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1 **FRUIT CUTICLE AS A MODULATOR OF POSTHARVEST**  
2 **QUALITY**

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## Fruit cuticle as a modulator of postharvest quality

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### Abstract

The composition and structure of the surface tissues have a noticeable influence on the postharvest storage potential of fruits, inasmuch as they behave as a barrier against drying, chemical attacks, mechanical injuries and microbial infections. Cuticle is made of cutin – a biological insoluble polyester – embedded in an impermeable wax complex, and its inner side interacts intimately with the underlying epidermal cell walls. The cuticle plays a decisive role in plant development, being its first communication system with the surrounding biotic and abiotic environment. Published reports on composition and biosynthesis of fruit cuticles are comparatively scarce, and many knowledge gaps exist as to what part they play in quality determination and postharvest performance. This review aims at collecting available information in relation to the role of fruit cuticle as a determinant factor of some important traits related to postharvest quality of produce, including water loss, susceptibility to several physical and biological stresses, and decreased fruit firmness. To our best knowledge, this is the first published work focusing on fruit cuticle as a major modulator of postharvest quality, and interlinking pre-existing disperse literature on this topic. A deeper comprehension of cuticle structure and functions will be of help in understanding postharvest biology and in designing new technological solutions.

*Keywords:* cuticle biochemistry; cutin; decay; disorders; firmness; water loss; wax

## 40 **1. Introduction**

41 Metabolic events that occur during maturation, ripening and postharvest evolution  
42 of fruits cause significant changes that reduce the marketable volume of the harvested  
43 production, the visual and organoleptic appeal to the consumer, the level of available  
44 vitamins and antioxidants, and the storage ability. These occurrences cause dramatic  
45 economic losses to the fruit crop sector.

46 The fruit cuticle has been largely disregarded with respect to its putative influence  
47 in modulating fruit development, and, in particular, fruit ripening and postharvest  
48 performance. However, the cuticle is synthesised by and covers the epidermis of the  
49 fruit, being the first barrier against abiotic and biotic conditions in which it develops  
50 (Domínguez et al., 2011a). The main function traditionally attributed to fruit cuticles is  
51 to minimise water loss, although it also limits the loss of substances from internal  
52 tissues, protects against physical, chemical and biological attack, and provides  
53 mechanical support to maintain plant organ integrity. The preservation of all these  
54 functions requires structural integrity of the cuticle throughout fruit expansion and  
55 development.

56 Cuticles contribute to traits such as maximum strain, breaking stress or elastic  
57 modulus, which affect the mechanical behaviour of fruit and other plant organs. The  
58 viscoelastic and strain-hardening properties of cuticles contribute to reinforcing the  
59 epidermal cell walls, while simultaneously conferring extensibility (Domínguez et al.,  
60 2011a). In turn, such biophysical properties are dependent to some extent upon external  
61 conditions such as temperature and relative humidity (Edelmann et al., 2005; Matas et  
62 al., 2005). Cuticle strength and rigidity decrease when temperature increases, the  
63 structure exhibiting a phase transition at a given temperature. The effect of this  
64 transition temperature on the elastic modulus is dependent on relative humidity, as

65 water is known to plasticise the plant cuticle (reviewed in Domínguez et al., 2011b).  
66 These two factors are thus among the most important ones in devising storage strategies  
67 for postharvest conservation. This review focuses specifically on the current available  
68 knowledge about the relevance of cuticle composition and properties for fruit quality  
69 during the postharvest period (see Fig. 1).

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## 72 **2. A brief overview of cuticle composition in fruits**

73 Cuticles are lipidic layers mainly composed by cutin, a polyester polymer rich in  
74 hydroxylated and epoxy-hydroxylated C<sub>16</sub> and C<sub>18</sub> fatty acids. This cutin matrix is  
75 embedded with amorphous waxes and a minor fraction of phenolics, while the plant  
76 surface is covered by epicuticular waxes, both amorphous and crystalline. On the inner  
77 side of the cuticle, cutin is mixed with pectin and glucan polysaccharides from the  
78 epidermal cell walls, the composition of which closely resembles that of primary cell  
79 walls (López-Casado et al., 2007). Cuticle also contains cutan, a non-ester network  
80 made of aliphatic compounds assembled mainly by ether bonds. Recent reviews have  
81 been published summarizing available information on the composition and biosynthesis  
82 of cutin and cuticular waxes (Kunst and Samuels, 2003, 2009; Nawrath and Poirier,  
83 2008; Pollard et al., 2008; Samuels et al., 2008). Some studies have shown evidence that  
84 cuticle composition differs significantly in different organs of the same plant, both  
85 regarding cutin (Espelie et al., 1979, 1980; Marga et al., 2001; Järvinen et al., 2010) and  
86 waxes (Radler, 1965, 1970; Baker et al., 1975). In order to shed light on the possible  
87 roles of cuticle in fruit quality and postharvest performance, therefore, it would be  
88 convenient to have data on the specific composition of fruit cuticles. Yet published

89 reports on cuticle composition of fruits are comparatively scarce, research efforts having  
90 been focused primarily on vegetative tissues.

91       Currently available information on cutin and cuticular wax composition in different  
92 fruit types is summarised in Table 1. In many cases, the composition of either cutin or  
93 cuticular waxes was reported uniquely, and thus for some fruit types the overview of  
94 cuticle constituents is still incomplete. In any case, this survey shows that fruit cuticles  
95 display substantial variability according to species, to genotypes within a given species,  
96 and to developmental stage. In most of the reports summarised in Table 1, *n*-alkanes  
97 and triterpenoids were identified as prominent components of cuticular waxes, in some  
98 cases accompanied by significant amounts of aldehydes. Among the *n*-alkanes, the C<sub>29</sub>  
99 hydrocarbon *n*-nonacosane is reiteratedly cited as a major compound, being the most  
100 abundantly present in cuticles of apple, citrus fruit and sweet cherry, while the C<sub>31</sub> *n*-  
101 hentriacontane was identified as the predominant alkane in other species such as pepper  
102 and tomato. Regarding the triterpenoid components of cuticular waxes, the triterpene  
103 ursolic and oleanoic acids dominate cuticular wax composition of apple, grape, peach  
104 and sweet cherry, whereas triterpenoid alcohols such as amyryns are predominant in  
105 citrus species, Asian pear, pepper and tomato.

