Journal of Plant Physiology **165** (2008) 1545—1562

Available online at www.sciencedirect.com

ScienceDirect

JOURNAL OF PLANT PHYSIOLOGY

www.elsevier.de/jplph

Physiological, biochemical and molecular changes occurring during olive development and ripening

Carlos Conde[a,*], Serge Delrot[b], Hernâni Gerós[a]

[a]*Departamento de Biologia, Universidade do Minho, Campus de Gualtar, 4710-057 Braga, Portugal*
[b]*Institute of Vine and Wine Sciences (ISVV), University Victor Segalen Bordeaux II, Unité Mixte de Recherches Ecophysiology and Grape Functional Genomics, INRA, 71 Avenue Edouard Bourlaux 33883, BP 81, Villenave d'Ornon, France*

Received 17 February 2008; received in revised form 13 April 2008; accepted 14 April 2008

KEYWORDS
Lipid synthesis;
Olive oil;
Phenolics;
Sugar transport;
Volatiles

Summary

Since ancient times the olive tree (*Olea europaea*), an evergreen drought- and moderately salt-tolerant species, has been cultivated for its oil and fruit in the Mediterranean basin. Olive is unique among the commercial important oil crops for many reasons. Today, it ranks sixth in the world's production of vegetable oils. Due to its nutritional quality, olive oil has a high commercial value compared with most other plant oils. Olive oil has a well-balanced composition of fatty acids, with small amounts of palmitate, and it is highly enriched in the moneonic acid oleate. This makes it both fairly stable against auto-oxidation and suitable for human health. Nevertheless, it is the presence of minor components, in particular phenolics, contributing for oil's high oxidative stability, color and flavor, that makes olive oil unique among other oils.

Moreover, as a result of their demonstrated roles in the prevention of cancer and cardiovascular diseases, olive phenolics have gained much attention during the past years. Also unique to virgin olive oil is its characteristic aroma. This results from the formation of volatile compounds, namely, aldehydes and alcohols of six carbon atoms, which is triggered when olives are crushed during the process of oil extraction. The biochemistry of the olive tree is also singular. *O. europaea* is one of the few species able to synthesize both polyols (mannitol) and oligosaccharides (raffinose and stachyose) as the final products of the photosynthetic CO_2 fixation in the leaf. These carbohydrates, together with sucrose, can be exported from leaves

Abbreviations: AAT, alcohol acyltransferase; ACP, acyl carrier protein; ADH, alcohol dehydrogenase; BCCP, biotin carboxylase carrier protein; DAG, diacylglycerol; DAGAT, diacylglycerol acyltransferase; FAS, fatty acid synthase; G3PAT, glycerol-3-phosphate acyltransferase; HDL, high-density lipoprotein; HPL, hydroperoxide lyase; KAS, ketoacyl-ACP synthase; LDL, low-density lipoprotein; LOX, lipoxygenase; LPAAT, lysophosphatidate acyltransferase; PCMBS, P-chloromercuribenzene sulfonate; RFO, raffinose family oligosaccharide; TAG, triacylglycerol.

*Corresponding author. Tel.: +351 253 604048; fax: +351 253 678980.
E-mail address: conde@bio.uminho.pt (C. Conde).

0176-1617/$ - see front matter
doi:10.1016/j.jplph.2008.04.018

to fruits to fulfill cellular metabolic requirements and act as precursors to oil synthesis. Additionally, developing olives contain active chloroplasts capable of fixing CO_2 and thus contributing to the carbon economy of the fruit. The overall quality of table olives and olive oil is influenced by the fruit ripening stage. Olive fruit ripening is a combination of physiological and biochemical changes influenced by several environmental and cultural conditions, even if most events are under strict genetic control.

Contents

Introduction

Olea europaea is an emblematic species and one of the most important and widespread fruit trees in the Mediterranean basin (Loumou and Giourga, 2003). Native to this region, wild olives were collected by Neolithic people as early as the 8th millennium B.C. The first domestic cultivation of olive trees is believed to have taken place on the island of Crete during the Minoan period around 1500–3000 BC (Riley, 2002). From here started the first exportations of olive oil not only to mainland Greece, but also to Northern Africa and Asia Minor. Olive tree cultivation and olive oil production became particularly intense and played an important role in the economy of the region. The olive culture then spread to the Romans. As the Romans extended the limits of their dominion, they took the olive with them and extended olive tree cultivation over the entire Roman Empire. Today, olive is one of the most extensively cultivated fruit crops in the world. Its cultivation area has tripled in the past 44 years, from 2.6 to 8.6 million hectares, with a worldwide production of table olives around 17 million tons (FAOSTAT, 2007). Over 750 million olive trees are cultivated worldwide, with about 95% in the Mediterranean basin. About 73% of the global olive oil production comes from European Union countries. Of European production, 97% comes from Spain, Italy, and Greece; Spain alone accounts for more than 40% of the world's olive oil production. In Portugal, *O. europaea* has a wide distribution, with a cultivated area of 430,000 hectares, predominantly in the center and south areas of the country. It represents an important economical and environmental species, making Portugal the eighth major olive producer country in the world, accounting for 280,000 tons of table olives and 40,000 tons of olive oil production per year.

O. europaea is a member of the Oleaceae family. This is a medium-sized family comprising 600 species in 25 genera distributed on all continents, except the Antarctic, from northern temperate to southern subtropical regions and from low to high elevations (Wallander and Albert, 2000). The family is considered monophyletic on the basis of several morphological synapomorphies and is easily circumscribed. The family members are trees, shrubs or woody climbers with opposite, simple or compound leaves without stipules. The flowers are hypogynous and tetramerous, generally with two stamens, but also with four stamens in some species. The corolla is actinomorphic and usually sympetalous. The phylogenetic relationships among the recognized family genera have been assessed by a cladistic analysis of DNA sequences from two non-coding chloroplast loci, the *rps16* intron and the *trnL-F* region (Wallander and Albert, 2000).