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Review

The fruit cuticle as a modulator of postharvest quality

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ABSTRACT

The composition and structure of fruit surface tissues have a noticeable influence on the postharvest storage potential of fruit, inasmuch as they behave as a barrier against drying, chemical attack, mechanical injuries and microbial infection. The 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 the first communication system with the surrounding biotic and abiotic environment. Published reports on the composition and biosynthesis of fruit cuticles are comparatively scarce, and many knowledge gaps exist on the part cuticles play in quality determination and postharvest performance. This review aims at collecting available information in relation to the role of the fruit cuticle as a determinant factor of some important traits related to postharvest quality, including water loss, susceptibility to physical and biological stresses, and decreased fruit firmness. To the best of our knowledge, this is the first published work focusing on the fruit cuticle as a major modulator of postharvest quality and interlinking existing dispersed literature on this topic. A deeper understanding of cuticle structure and function will be of help in understanding postharvest biology and in designing new technological solutions.

1. Introduction

Metabolic events that occur during maturation, ripening and postharvest development in fruit cause significant changes that reduce the marketable volume of the harvested product, the visual and organoleptic appeal to the consumer, the level of available vitamins and antioxidants, and storage ability. These occurrences cause large economic losses to the fruit crop sector.

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

Cuticles contribute to traits such as maximum strain, breaking stress or elastic modulus, which affect the mechanical behaviour of fruit and other plant organs. The viscoelastic and strain-hardening properties of cuticles contribute to reinforcing the epidermal cell walls, while simultaneously conferring extensibility (Domínguez et al., 2011a). In turn, such biophysical properties are dependent to some extent upon external conditions such as temperature and relative humidity (Edelmann et al., 2005; Matas et al., 2005). Cuticle strength and rigidity decrease when temperature increases, the structure exhibiting a phase transition at a given temperature. The effect of this transition temperature on the elastic modulus is dependent on relative humidity, as water is known to plasticise the plant cuticle (reviewed in Domínguez et al., 2011b). These two factors are thus among the most important ones in devising storage strategies for postharvest preservation. This review focuses specifically on the current available knowledge on the relevance of cuticle composition and properties for fruit quality during the postharvest period (see Fig. 1).

2. A brief overview of cuticle composition in fruit

Cuticles are lipidic layers mainly composed by cutin, a polyester polymer rich in hydroxylated and epoxy-hydroxylated C_{16} and C_{18} fatty acids. This cutin matrix is embedded with amorphous waxes and a minor fraction of phenolics, while the plant surface is

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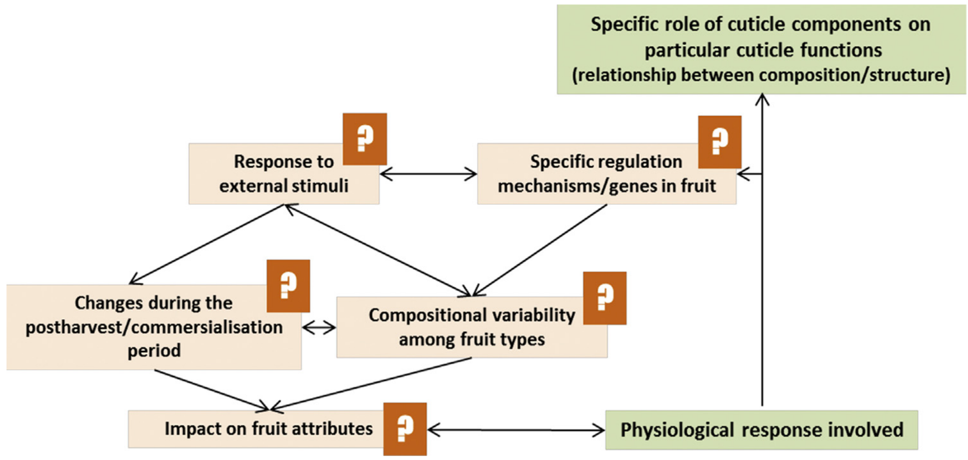

Fig. 1. Major unanswered questions on the interactions between cuticle characteristics and fruit quality attributes impacting postharvest management.