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### 108 **3. Cuticle biosynthesis during fruit maturation and ripening**

109       Some studies have addressed cuticle biosynthesis during fruit development, mainly  
110 from a morphological or quantitative perspective. Cuticle deposition reportedly ceases  
111 early during fruit development, prior to the onset of the ripening process and frequently  
112 before the fruit has attained maximum size, resulting in decreased amount of cuticle per  
113 surface area and thus in reduced cuticle thickness in ripe fruit (Rosenquist and

114 Morrison, 1988; Comménil et al., 1997; Belding et al., 1998; Dong et al., 2012; Liu et  
115 al., 2012). In some cases, early-arrested deposition of cuticular components and the  
116 associated decline in cuticle thickness causes microcracks as surface strain increases  
117 when fruit expands (Sala et al., 1992; Knoche et al., 2004; Knoche and Peschel, 2007;  
118 Peschel et al., 2007; Khanal et al., 2011; Becker and Knoche, 2012). A notorious  
119 exception to this generally observed trend is tomato, for which a continuous increase in  
120 cuticular waxes and cutin monomers has been found during fruit development (Kosma  
121 et al., 2010).

122 In contrast, the compositional evolution of specific cuticular components during  
123 fruit maturation has been reported for only a few species, including grape berries  
124 (Comménil et al., 1997), apple (Belding et al., 1998; Dong et al., 2012), sweet cherry  
125 (Peschel et al., 2007), tomato (Saladié et al., 2007; Kosma et al., 2010) and orange (Liu  
126 et al., 2012). This has revealed substantial differences in the time-course changes of  
127 particular wax and cutin constituents for each fruit type, thus illustrating the need to  
128 undertake such studies on a case-by-case basis.

129 In spite of the important implications for fruit quality and postharvest performance,  
130 little efforts have been devoted to the study of cuticle formation in fruit, particularly  
131 from the biochemical and molecular perspectives, although some information exists for  
132 tomato (Vogg et al., 2004; Leide et al., 2007; Mintz-Oron et al., 2008; Isaacson et al.,  
133 2009; Nadakuduti et al., 2012; Yeats et al., 2012a; Shi et al., 2013), sweet cherry (Alkio  
134 et al., 2012), and apple (Albert et al., 2013). These works have allowed the  
135 identification of genes potentially involved in cuticular wax or cutin biosynthesis in  
136 fruit surfaces, which should facilitate further research on the formation of this important  
137 outer layer.

138 For tomato, a very long-chain fatty acid  $\beta$ -ketoacyl-CoA synthase (*LeCER6*),  
139 required for the biosynthesis of very long-chain ( $>C_{30}$ ) *n*-alkanes and aldehydes, has  
140 been identified and characterized (Vogg et al., 2004), and its loss-of-function mutant  
141 fruit demonstrated to display altered cuticle permeability and transpiration properties  
142 (Leide et al., 2007). Accordingly, Mintz-Oron et al. (2008) reported progressively  
143 increased expression of *SICER6* (referred to as *LeCER6* in the previous papers by Vogg  
144 et al., 2004, and Leide et al., 2007) throughout maturation and ripening of tomato fruit.  
145 Some other cuticle-related genes have been also identified in tomato which are involved  
146 in cutin deposition (Isaacson et al., 2009; Nadakuduti et al., 2012; Yeats et al., 2012b;  
147 Shi et al., 2013), as well as a transcription factor that regulates fruit cuticle formation  
148 and epidermal patterning (Shi et al., 2013). Scarce information is currently available for  
149 fruit other than tomato, but recent studies on sweet cherry (Alkio et al., 2012) and apple  
150 (Albert et al., 2013) have also allowed the identification of a range of genes potentially  
151 involved in cuticle formation during fruit development, including some related to the  
152 biosynthesis of wax and cutin components, transcription factors and cuticular lipid  
153 transporters.

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155

#### 156 **4. Changes in fruit cuticle composition after harvest**

157 Limited research attention has been apparently focused on changes in fruit cuticle  
158 composition during storage or in response to particular postharvest procedures, but  
159 some published studies are available for apple, which reveal considerable cultivar-  
160 associated variability. Morice and Shortland (1973) did not observe any changes in wax  
161 amount or composition of ‘Sturmer’ apple fruit throughout storage at 3 °C for up to nine  
162 months, while total wax amount in ‘Granny Smith’ and ‘Dougherty’ samples increased



163 to different extent during that time. Changes in fatty acid composition were also  
164 observed, the most notorious one being an 11-fold rise in linolenic acid found for  
165 ‘Granny Smith’ fruit. Controlled atmosphere (CA) storage and, especially, shelf life  
166 thereafter, affected wax properties, structure and chemical composition in fruit of three  
167 apple cultivars (Veraverbeke et al., 2001a), particularly for extended storage periods.  
168 The main changes in wax components referred to the alkane and ester fractions,  
169 apparently due to ester hydrolysis which led to augmented content in free fatty acids and  
170 in the secondary alcohol nonacosan-10-ol. The presence of an alcohol instead of an  
171 alkane can account for wax glossiness, which is correlated with alcohol content.

172 Total wax amount decreased sharply in ‘Red Fuji’ apples during storage at 0 °C for  
173 seven months, and wax composition was also modified (Dong et al., 2012). The alkanes  
174 *n*-nonacosane, *n*-heptacosane and *n*-nonacosene, prominent among the hydrocarbon  
175 present in surface waxes of this cultivar and required for the formation of crystalline  
176 wax structures, decreased over the storage period. In contrast, the content of nonacosan-  
177 10-ol, essential for the development of cuticular wax crystals, and of nonacosan-10-one,  
178 decreased over the first months of cold storage followed by a sharp increase for longer  
179 storage periods. Interestingly, 1-methylcyclopropene (1-MCP) treatment largely  
180 attenuated both the decline in *n*-nonacosane and the increase in nonacosan-10-ol and  
181 nonacosan-10-one levels observed for untreated fruit, indicating that wax composition  
182 of ‘Red Fuji’ apples is an ethylene-dependent attribute. 1-MCP treatment also delayed  
183 the development of certain wax constituents during cold storage for up to six months of  
184 ‘Autumn Gold’ and ‘Royal Gala’ fruit, although only a few of them were unequivocally  
185 identified (Curry, 2008), among them nonacosan-10-ol, the increase in which after long-  
186 term storage was partially suppressed in 1-MCP-treated fruit. These observations agree  
187 with recent work on ‘Navelate’ orange fruit, where ethylene treatment ( $2 \mu\text{L L}^{-1}$ )

188 increased both total and soft epicuticular waxes and induced structural changes in  
189 surface waxes during shelf life at 22 °C for up to three weeks (Cajuste et al., 2010).

