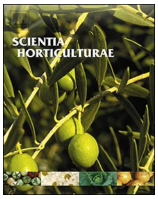
Scientia Horticulturae 232 (2018) 145–152

Contents lists available at ScienceDirect

Scientia Horticulturae

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



Review

The cuticle as a key factor in the quality of horticultural crops

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ARTICLE INFO

Keywords:
Biosynthesis
Cuticle
Quality
Crops
Biotic and abiotic stress

ABSTRACT

In recent years, there has been a major increase in the commercialization of horticultural crops in response to population increase. However, several important factors associated with pre- and post-harvest conditions, including drought stress, pathogen infection, water loss and climate change are limiting the commercialization potential of many horticultural crops, thereby compromising agricultural sustainability. The cuticle, which is composed of cutin and waxes, provides a critical structural barrier between a plant parts and its environment. Cuticle biosynthesis is influenced by many factors during plant development and contributes to the pre- and post-harvest quality of many horticultural crops. However, many aspects of the structure-function relationships of many aspects of the plant cuticle are not well understood. Studies focusing on cuticles are increasingly important due to the major challenges of crop production, such as diseases and abiotic stresses. In this review, we focus on the cuticle as a key factor in the quality of horticultural crops and provide an overview of the recent research and conclusions in the field.

1. Introduction

The aerial organs of terrestrial plants synthesize a hydrophobic cuticle as a protective barrier to avoid uncontrolled water loss. The cuticle is synthesized by the epidermal cell layer and is composed mainly of cutin and wax lipids (Kunst and Samuels, 2003). Cuticle biosynthesis comprises three processes: a) biosynthesis of lipids and elongation to form monomers; b) transport and export; and c) cuticle assembly. These processes are different among species and organs, including the patterns of cutin and wax deposition, suggesting that they are regulated by different mechanisms (Wang et al., 2016). The regulation of cuticle biosynthesis is complex and involves interacting signaling networks associated with the response to biotic and abiotic stresses, issues that are discussed in several reviews by Kunst and Samuels (2003), Samuels et al. (2008), Yeats and Rose (2013), Hen-Avivi et al. (2014), Martin and Rose (2014) and Fich et al. (2016).

Some cuticle properties, such as its flexibility and ability to self-repair, are of considerable economic significance and the variation in fruit cuticle composition may underlie differences in several traits such as resistance to biotic and abiotic stress (Riederer and Schreiber, 2001; Shi et al., 2013a). Despite the critical roles of the cuticle, its importance has been underappreciated and the structural bases of many of its roles are not well understood. Current knowledge of cuticle structure and composition have benefited from studies of *Arabidopsis thaliana* and tomato (*Solanum lycopersicum*) fruit, as well as transgenic lines with abnormal cuticles. This information has been useful for understanding the role of the cuticle in stress responses (Shi et al., 2013a).

The cuticle has several biological roles, which are important for fruit quality and post-harvest shelf-life, such as desiccation control, limiting microbial infection, and physiological disorders (Martin and Rose, 2014). It also influences fruit softening and postharvest fruit quality (Saladié et al., 2007). Some of the roles of the cuticle that are discussed in this review are shown in Fig. 1. In addition, we have included sections discussing the importance of the cuticle in resistance to disease, biotic and abiotic stress.

2. The role of the cuticle in disease, biotic and abiotic stresses: challenges for maintaining crop quality

Biotic and abiotic stresses influence the crop life cycle and compromise agricultural sustainability, with consequent effects on plant resources, biodiversity and global food security (Ahuja et al., 2017). To resist adverse environmental conditions, plants have developed adaptive stress responses, such as the protective barrier known as the cuticle, whose biosynthesis and properties are influenced by many environmental factors such as temperature, UV-B radiation, light, humidity, ozone, and elevated carbon dioxide levels (Baker, 1974; Giese, 1975; McQuattie and Rebbeck, 1994; Shepherd et al., 1995; Matas et al., 2005). Variations in cuticular wax load depending upon growing conditions have been observed (Hunsche and Noga, 2011), as have changes in the wax chemical composition, morphology and surface wettability following changes in humidity. For instance, *Brassica oleracea,*

