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Review

Strengthening fruit-skin resistance to growth strain by application of plant growth regulators

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ABSTRACT

Russeting and cracking of fruit skin are major disorders that limit fruit quality and marketability. The causes suggested to be environmental condition, orchard management and failure of the skin to resist surface tensions due to fruit expansion. Basically, fruit skin is made of epidermis cells and cuticular matrix. Increased cuticle thickness, higher epidermal cell density and cell morphology that support strong adhesion between neighboring cells are characteristic of fruits tolerant to cracking compared to susceptible genotypes.

Apple is being increasingly considered as a model for fruit development studies. Recently, spraying a mixture of gibberellin A4 plus A7 (GA_{4+7}) and the cytokinin 6-benzyl adenine (BA) at cell division stage of apple fruit development was shown to result with reduced incidence of skin cracking by maintaining a higher number of epidermal cells compared to untreated fruit.

Various treatments with plant growth regulators (PGR) were tested for controlling cracking incidence in other fruits, including tomato, pear, persimmon, apricot, grape, mandarin and kiwi. We hypothesize a common mechanism for BA + GA_{4+7} effect on fruit skin, and propose to view the skin as a tissue whose characteristics may be manipulated to improve its resistance to environmental and growth strains.

The review paper links practical approaches in the orchard to control costly yield losses with (limited) knowledge on fruit skin anatomy and development, and discussed the hypothesis that similar treatments may be applied with various agricultural important fruits.

Contents

1. General introduction

Fleshy fruits are covered with an outer protective layer known as peel, skin or rind, depending on the botanical definition. This layer may be thin, such as in grape, tomato or apple, or thick as in citrus fruits and pomegranate, where it consists of inner and outer layers called albedo and flavedo, respectively. The peel should be able to resist the strain caused by growth but not limit fruit expansion, and at the same time provide protection against pests, pathogens and extreme environmental conditions.

Fruit cracking is one of the main disorders limiting fruit quality and yield. The phenomenon occurs mainly in the pre-harvest stage and initiates at the surface of the fruit, where cracks traverse the cuticle and penetrate the inner tissues; extreme cracking can result in fruit splitting. Cracks mar fruit appearance, allow water loss and

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pathogen invasion, decrease storage and shelf life, and therefore reduce fruit marketability.

The cracking phenomenon affects many types of fruit: apple, sweet cherry, grape, pomegranate, persimmon, litchi, citrus and tomato, among others. It can be caused by external conditions that affect fruit development, such as orchard management (irrigation and nutrition) and environmental conditions (temperature, humidity, wind and light), and by fruit characteristics (shape, size, and firmness), and anatomy and strength of the fruit skin (Khadivi-Khub, 2015).

Apart from agricultural considerations, the cracking phenomenon, its causes and treatments enable a unique examination of peel characteristics at the cellular level. For simplicity, the peel is made up of one or two epidermal cell layers covered on the external side with cuticular matrix made up of cutin and wax, and underlain by two to three layers of hypodermal cells. In the present review, we focus on the outermost layers—the epidermis and cuticle—and use the terms skin or peel according to context.

2. Fruit-skin anatomy

The cuticular layer is a continuous hydrophobic structure, composed predominantly of two components: cutin, a polymer of hydroxylated and epoxy-hydroxylated C16 and C18 esterified fatty acids, and wax—very-long-chain fatty acids and their derivatives, such as alkanes, alcohols, aldehydes and esters; both cutin and wax are produced and secreted by the epidermal cells (Hen-Avivi et al., 2014; Yeats and Rose, 2013). The waxes are unpolymerized, and are embedded in and deposited on the cutin matrix; the latter is connected to the polysaccharides of the outer cell wall of the underlying epidermal cells (Domínguez et al., 2011a; Lopez-Casado et al., 2007). Monomer composition of the cuticle may differ among species and different plant organs may contain additional metabolites, such as phenolics and flavonoids (Domínguez et al., 2011b). In addition, cuticle composition during fruit development may follow different patterns, including increases in cuticle thickness, density and stiffness (Espana et al., 2014). Lack of coordination between cuticle deposition and growth expansion of the fruit surface has been implicated in a number of surface disorders, including fruit russeting and cracking (Knoche et al., 2004).