190

191

## 192 **5. Cuticle as determinant of postharvest quality attributes of fruits**

193 Fruit cuticles influence post-harvest shelf life, and are associated with some  
194 important quality disorders such as cracking (Edelmann et al., 2005; Matas et al., 2005).

195 Published research on the relationship between cuticle properties or composition and  
196 quality attributes of fruit commodities has reported on three main aspects, namely water  
197 permeability and loss, susceptibility to infections and physiological disorders. Of late,  
198 though, some new evidence suggests a possible important role of cuticle composition  
199 and/or properties on postharvest firmness changes, which is worth of further  
200 consideration.

201 Given the hydrophobic nature of cuticle components and its capacity to function as  
202 a barrier, it has generally been assumed that this thin, outer layer of aerial organs of  
203 plants serve mainly protective purposes. For instance, intracuticular waxes have a  
204 dominant role in minimising non-stomata water loss across the cuticle. Cutin is involved  
205 in waterproofing leaves and fruits of higher plants, in regulating nutrient flow, and in  
206 minimising pathogen attack (Heredia, 2003). It has been reported that some fungi  
207 infecting important crops produce cutinases, which aid infection through their esterase  
208 activity (Sweigard et al., 1992). Plants with altered cutin deposition show a wide range  
209 of phenotypes, including defective development and growth, altered morphology,  
210 permeability and stomata structure, as well as increased sensitivity to stress and  
211 infections (Pollard et al., 2008). Evidence also indicates that cuticle structure and links  
212 among its components must be a central aspect of cuticular functionality as well. For

213 example, Li et al. (2007) overexpressed simultaneously *GPAT5* and *CYP86A1* in  
214 *Arabidopsis*, respectively a glycerol-3-phosphate acyltransferase and a fatty acid  $\omega$ -  
215 hydroxylase required for cutin assembly, and observed increased permeability of  
216 cuticles in spite of increased cutin and unchanged wax accumulation.

217 If we focus specifically on fruit produce, cuticle properties are very relevant from a  
218 physiological point of view, and often have considerable economic importance. Apart  
219 from its general role of minimising water loss (Riederer and Schreiber, 2001), cuticle  
220 limits solute loss from the inner tissues and protects against biotic and abiotic factors in  
221 the surrounding environment. Yet the mechanical properties of fruit cuticles change  
222 with relative humidity and temperature (Edelmann et al., 2005; Matas et al., 2005), and  
223 this observation is relevant for postharvest performance of fruit produce. Riederer and  
224 Schreiber (2001) found that cuticular permeability to water increases by a factor of 2 in  
225 the temperature range 15 °C to 35 °C and relates directly to solute transport through the  
226 cuticle, in agreement with the general observation that heating chemical solutions  
227 improves in many instances their absorption by fresh fruit. Cuticular permeability is  
228 also impacted by organic compounds of both biogenic and anthropogenic (for instance,  
229 those used in pesticides) origin, which may increase cuticular permeability apparently  
230 through a plasticising action on wax structure (reviewed in Riederer and Schreiber,  
231 2001).

232

### 233 ***5.1. Water loss***

234 Post-harvest water loss of fruit results from fruit respiration and diffusion through  
235 the fruit cuticle. Although water potential gradient from inside to outside the fruit varies  
236 throughout storage according to temperature and relative humidity, considerable  
237 species- and cultivar-related variability exists in water loss, which indicates differences

238 in cuticular permeability to water. This variability arises from a combination of fruit  
239 maturity, environmental conditions, and genetic differences in factors such as cuticle  
240 thickness, presence of pores or cracks, and quantity, distribution or chemical nature of  
241 cuticular components (Lownds et al., 1994; Maguire et al., 1999; Knoche et al., 2000;  
242 Peschel et al., 2003; Gibert et al., 2010).

243 Contradictory results have been reported as to the relevance of cuticle thickness for  
244 weight loss during storage. Significant differences in wax deposition and cuticle  
245 thickness were observed in ozone-treated 'Casselman' plums as compared to control  
246 fruit, and suggested to have contributed to differences in weight loss (Crisosto et al.,  
247 1993a). Pepper fruit displaying high epicuticular wax contents also lost weight at  
248 significantly lower rates (Lownds et al., 1993). In other cases, the positive effects on  
249 weight loss reduction of given postharvest treatments have been shown to be  
250 independent of cuticle thickness. For example, decreased weight loss in heat-treated  
251 cactus pears was suggested to arise from rearrangement of the epicuticular wax layers,  
252 which minimised cracks and fissures, as no treatment effects were found on cuticle  
253 thickness or respiration rates of fruit (López-Castañeda et al., 2010). Indeed, when water  
254 permeability values of cuticles from 61 plant species were reviewed in a survey which  
255 included mostly leaf, but also a few fruit cuticles (Riederer and Schreiber, 2001), it was  
256 concluded that this property was not correlated to thickness or wax coverage, most  
257 water apparently diffusing as single molecules across a lipophilic barrier.

258 The thickness of the cuticular wax layer is usually estimated gravimetrically by  
259 extracting in organic solvent, drying and weighing the wax, and then relating it to the  
260 surface units of skin or cuticular membrane used for the extraction. However, this  
261 procedure implies tissue destruction and damage to the wax layer, and thus does not  
262 allow assessing changes in cuticle structure, which may prove more relevant than

263 thickness or amount for water permeability properties of cuticle. Instead, Veraverbeke  
264 et al. (2001b) used confocal laser scanning microscopy (CLSM) to visualise the changes  
265 in cuticle structure and thickness during long-term (nine months) ultra-low oxygen  
266 (ULO) storage of ‘Elstar’, ‘Jonagold’ and ‘Jonagored’ apple fruit. This approach  
267 allowed the use of the same fruit throughout the experimental time, and showed  
268 profound differences in the wax layer according to cultivar and storage period, likely  
269 related to water loss rates of each particular cultivar. During storage of all three  
270 cultivars, the wax layer smoothed to cover the cracks, likely as a protection against  
271 moisture loss, and the wax penetrated into the cutin layer. Further research on the same  
272 apple cultivars demonstrated that the diffusion coefficient of wax was at least a hundred  
273 times smaller than that of cutin (Veraverbeke et al., 2003a), and revealed considerable  
274 cultivar-related differences in diffusion properties of the cuticle. Based on these  
275 investigations, a model for the prediction of moisture loss across the cuticle of apple  
276 during storage was developed (Veraverbeke et al., 2003b) and validated partially  
277 (Veraverbeke et al., 2003c).