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https://doi.org/10.1016/j.scienta.2018.01.005
Received 13 October 2017; Received in revised form 31 December 2017; Accepted 4 January 2018

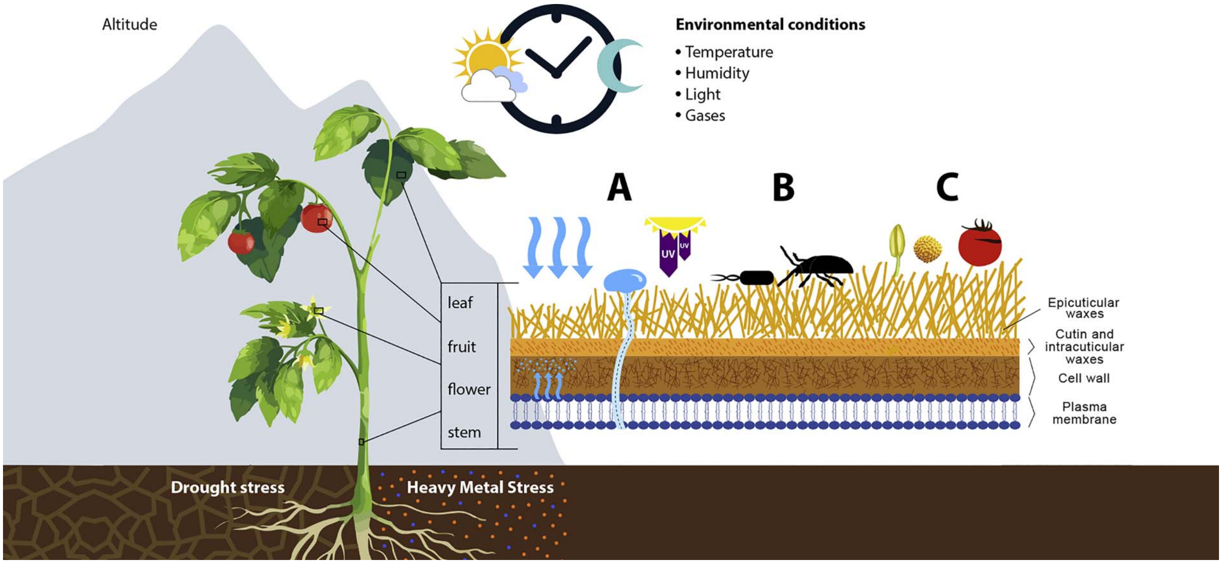

Fig. 1. The physiological roles of the cuticle in crop plants. The cuticle covers leaves, stems, flowers and fruits, protecting them against biotic and abiotic stress and diseases. Many environmental conditions influence cuticle biosynthesis. A, the cuticle protects against abiotic stress by reducing water loss, restricts disease via the "lotus effect" and reduces UV radiation damage. B, the cuticle protects against biotic stresses, such as those caused by bacteria, viruses and insects. C, the cuticle roles in diseases, such as in anther and exine formation as well as fruit russeting.

Eucalyptus gunnii and *Tropaeolum majus* grown under 98% relative humidity (RH) showed a decrease in total wax and wax crystal density, but a significant increase in leaf surface wettability. Conversely, under 20–30% RH, increased total wax amounts and reduced surface wettability were observed (Koch et al., 2006). In the Compositae family, the amount of total wax was significantly higher and levels of *n*-alkanes were the largest component in plants growing at high altitudes, while primary alcohols were the main wax components at low altitudes, suggesting that variations in cuticle components might be an adaptive response to altitude (Guo et al., 2016a). Recent studies of the role of the cuticle in responses to climate changes have shown that the presence of low oxygen levels (hypoxia) correlate with lower total wax and cutin levels and a downregulation of cuticle associated genes. This induced change in cuticle ultrastructure leads to increased permeability, allowing the plant to cope with oxygen deficiency (Kim et al., 2017).