covered by epicuticular waxes, both amorphous and crystalline. On the inner side of the cuticle, cutin is mixed with pectin and glucan polysaccharides from the epidermal cell walls, the composition of which closely resembles that of primary cell walls (López-Casado et al., 2007). The cuticle also contains cutan, a non-ester network made of aliphatic compounds assembled mainly by ether bonds. Recent reviews have summarised available information on the composition and biosynthesis of cutin and cuticular waxes (Kunst and Samuels, 2003, 2009; Nawrath and Poirier, 2008; Pollard et al., 2008; Samuels et al., 2008). Some studies have shown that cuticle composition differs significantly in different organs of the same plant, both regarding cutin (Espelie et al., 1979, 1980; Marga et al., 2001; Järvinen et al., 2010) and waxes (Radler, 1965, 1970; Baker et al., 1975). In order to shed light on the possible roles of the cuticle in fruit quality and postharvest performance, therefore, it would be convenient to have data on the specific composition of fruit cuticles. Yet published reports on cuticle composition of fruit are comparatively scarce, research efforts having been focused primarily on vegetative tissues.

Currently available information on cutin and cuticular wax composition in different fruit types is summarised in Table 1. In many cases, the composition of either cutin or cuticular waxes has been reported separately, and thus for some fruit types the overview of cuticle constituents is still incomplete. Regardless of this, this survey shows that fruit cuticles display substantial variability according to species, genotypes within a given species, and developmental stage. In most of the reports summarised in Table 1, *n*-alkanes and triterpenoids have been identified as prominent components of cuticular waxes, in some cases accompanied by significant amounts of aldehydes. Among the *n*-alkanes, the C_{29} hydrocarbon *n*-nonacosane is regularly cited as a major compound, being the most abundant in cuticles of apple, citrus fruit and sweet cherry, while the C_{31} *n*-hentriacontane has been identified as the predominant alkane in other species such as pepper and tomato. With respect to the triterpenoid components of cuticular waxes, the triterpene ursolic and oleanoic acids dominate cuticular wax composition of apple, grape, peach and sweet cherry, whereas triterpenoid alcohols such as amyrins are predominant in citrus species, Asian pear, pepper and tomato.

3. Cuticle biosynthesis during fruit maturation and ripening

Some studies have addressed cuticle biosynthesis during fruit development, mainly from a morphological or quantitative perspective. Cuticle deposition reportedly ceases early during fruit development, prior to the onset of the ripening process and frequently before the fruit has attained maximum size, resulting in decreased amounts of cuticle per surface area and thus in reduced cuticle thickness in ripe fruit (Rosenquist and Morrison, 1988; Comménil et al., 1997; Belding et al., 1998; Dong et al., 2012; Liu et al., 2012). In some cases, early-arrested deposition of cuticular components and the associated decline in cuticle thickness causes microcracks as surface strain increases when fruit expand (Sala et al., 1992; Knoche et al., 2004; Knoche and Peschel, 2007; Peschel et al., 2007; Khanal et al., 2011; Becker and Knoche, 2012). A notable exception to this generally observed trend is tomato, for which a continuous increase in cuticular waxes and cutin monomers has been found during fruit development (Kosma et al., 2010).

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

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

For tomato, a very long-chain fatty acid β-ketoacyl-CoA synthase (LeCER6), required for the biosynthesis of very long-chain ($>C_{30}$) *n*-alkanes and aldehydes, has been identified and characterised (Vogg et al., 2004), and its loss-of-function mutant fruit displayed altered cuticle permeability and transpiration properties (Leide et al., 2007). Accordingly, Mintz-Oron et al. (2008) reported progressively increased expression of *SlCER6* (referred to as *LeCER6* in the previous papers by Vogg et al., 2004, and Leide et al., 2007) throughout maturation and ripening of tomato fruit. Some other cuticle-related genes have been also identified in tomato which are involved in cutin deposition (Isaacson et al., 2009; Nadakuduti et al., 2012; Yeats et al., 2012b; Shi et al., 2013), as well as a transcription factor that regulates fruit cuticle formation and epidermal