278 In addition to the significance of cuticle thickness in weight loss as discussed  
279 above, experimental evidences also exist on the role of particular cuticle components in  
280 cuticular permeability, waxes having been generally shown as the major cuticular  
281 components accounting for its function as an impermeability barrier. Removal of  
282 surface waxes of ‘Calrico’ peaches resulted in significantly higher water loss rates  
283 (Fernández et al., 2011). The peel of the glossy *sticky peel* tomato mutant is more elastic  
284 and shows increased cuticular permeability than the wild type, apparently associated to  
285 a lower proportion of long-chain alkanes in epicuticular waxes (Nadakuduti et al.,  
286 2012). Similarly, biochemical characterisation of the cuticular waxes of the LeCER6  
287 loss-of-function tomato mutant showed decreased content in very long-chain *n*-alkanes

288 along with elevated levels of amyryns, with an associated 3- to 8-fold increase in water  
289 loss per fruit surface area in comparison with the wild-type fruit in spite of the fact that  
290 the mutant has thicker cuticles (Vogg et al., 2004; Leide et al., 2007). Because the  
291 difference in water loss between the mutant and the wild type was abolished by  
292 chloroform extraction of total waxes, but not when only the epicuticular waxes were  
293 removed (Vogg et al., 2004), it was concluded that the main portion of the transpiration  
294 barrier is located in the intracuticular wax layer, whose core properties are defined by  
295 the *n*-alkanes but modulated by the presence of triterpenoids. The physiological and  
296 biochemical characterisation of three *cutin deficient* tomato mutants (*cd1*, *cd2* and *cd3*)  
297 provided interesting clues as to the possible role of each type of cuticle component on  
298 cuticle function (Isaacson et al., 2009). For instance, despite severely impaired cutin  
299 deposition in all three mutant lines, only *cd1* fruit show dramatically increased water  
300 loss during the postharvest period, suggesting that the cutin matrix does not play a  
301 central role in limiting water loss and that waxes are the primary barrier against  
302 dehydration. Interestingly, the total amount of waxes in cuticles of wild type and *cd*  
303 fruit is similar, but wax composition differs in each *cd* line. It was concluded that  
304 reduced wax alkanes and enhanced triterpenoids would lead to an increase in the  
305 amorphous portion of the cuticular waxes thus impairing cuticle function as a barrier  
306 against water loss. This model questions a role for cutin as a significant hydrophobic  
307 barrier, and rather attributes it the function of providing a framework into which the  
308 intracuticular wax compounds can adopt a functional structure for restricting water  
309 movement.

310 Total cuticular wax amounts were likewise directly related to postharvest water loss  
311 during storage of pepper fruit from 10 cultivars, while no association was found to total  
312 cuticle amount, total cutin or to the amount of individual cutin or wax constituents

313 (Kissinger et al., 2005). In contrast, Parsons et al. (2012) reported significant  
314 correlations of water loss in *Capsicum* sp. fruit not only to wax, but also to cutin  
315 monomer composition. Simple straight-chain aliphatic cuticle components were more  
316 closely related to the formation of impermeable barriers than isoprenoid compounds, the  
317 ratio alkane to triterpenoids plus sterols being negatively correlated to dehydration in  
318 accordance with previous observations for tomato (Isaacson et al., 2009). Moreover,  
319 water loss rates were associated to total cutin content, to total C<sub>16</sub> monomers, and to 16-  
320 hydroxypalmitic acid. The analytical procedures in both cases were similar, involving  
321 enzymatic isolation of cuticles, chloroform/methanol dewaxing and N,O,-  
322 bis(trimethylsilyl)trifluoroacetamide (BSTFA) derivatisation of cutin monomers. These  
323 discrepancies may thus have arisen from the different *Capsicum* genotypes used in each  
324 case, and suggest relevant cultivar-related differences in cuticle functionality.

325       However, cuticle properties and their effect on fruit characteristics may be only  
326 partially related to cuticular chemical components. Hovav et al. (2007) developed a  
327 novel tomato genotype via introgression from the wild tomato species *Solanum*  
328 *habrochaites*, which is prone to cuticle microfissuring and fruit dehydration. This  
329 phenotype was demonstrated to be inherited as a single gene (*Cuticular Water*  
330 *Permeability; Cwp1*) which is expressed mainly in the epidermal tissue and codes for a  
331 protein of unidentified function. Because no significant differences were observed  
332 between the wild-type and the introgressed genotypes in either wax or cutin  
333 components, it was hypothesised that the CWPI protein is likely to affect the  
334 rheological properties of the skin by a yet unclear mechanism, or may impact on other  
335 components of epidermal development such as cell division or expansion.

336

## 337       **5.2. Susceptibility to infections**

338 Disease resistance of fruit declines with ripeness stage and with storage period. In  
339 some cases, hyphae of the pathogen organism can infect the fruit by direct penetration  
340 of the cuticle, sometimes forming highly specialised structures. For example,  
341 *Colletotrichum acutatum* penetrates the cuticle layer of *Capsicum* spp. fruit by forming  
342 a highly branched, thick-walled hypha within 24h post-inoculation (Liao et al., 2012).  
343 This structure has only been found in the cuticle layer of *Capsicum* fruit, as it was not  
344 found when the pathogen was inoculated onto pepper petals, mango leaves, or tomato  
345 and eggplant fruits. Although many other common postharvest pathogens are unable to  
346 penetrate directly the host cuticle and require surface injuries or natural opening such as  
347 lenticels and stomata (Coates and Johnson, 1997), fruit become progressively more  
348 susceptible to wounds and mechanical damages in general after long-term storage, thus  
349 opening a route for the development of infections. Some of these injuries can be  
350 microscopic such as those arising from surface microcracking to which some fruit  
351 species are particularly prone, and which is directly dependent on cuticle amount,  
352 composition and mechanical properties. The protective effect of ethylene treatment  
353 against disease incidence by *Penicillium digitatum* in 'Navelate' oranges has been  
354 ascribed to the synthesis of new waxes in treated fruit, which may cover stomata, cracks  
355 or areas lacking wax that are generated during storage, thus imposing a physical barrier  
356 to infection (Cajuste et al., 2010).