Little information is available on fruit epidermis development, although the morphology of the epidermal layer may contribute to cracking resistance. For example, high epidermal cell density implies more cell walls per unit surface area, reducing the cutin-to-polysaccharide ratio. This confers elasticity (Lopez-Casado et al., 2007) and provides stronger structural support for the cuticle. In addition, less elongated and more rounded epidermal cells potentially distribute pressure more evenly throughout the cell and to the overlying wall and cuticle, reducing the pressure on any one area (Considine and Brown, 1981) and the probability of skin failure and cracking disorder (Emmons and Scott, 1998). Furthermore, a link between epidermal development and cuticle formation has been reported. SHINE clade transcription factors were found to regulate the transcriptional network that acts in epidermal patterning and fruit-cuticle formation, and links cutin metabolism with the more global program of epidermal cell patterning and organ formation in tomato fruit (Shi et al., 2013, 2011).

In accordance with the aforedescribed skin biomechanics, studies on berry fruit genotypes that are tolerant or susceptible to skin cracking have indicated that cuticle thickness and epidermal cell density are positively correlated with cracking resistance (Emmons and Scott, 1998; Matas et al., 2004). Similarly, a cracking-susceptible apple cultivar had less crystalline wax and a thinner cuticle layer (Konarska, 2013). These observations imply that manipulations of epidermal cell density and cuticle thickness and composition might enable strengthening the peel and controlling cracking incidence.

3. Apple skin as a model for studying peel cracking in orchard fruits

Apple is becoming an increasingly popular model for fruit-development studies (Eccher et al., 2013). Apple skin is composed of a single- or double-layered epidermis covered by a cuticle and underlain by multiple layers of hypodermis cells; the outer surface of the cuticle is covered by wax crystals and the inner surface is characterized by cuticle extensions ("pegs") between adjacent epidermal cells (Khanal et al., 2014; Konarska, 2013). Cuticle morphology and composition vary among cultivars, and change in response to environmental stresses as well as during fruit development (Belding et al., 1998). The cuticle layer, being in contact with the external environment, contains micro-cracks and fissures of varied widths and depths that do not extend to the epidermal cell walls (Konarska, 2013) and are of no agricultural significance.

The development of fleshy fruit in most species is characterized by a short cell-division phase followed by continuous cell expansion until ripening (Azzi et al., 2015). In apple, fruit growth follows a sigmoidal extension pattern (Knoche et al., 2011). After an initial lag phase with little change in mass, fruit volume and hence surface area increase rapidly, reaching a maximum rate around the middle of the season before decreasing again toward maturity (Eccher et al., 2013; Ginzberg et al., 2014).

It is worth noting that fruit exposure to extreme growth conditions at early stages of development is critical for the development of cracking several months later, at the end of growth; e.g., a warm and dry climate during the cell-division stage of apple development resulted in increased cracking incidence that only became evident close to harvest time (Ginzberg et al., 2014). This observation suggests that extreme events during growth weaken the skin; however skin failure only becomes evident if it fails to resist growth tensions. Additional causes for cracking have been reviewed by Khadivi-Khub (2015).

4. Plant-growth regulators (PGRs) in the orchard

PGRs have been used for many years in orchards, mainly for fruit thinning (Davis et al., 2004) and to control fruit shape and size. Exogenous application of synthetic cytokinin has been shown to increase fruit size in several crops, such as kiwifruit (Biasi et al., 1991; Kim et al., 2006), persimmon (Itai et al., 1995), pear (Shargal et al., 2006; Stern and Flaishman, 2003), grape (Reynolds et al., 1992), and apple (Stern et al., 2006). Bigger fruit resulted from extension of the cell-division growth phase of pulp parenchyma cells in treated fruit (Shargal et al., 2006). High endogenous levels of gibberellic acid (GA) have been associated with thicker cuticle and lower incidence of russeting in apple (Eccher, 1986; Eccher and Hajnajari, 2006). Similarly, auxin application stimulates cell enlargement in apples (Wismer et al., 1995) and cherry fruit (Stern et al., 2007b), and increases peel thickness in mandarin (Stander et al., 2014).

At the cellular level, cytokinins play a key role in stimulating cell division and promoting cell differentiation by controlling the cell cycle at both the G_1/S and G_2/M transitions (recently reviewed by Schaller et al., 2014). GA has been shown to mainly regulate cell expansion by mediating destabilization of the growth repressors DELLA proteins (Band et al., 2012; Ubeda-Tomas et al., 2009). The positive effect of GA on cell elongation has been correlated with GA-mediated promotion of the transverse orientation of outer tangential wall microtubules of epidermal cells (Wenzel et al., 2000). Microtubules are thought to provide a spatial template for the ori-