The cuticle wax profile and ultrastructure may also vary by season and even with fruit position on trees such as orange (*Citrus sinensis* (L.) Osbeck) and these changes are associated with changes in environmental conditions and the effects of both biotic and abiotic stresses during each season (El-Otmani et al., 1989; Gülz et al., 1991; Jenks et al., 2002).

It is important to consider the cuticle anti-adhesive properties and their role in pesticide retention and/or absorption, since the persistence of pesticide residues may be a potential risk to consumers. Riccio et al. (2006) reported that epicuticular waxes influence the penetration of the insecticide, chlorpyrifos-methyl, into the pulp of some fruits. It has also been reported that higher cuticular wax load and lower contact angles are related to the uptake of leaf-applied agrochemicals (Hunsche and Noga, 2011). The hydrophobic properties of epicuticular waxes confer water-repellent properties, resulting in a self-cleaning surface and "the lotus-effect" (Neinhuis and Barthlott, 1997), where water droplets roll off plant surfaces, carrying with them contaminating particles such as dust and fungal spores.

The cuticle has been associated with several horticultural diseases in both pre- and postharvest contexts. It also prevents organ fusion, as exemplified by the tomato recessive *positional sterile* (*ps*) mutation, where cuticle composition is altered by an almost complete absence of *n*-alkanes and aldehydes, resulting in floral organ fusion and positional sterility (Leide et al., 2007). Furthermore, overexpression of the *CFLAP1* and *CFLAP2* transcription factors has been shown to lead to changes in the expression of genes involved in the fatty acid, cutin and wax biosynthetic pathways, and to cause multiple cuticle defective phenotypes, such as organ fusion, breakage of the cuticular layer and decreased epicuticular wax crystal load (Li et al., 2016). Interestingly, it has been proposed that epicuticular wax structure and chemical composition, rather than total wax load, influences rind staining and peel pitting of Fortune mandarin (*Citrus reticulata*) fruits (Sala, 2000). It has also been reported that cuticle microcracking can generate pathways for pathogen invasion in cucumber fruit (Martínez and Fernández-Trujillo, 2007). In cactus pear (*Opuntia ficus-indica* Mill. (L.) cv. Gialla), heat treatment caused a partial melting of the epicuticular wax layers, leading to a modified cuticle structure and sealing of micro-wounds and cracks. This was considered a contributing factor in the protection against pathogen wounding that reduced decay during storage, retention of visual quality and prevention of chilling injury (Schirra et al., 1999).

The cuticle plays a role during ripening and storage, and the epicuticular wax composition and morphology, in particular, are considered to be an integral part of fruit ripening. These changes can reduce non-chilling peel pitting and disease incidence caused by *Penicillium digitatum* in orange fruit (*Citrus sinensis*), suggesting that the formation of new waxes in fruit treated with ethylene may partially cover stomata, cracks or areas lacking wax (Cajuste et al., 2010). Finally, during fruit storage, changes in wax compounds and wax morphology lead to skin greasiness in apples (*Malus domestica*) (Yang et al., 2017).

2.1. Drought stress

Drought stress (DS) is one of the main limitations to global agricultural production, and future water-limiting environments caused by climate changes will further exacerbate a reduction in the production and quality of horticultural crops. Plants have evolved diverse adaptive strategies and mechanisms to avoid such stress, including stomatal closure, promotion of root growth and alteration of the water potential components to allow water uptake, among others. Cuticular wax biosynthesis has also been shown to contribute to drought resistance (Seo and Park, 2011), and plant species that grow in naturally dry conditions provide an opportunity to understand the role of the cuticle under DS. For example, transcriptomic analysis of the desert plant, *Reaumuria*