357 Relationships between infection susceptibility and cuticle thickness and structure  
358 have been suggested for apple fruit (Konarska, 2012). Lower incidence of rots and  
359 longer post-harvest life in cranberries has also been attributed to thicker cuticle and wax  
360 accumulation at the calyx end, which would retard the entry of microorganisms into the  
361 fruit during wet harvest (Özgen et al., 2002), a harvesting practice in which the fields  
362 are flooded in order to facilitate gathering of fruit. Similarly, cuticle thickness and wax



363 contents correlated positively with resistance to *Botrytis cinerea* in up to 42 genetically  
364 diverse cultivars and selections of table grapes (Marois et al., 1986; Mlikota Gabler et  
365 al., 2003). Cuticle density and thickness have been shown likewise to be related to stone  
366 fruit susceptibility to infection by *Monilia fructicola*, yet this could only partially  
367 explain the differences in fruit predisposition to this rot (Crisosto et al., 1997),  
368 suggesting a role for particular cuticular components in modulating disease resistance.  
369 For instance, when ‘Thomson Seedless’ grape berries were dipped in chloroform to  
370 remove epicuticular waxes, a significant increase in susceptibility to infection by *B.*  
371 *cinerea* was observed (Marois et al., 1985). In contrast, the cutin content of the cuticle,  
372 rather than waxes, and cuticle thickness, were suggested as indicators of susceptibility  
373 to *B. cinerea* infection in ‘Pinot noir’ grapes (Comménil et al., 1997). A major role for  
374 cutin in determining susceptibility to infections is also supported by observations that  
375 epicuticular wax content and appearance were unchanged in grapes of four seedless  
376 cultivars after dipping in hot ethanol, despite the fact that dipped fruit were more  
377 susceptible to subsequent infection (Mlikota Gabler et al., 2005). No apparent  
378 relationship was found either between the severity of the sooty blotch disease caused by  
379 *Peltaster fructicola* and *Leptodontidium elatius* and the major epicuticular wax  
380 components of five different apple cultivars (Belding et al., 2000).

381       The relative importance of particular cutin and wax components to resistance  
382 against infection is poorly understood, but some research efforts have been focused on  
383 this aspect. Bostock et al. (1999) studied the basis for the high resistance of ‘Bolinha’  
384 peach to infection by the brown rot fungus *M. fructicola*, and found that the phenolic  
385 chlorogenic and caffeic acids, otherwise quantitatively minor cuticular components,  
386 were present in high amounts on the surface of the resistant fruit and suppressed  
387 cutinase activity levels in cultures of *M. fructicola*. A series of cinnamic and benzoic

388 acid derivatives also suppressed the activity of cutinase, an enzyme that pathogenic  
389 fungi can use to aid penetration of the cuticle. Likewise, *in vitro* assays demonstrated  
390 inhibiting effects of *n*-alkanes and triterpenoids on spore germination and mycelial  
391 growth of *Alternaria alternata*, a causal agent of Alternaria rot of pears, suggesting a  
392 major contribution to the antifungal properties of the cuticular waxes of Asian pear (Yin  
393 et al., 2011).

394       Recent efforts to characterise genes involved in fruit cuticle development will allow  
395 identifying or confirming key elements for specific cuticle functions. For instance, all  
396 three *cd* tomato mutants (Isaacson et al., 2009) have as little as only 5-10% cutin  
397 amount as compared to the wild-type, with an associated increase in pathogen  
398 susceptibility. Similarly, silencing of the transcription factor SISHN3 and the fatty acid  
399  $\omega$ -hydroxylase SICYP86A69 in tomato led to increased predisposition to infection by  
400 the fungus *Colletotrichum coccodes* and postharvest water loss (Shi et al., 2013).  
401 Biochemical characterisation of cuticles of mutant fruit showed that higher  
402 susceptibility to infection was related to sharply decreased content of specific cutin  
403 monomers, particularly of the C<sub>16</sub> class and, for the mature green stage, also of the  
404 phenolic compounds benzoic acid and *trans*-coumaric acid.

405

### 406       **5.3. Physiological disorders**

407       The outer surface layers of fruit, including cuticles as well as epidermal and  
408 subepidermal tissues, constitute the skin and represent the main structures conferring  
409 mechanical strength to fruit. The skin surrounds a mass of more deformable material;  
410 when skin failure occurs, cracks develop (Matas et al., 2005; Becker and Knoche,  
411 2012). This cuticular cracking appears mainly in ripe fruits and, when severe enough to  
412 be visible, it represents an important problem for many commodities, causing large

413 economic losses due to negative effects on fruit appearance, acceleration of water loss  
414 and creation of an entry for pathogens. Cracks may also help accelerate oxidative  
415 processes thus favouring browning alterations. On the other side, microcracks on the  
416 surface can be an important pathway for the uptake of minerals such as calcium.  
417 Transport of exogenously applied  $\text{Ca}^{2+}$  through apple cuticles has been shown to occur  
418 mainly through lenticels and cracks in the cuticle (Harker and Ferguson, 1988), and  
419 epicuticular wax cracks become wider and deeper as storage period increases, thus  
420 intensifying  $\text{Ca}^{2+}$  uptake by fruit (Roy et al., 1999). Heat-treated ‘Golden Delicious’  
421 apples absorbed significantly less calcium than untreated fruit (Roy et al., 1994; Lurie et  
422 al., 1996), this effect being attributed to wax softening leading to smoothing or  
423 elimination of the deep cracks present in epicuticular waxes of non-heated controls.

424       Cracking typically occurs when maturation and harvest coincide with a period of  
425 high humidity, causing water movement from branches and leaves to the fruit owing to  
426 a large difference in their water potentials. The cracking disorder has been especially  
427 studied in sweet cherry fruit (Sekse, 1995, 1998, 2008; Knoche et al., 2000, 2001, 2002;  
428 Knoche and Peschel, 2002; Peschel and Knoche, 2005). Removal of epicuticular wax  
429 had no effect on the frequency of water-induced microcracks in seven different  
430 cultivars, but hydration increased fracture strain while decreasing fracture stress and  
431 elasticity modulus (Knoche and Peschel, 2006). No relationship was found either  
432 between cracking susceptibility and skin elasticity, cuticle thickness or the content of  
433 different minerals, with the exception of calcium the levels of which were higher in the  
434 cracking-resistant cultivar ‘Sue’ (Lane et al., 2000). While the physical properties of the  
435 epidermal and subepidermal cells might be relevant for cracking susceptibility, which  
436 would explain the observed impact of calcium, the cessation of cuticle deposition during  
437 early sweet cherry development has been reported to associate with down-regulation of

438 several genes putatively involved in cuticle formation (Alkio et al., 2012). The increase  
439 in strain imposed on the surface as fruit expands would lead to the formation of  
440 microcracks. The identification of these candidate genes will allow cause/effect studies  
441 on cuticle composition or properties and the development of this disorder.

