandi et al., 2012; Rondanini et al., 2014) and manipulative evidence (García-Inza et al., 2014) in the field that show that oleic acid decreases in oil from the whole fruit as temperature increases. This response is opposite to that generally found in crops that accumulate oil in the seed. In sunflower (Canvin, 1965), maize and soybean (Zuil et al., 2012 and references cited therein) high temperature during fruit growth is associated with an increase in oleic acid concentration. This differential response to temperature could be due to the different fruit structures involved (principally mesocarp in olive and seed in oil-seed crops). The objective of the present work was to elucidate the effect of temperature on olive seed and mesocarp dry weights, oil concentrations and oil fatty acid composition of oils from both oil-bearing fruit structures. To do this, advantage was taken of the fact that seed oil accumulation is completed about a half of the way through the fruit growth phase, while oil continues to accumulate in the mesocarp almost right through to fruit maturity.

2. Materials and methods

2.1. Experimental site and temperature treatments

The experiment was conducted in 2011 at Los Molinos (28°43′ S, 66° 56′ W, 1400 m above sea level (masl)), La Rioja province, Argentina. This location was selected because of its altitude, which makes the site cooler and allowed us to attain a broader range of temperatures. The orchard was planted in 1940 at 6 m between trees and 12 m between lines. The plants were flood-irrigated every 20 days all year round, and fertilized with 40 kg of goat manure per plant at pit hardening stage. Mean daily solar radiation during Periods A and B of our experiments were 22.2 and 18.9 MJ m^{-2} d^{-1} respectively, similar to regional averages for equivalent periods (21.8 and 20.8 MJ m^{-2} d^{-1} for La Rioja (420 masl) and Aimogasta (800 masl), respectively, for the 2009–2012 period).

The cultivar Arauco (Barranco et al., 2000) was used for this study. More details on the experimental site and characteristics of the cultivar can be found in García-Inza et al. (2014). Full bloom was registered on 24 October 2010 and pit hardening on 30 December 2010. The latter was considered to have occurred when it proved impossible to slice the endocarp of the sampled fruit right through with a sharp knife (see García-Inza et al., 2014 for further details).

The temperature manipulation experiment involved two sub-phases of fruit growth. Period A, covered from 25 November 2010 to 23 February 2011, when most of the seed oil accumulation phase and the initial sub-phase of mesocarp oil accumulation occurred. Period B, covered from 1 March 2011 to 13 May 2011, including pit hardening to final harvest interval, thus including the second sub-phase of mesocarp oil accumulation. These treatment periods were selected to probe possible differential responses to temperature on seed and mesocarp fruit structures. During each of the two Periods four thermal levels were applied: a control at ambient temperature, two heating levels (5 °C and 10 °C warmer than control), and a cooling level (3 °C cooler than the control). The experimental design was a randomized complete block with four replicates where a tree was taken as a block, and each treatment was present within each block. Once the Period A treatment was completed, the chambers were moved to different branches of the same tree to begin the Period B treatment. In both Periods, we selected external fruiting branches of around 20 cm in length bearing between 5–8 fruit per branch from the South-oriented (± 25 °) surface of the crown of the trees, at 2–3 m height. The proportion of total fruit on the trees involved in the experiment represented only about 0.34% of the fruit production of the tree (data not shown). Additionally, chambers were widely spaced in the canopy of the tree, and treated fruiting branches were positioned on different main branches (i.e., a branch older than 4 years age). Proietti and Tombesi (1996) noted that main branches on an olive tree are largely independent. Both the very small proportion of fruit involved in the experiment and the spacing between treatments make independence between treatments probable and compensation among them unlikely. Selected branches were enclosed in acrylic chambers of 22 × 22 × 10 cm (length, width and height respectively) during the treatment Period. Sides and bases of the chambers were covered with reflective bubble wrap insulation and a shade cloth (30% transmittance) located 10 cm above the lid was used