442 Cuticle density has been related to the development of disorders such as flesh  
443 browning during storage of apples (Jobling, 2002). Gas diffusion through fruit tissues  
444 can be limited under certain controlled atmosphere conditions, resulting in too low O<sub>2</sub>  
445 and too high CO<sub>2</sub> levels which cause browning damage in the cortex. Some apple  
446 varieties are particularly susceptible to russetting and lenticel breakdown, originated  
447 when cuticle surrounding lenticels cracks under conditions of rapid fruit growth and  
448 worsened along storage (Curry, 2003). In turn, the severity of those cracks is related to  
449 the structure of surface waxes, and impacted by humidity conditions during the growing  
450 season (Faust and Shear, 1972). Cuticular free phenolic compounds are correlated  
451 negatively with the formation of conjugated trienes during storage of apples, and thus  
452 with the development of superficial scald (Ju and Bramlage, 2000), possibly mediated  
453 by the antioxidant activity of these compounds. The skin spot disorder, an important  
454 physiological alteration in 'Elstar' apple fruit after removal from controlled atmosphere  
455 storage, is associated to microcracks in the cuticle, apparently arising from oxidative  
456 damage through those cracks upon removal from storage (Grimm et al., 2012).

457 Other alterations are likewise related apparently to the loss of integrity of the  
458 cuticle structure and functionality. The development of skin discolouration in stone fruit  
459 species such as peach and nectarine has been ascribed to abrasion injuries in the cuticle,  
460 which expose the epidermal cells to alterations in pH or content of metallic ions, thus  
461 inducing changes in anthocyanin colour (Crisosto et al., 1993b).

462 In relation to citrus fruit, epicuticular wax morphology is related to water  
463 permeability of cuticles in 'Fortune' mandarins, higher permeability values coinciding  
464 with higher incidence of peel pitting (Vercher et al., 1994). Morphological changes in  
465 the surface waxes might also underlie the protective role of ethylene against peel pitting  
466 in oranges, although no satisfactory relationship was found to water stress or to  
467 compositional changes in waxes (Cajuste et al., 2010). No correlation was observed  
468 either between epicuticular wax content and susceptibility to rindstaining of orange fruit  
469 (Sala et al., 1992), suggesting that compositional alterations rather than total amount of  
470 waxes are relevant for the development of the alteration. This view is supported by the  
471 finding that higher incidence of rindstaining in 'Fortune' mandarins is associated with  
472 lower content of *n*-alkanes and esters, and with higher proportion of ketones and fatty  
473 acids (Sala, 2000), possibly in relation to the severe damages observed in the structure  
474 of the epicuticular wax layer and resulting increase in flavedo water permeability and  
475 water loss. Finally, greater incidence of chilling injury in grapefruit after cold storage  
476 may be mediated by differences in epicuticular wax morphology and composition,  
477 specifically by an increase in the content of *n*-alkanes (McDonald et al., 1993).

478

#### 479 ***5.4. A role in post-harvest firmness changes?***

480 Mechanical factors, chiefly tissue firmness, have the most influence on fruit texture.  
481 Firmness changes of fruit during ripening and after harvest have been the object of  
482 intensive research efforts throughout more than 40 years. The primary focus of research  
483 on fruit softening has been placed on cell wall metabolism (reviewed in Goulao and  
484 Oliveira, 2008) and has generally overlooked other possible physiological processes  
485 involved. Genetically suppressed expression of several ripening-related cell wall-  
486 modifying proteins has generally failed to counteract firmness loss to a significant

487 extent (Rose et al., 2003), leading to the view that ripening-related cell wall disassembly  
488 results from the cooperative action of many different activities. In this context, some  
489 reports suggest that cuticle composition and architecture may also play a key role in  
490 firmness changes of fruit.

491       The cuticle provides structural support for those fruit lacking hard internal tissue. It  
492 may function as an external structural element that adds mechanical support for tissue  
493 integrity. Cuticular wax components of grape berries are tightly bound and highly  
494 ordered at the molecular order, and the resulting barrier structure protects but also  
495 imparts consistency to fruit (Casado and Heredia, 1999). The biomechanics of tomato  
496 fruit skin and isolated cuticle have been investigated for three cultivars differing in  
497 cracking susceptibility and fruit shape, and it was concluded that cuticle is a  
498 mechanically important component of the tomato fruit (Bargel and Neinhuis, 2005).  
499 Stiffness of skin and cuticle increased during maturation and ripening, and failure stress  
500 and failure strain decreased, although some cultivar-related discrepancies were  
501 observed. The modifications in these properties at the final stages of ripening have  
502 implications for handling and storage potential. Mechanical properties of cuticle are  
503 altered according to storage conditions such as temperature and relative humidity  
504 (Edelmann et al., 2005; Matas et al., 2005); this can also be of relevance for changes in  
505 firmness. Despite that, the structure-function relationships between cuticle  
506 composition/structure and biomechanical properties have not been intensively explored.  
507 Bargel et al. (2006) hypothesised that the amount of phenolic compounds is correlated  
508 with rigidity of the cutin matrix at full maturity. Accordingly, the mechanical  
509 characterisation of cuticles isolated from mature green and red ripe ‘Cascada’ tomato  
510 fruit revealed that phenolics present in the cutin network are likely candidates to  
511 account for rigidity, whereas the polysaccharide components provide the elastic

512 behaviour of the whole cuticle (López-Casado et al., 2007), which suggests a role in  
513 determining at least some fruit textural attributes. These attributes include firmness as  
514 well as other physical characteristics related to deformation or fracture. A survey of the  
515 chemical composition, density and tensile properties of fruit cuticles in 27 persimmon  
516 varieties revealed that density and polysaccharide constituents contribute to cuticle  
517 strength and elasticity, while cutin is related to viscoelasticity (Tsubaki et al., 2012), and  
518 related these properties to the mechanical characteristics specific to each of the cultivars  
519 considered in the study.

520       Some studies have shown parallels between firmness loss and changes in cell  
521 turgor, which were apparently under cellular control and not simply a consequence of  
522 loss of membrane integrity (Shackel et al., 1991). Solutes accumulate in the apoplast  
523 during ripening of tomato (Almeida and Huber, 1999; Shackel et al., 1991),  
524 concomitantly with transpiration-related water loss favouring efflux of water from the  
525 fruit. Moisture loss has been actually identified recently as the major cause of firmness  
526 changes during postharvest storage of blueberry fruit (Paniagua et al., 2013), which  
527 otherwise displays only small changes in cell walls after harvest. A relationship of  
528 turgor loss to mechanical properties has also been observed for apples and nectarines  
529 (Lin and Pitt, 1986; Heyes and Sealey, 1996). This points to the regulation of water  
530 transpiration as a possible mechanism involved in firmness loss, and thus also suggests  
531 a role for fruit cuticle in the process.

532       Further insight on a possible role of cuticle in firmness changes has been provided  
533 by the characterisation of the otherwise normally ripening tomato mutant *DFD*  
534 (*'delayed fruit deterioration'*). These fruit remain firm for at least six months and show  
535 high resistance to opportunistic pathogens although the degree of cell wall disassembly,  
536 the reduction in cell-to-cell adhesion and the rates of gene expression related to cell wall

537 degradation are similar to those in the normally softening cultivar ‘Ailsa Craig’ (Saladié  
538 et al., 2007). Detailed characterization of this mutant demonstrated minimal  
539 transpiration water loss and substantially enhanced cell turgor arising from remarkable  
540 differences in fruit cuticle composition and structure. These results suggest that turgor  
541 and transpiration water loss are important determinants in the softening process of  
542 tomato. Since cuticle properties help modulating water loss, this external structure may  
543 contribute significantly to fruit texture. However, this may be restricted to fruit  
544 displaying thick and well developed cuticles, while the role of this outer layer of fruit  
545 surface might be considerably less in species characterized by weaker cuticles such as  
546 strawberries, for instance.

547

548

## 549 **6. Conclusions**

550 Biological surrounding structures represent the first contact of the plant cells and  
551 organs with the environment in which they grow, triggering signalling pathways that  
552 stand for the first line of defense and adaptation against biotic and abiotic stresses.  
553 Biotic and abiotic conditions keep modulating fruit development after harvest, and are  
554 important determinants of storage potential and quality of produce with vital impact on  
555 economic revenues for the sector. While the importance of the cell wall, that surrounds  
556 the plant cell, is widely recognised and has held large attention in studies on postharvest  
557 biology and technology of fruit produce, the role of the cuticle, that surrounds the fruit,  
558 has received much less attention. Major questions related to the interactions between  
559 fruit quality attributes and the composition and physiological roles of fruit cuticles,  
560 which demand detailed explanation, are illustrated in Fig. 1. From this review, it can be  
561 concluded that much more emphasis should be given to investigating fruit cuticles,



562 under a multidisciplinary approach including developmental biology, fruit physiology,  
563 physics and postharvest technology. On the other hand, knowledge of the background of  
564 each specific genotype is needed to understand general and specific postharvest  
565 behaviour. Even so, many knowledge gaps exist regarding the specific cuticle  
566 composition in individual fruit species and varieties (Table 1) that need to be addressed.  
567 From the technological point of view, huge benefits may also arise from a more  
568 comprehensive knowledge of the fruit cuticle composition and physiological role. A  
569 more detailed knowledge of the fine structure and role of cuticle biology and biophysics  
570 would be crucial to optimise tailor-made postharvest strategies aimed at improving  
571 quality maintenance and storage capability. To our best knowledge, this review is the  
572 first published work focusing on fruit cuticles as major factors modulating postharvest  
573 quality, and gathering and interlinking strewn literature on this topic.

574

575

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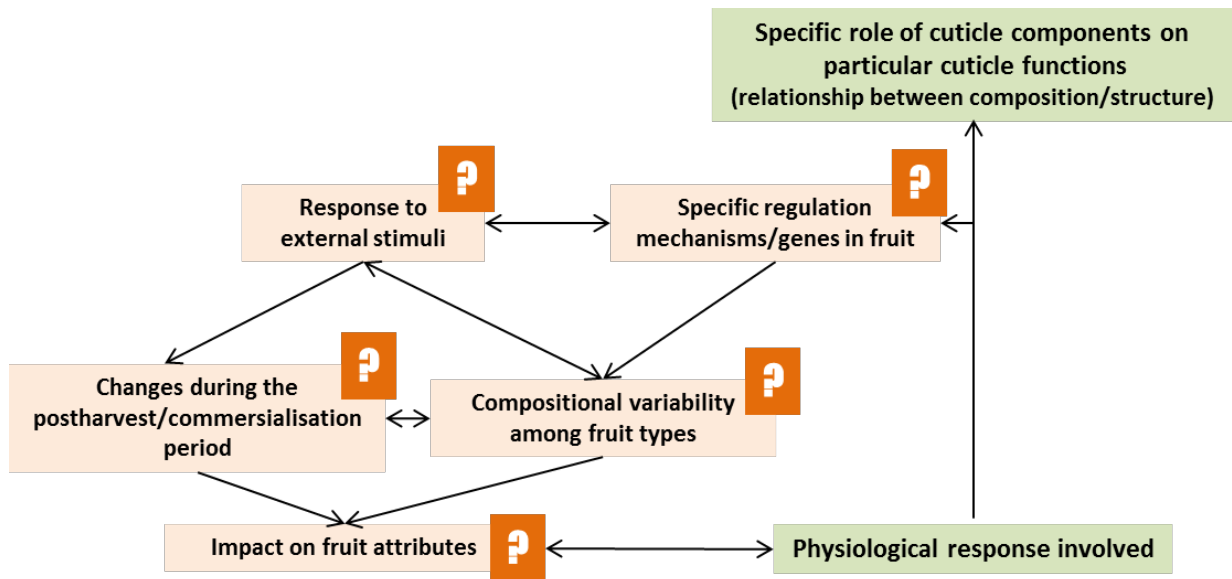
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**Figure 1.** Major unanswered questions on the interactions between cuticle characteristics and fruit quality attributes impacting postharvest management.

**Table 1.** A summary of the main reported constituents of cuticular waxes and cutin in fruits (n/r, not reported).

Fruit species	Cutin	Waxes				References
	Main monomer type	Carbonyl compounds	Alcohols	Alkanes	Terpenes	
<b>Apple</b>	18-OH C <sub>18</sub>	Fatty acids: C <sub>16:0</sub> , C <sub>18:2</sub> Other: C <sub>29</sub> -10-one (cultivar-specific)	Primary: C <sub>24</sub> , C <sub>26</sub> Secondary: C <sub>29</sub> -10-ol (cultivar-specific)	C <sub>29</sub>	Ursolic acid	Morice and Shortland, 1973; Espelie et al., 1979; Belding et al., 1998, 2000; Veraverbeke et al., 2001a; Dong et al., 2012
<b>Asian pear</b>	n/r	Fatty acids: C <sub>16:0</sub> , C <sub>18:2</sub>	Primary: C <sub>18</sub>	C <sub>29</sub> , C <sub>27</sub>	$\alpha$ -Amyrin	Yin et al., 2011
<b>Citrus</b>		Terpenoids > aldehydes > alkanes > alcohols (detailed composition not analysed)				
Grapefruit	16-OH-10-oxo C <sub>16</sub>					Espelie et al., 1980; McDonald et al., 1993
Lemon	n/r	Aldehydes: C <sub>24</sub> , C <sub>26</sub> , C <sub>28</sub>	n/r	C <sub>29</sub> , C <sub>31</sub>	n/r	Baker et al., 1975
Mandarin	n/r	Alkanes > esters > carbonyl compounds > primary alcohols > triterpenes (detailed composition not analysed)				Sala, 2000
Orange	n/r	Aldehydes: C <sub>24</sub> , C <sub>26</sub> , C <sub>28</sub>	Primary: C <sub>25</sub>	C <sub>29</sub> , C <sub>31</sub>	Amyrins	Baker et al., 1975; Cajuste et al., 2010; Liu et al., 2012
<b>Grape</b>	n/r	Aldehydes: C <sub>28</sub> , C <sub>30</sub>	Primary: C <sub>24</sub> , C <sub>26</sub> , C <sub>28</sub>	C <sub>25</sub> , C <sub>27</sub> , C <sub>29</sub> , C <sub>31</sub>	Oleanoic acid	Radler and Horn, 1965; Radler, 1965, 1970; Comménil et al., 1997; Casado and Heredia, 1999
<b>Other berries</b>						
Bilberry	9,10,18-triOH C <sub>18</sub> 9,10-epoxy-18-OH C <sub>18</sub>	n/r	n/r	n/r	n/r	Kallio et al., 2006
Black chokeberry	18-OH-9,10-epoxy C <sub>18:1</sub> 18-OH-9,10-epoxy C <sub>18:0</sub> 9(10),16-diOH C <sub>16:0</sub>	n/r	n/r	n/r	n/r	Järvinen et al., 2010
Black currant	10(9,8),16-OH C <sub>16</sub>	n/r	n/r	n/r	n/r	Kallio et al., 2006
Cloudberry	9(10),16-diOH C <sub>16:0</sub>	n/r	n/r	n/r	n/r	Järvinen et al., 2010
Cranberry	9,10-epoxy-18-OH C <sub>18</sub>	n/r	n/r	n/r	n/r	Kallio et al., 2006
Crowberry	9(10),16-diOH C <sub>16:0</sub> 18-OH-9,10-epoxy C <sub>18:0</sub> 18-OH C <sub>18:1</sub>	n/r	n/r	n/r	n/r	Järvinen et al., 2010
Lingonberry	9,10-epoxy-18-OH C <sub>18</sub> 9,10,18-triOH C <sub>18</sub>	n/r	n/r	n/r	n/r	Kallio et al., 2006
Raspberry	9(10),16-diOH C <sub>16:0</sub>	n/r	n/r	n/r	n/r	Järvinen et al., 2010
Rosehip	9(10),16-diOH C <sub>16:0</sub>	n/r	n/r	n/r	n/r	Järvinen et al., 2010



Rowanberry	9(10),16-diOH C <sub>16:0</sub>	n/r	n/r	n/r	n/r	Järvinen et al., 2010
Sea buckthorn	9,10-epoxy-18-OH C <sub>18</sub>	n/r	n/r	n/r	n/r	Kallio et al., 2006
Strawberry	9(10),16-diOH C <sub>16:0</sub>	n/r	n/r	n/r	n/r	Järvinen et al., 2010
<b>Pepper</b>	9,16-diOH C <sub>16</sub> 9-epoxy-18-OH C <sub>18</sub>	Fatty acids: C <sub>24</sub> , C <sub>26</sub> , C <sub>32</sub> (major chain length class)	n/r	C <sub>31</sub>	Amyrins	Kissinger et al., 2005; Parsons et al., 2012
<b>Persimmon</b>	578-1378 µg/cm <sup>2</sup> (detailed composition not analysed)	337-770 µg/cm <sup>2</sup> (detailed composition not analysed)				Tsubaki et al., 2012
<b>Stone fruits</b>						
Peach (melting)	18-OH C <sub>18:1</sub>	Fatty acids: C <sub>18:2</sub>	Secondary: C <sub>29</sub> -10-ol	C <sub>29</sub>	Ursolic and oleanoic acids	Belge et al. (unpublished)
Peach (non-melting)	18-OH C <sub>18:1</sub>	Fatty acids: C <sub>18:2</sub>	Secondary: C <sub>29</sub> -10-ol	C <sub>29</sub>	Ursolic and oleanoic acids	Fernández et al., 2011; Belge et al. (unpublished)
Sweet cherry	9(10),16-diOH C <sub>16:0</sub> 9,10,18-triOH C <sub>18:0</sub> (cultivar-specific)	Fatty acids: C <sub>18:2</sub>	Primary: C <sub>23</sub> , C <sub>30</sub> Secondary: C <sub>29</sub> -10-ol	C <sub>29</sub> , C <sub>27</sub>	Ursolic and oleanoic acids	Peschel et al., 2007; Belge et al. (unpublished)
<b>Tomato</b>	10,16-diOH C <sub>16:0</sub>	Fatty acids: C <sub>30</sub> , C <sub>32</sub>	Primary: C <sub>32</sub>	C <sub>31</sub> (C <sub>29</sub> , C <sub>33</sub> )	Amyrins	Vogg et al., 2004; Saladié et al., 2007; Hovav et al., 2007; Leide et al., 2007; Mintz-Oron et al., 2008; Isaacson et al., 2009; Kosma et al., 2010; Nadakuduti et al., 2012; Yeats et al., 2012; Shi et al., 2013
<b>Wild tomato</b>	Mid-chain epoxy-triOH C <sub>18</sub> (cultivar-specific)	Fatty acids: C <sub>16</sub> -C <sub>28</sub> (cultivar-specific)	Primary: C <sub>22</sub> -C <sub>30</sub> (cultivar-specific)	C <sub>29</sub> , C <sub>31</sub> (cultivar-specific)	Amyrins	Leide et al., 2007; Yeats et al., 2012