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Chapter

The First Signal to Initiate Fruit Ripening is Generated in the Cuticle: An Hypothesis

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Abstract

The paradigm that has prevailed for a long time sustains that ethylene is the first signal that initiates fruit ripening. However, in this manuscript, we present the hypothesis that a signal generated from the cuticle induces the synthesis of ethylene, and therefore, it is the initial signal that triggers the fruit-ripening phenomena. Among the experimental evidence supporting the hypothesis, we can mention that cuticle components released during the plant pathogenic attack can induce the synthesis of ethylene in plants. Also, it has been found that in fungi, a cuticle component can activate a transcription factor by phosphorylation, which induces the transcription of a gene encoding a cutinase. Besides, studies with plant tissues experiencing a high rate of cell expansion have shown that there is a careful synchronization between the demand of cuticle components and biosynthesis, which suggests that the plant cell can sense the moment in which the fruit would stop growing by cell expansion, and initiate the ripening phenomena. In this chapter, experimental evidences supporting the physiological role of the fruit cuticle in the fruit ripening phenomena will be presented and reviewed with the goal to show a possible role of the fruit cuticle in the onset of fruit ripening.

Keywords: cuticle, components, signal, fruit, ripening

1. Introduction

The focus of the chapter is to show the physiological role of the fruit cuticle changes mentioned during fruit ripening. The different reports in which the changes in gene expression related with the biosynthesis, transport, and assembly of the different cuticle components during fruit development will not be discussed, unless they are relevant to support the hypothesis of this work. Readers interested in this subject can consult several excellent reviews [1–3].

Cuticle is a thin layer made of large molecular weight molecules with hydrophobic characteristics as well as polysaccharides and phenolic compounds. Its hydrophobic

physical properties make the diffusion of non-lipophilic molecules such as water or other charged molecules very difficult [4]. In this way, the cuticle plays a very important role of reducing the water loss in the surrounding environment, which is one of the cuticle's most important physiological functions. Besides that, the cuticle plays a role as a defense of the fruit against different biotic and abiotic stresses such as fungi and bacteria infection, heat, mechanical support, responses to mechanical injury, responses to heat, protection against the negative effects of UV light, plant development, as well as physiological disorders such as fruit cracking [5–9].

The role of ethylene as a signal to begin fruit ripening is very old knowledge. Indeed, there are many experimental evidence in support that ethylene plays an important role in inducing the expression of genes, which carries out the different changes that the fruit shows during fruit ripening [10, 11]. However, it is important to challenge this idea in pursuit of a signal, which can begin the synthesis of ethylene. Based on the above mentioned, it is clear that the cuticle plays an important role in several fruit physiological phenomena. Further, the cuticle composition is very complex, and the possibility of a signal enzymatically released from the cuticle components when the fruit has finished growing by cell expansion can in turn induce the biosynthesis of ethylene to start the fruit ripening. In fact, it has been suggested that cuticle can control the fruit growth rate. Alternatively, it is possible to think a change in cuticle biomechanics can be sensed by a receptor to start the fruit ripening.

The main goal of the present chapter is to provide evidence supporting the hypothesis that the cuticle is playing an important role in the onset of fruit ripening.

2. Changes in the bio-mechanical properties of the cuticle during fruit ripening

The study of the biomechanical properties has suggested that the cuticle shows several characteristics that allows to conclude that it is similar to the ones present in smart materials [12]. Comparing the mechanical properties of tomato fruit cuticle with leaf cuticles from several species, it is possible to observe that the tomato fruit cuticle shows a higher tendency to deform as compared with leaf, as concluded from the much lower Young's moduli of the tomato fruit cuticle. This most likely is related to the need of the fruit cuticle to yield under the stress of a lower force because the fruit must increase the size without cracking [13]. Moreover, an increase in the Young's moduli from mature green to red ripe tomato fruits had been observed in several tomato cultivars [14].

Besides the above mentioned, it was found that the cuticle physical properties do not have any correlation with the thickness [13]. Comparison between the cuticle of non-ripening tomato mutants such as *alcobaca*, *rin*, and *nor* with the normal ripening variety of tomato fruit 'Ailsa Craig' found that there was a difference in cuticle lipid composition [15]. Specifically, a larger amount of trihydroxy C18 fatty acids was found during the stages of small green, mature green, and red ripe equivalent in the non-ripening mutants such as *alcobaca*, *rin*, and *nor* as compared with the 'Ailsa Craig' (AC) tomato. The authors suggested that the presence of more C18 compounds could be related with a more elastic cuticle [15]. On the other hand, by studying tomato fruit varieties with large or low amount of flavonoids, it was found that the amount of flavonoids in the cuticle induces an increase in the Young's moduli [14]. In agreement, the inhibition of the chalcone synthase gene by virus inducing gene silencing in two tomato cultivars induced a lower amount of flavonoids and a decrease

in the Young's moduli as a consequence [16]. Besides, the viscoelastic properties of the tomato fruit cuticle during the last stages of tomato fruit ripening has been ascribed to the increased amount of phenolics, which interacts with cutin and the different polysaccharide compounds [17, 18]. On the other hand, it has been mentioned that the whole cuticle is behind the elastic properties of cuticle, whereas the viscoelastic behavior of tomato cuticle is related to the cutin component [19]. Wax is related positively to the level of the Young's moduli or stiffness as it was concluded from experiments in which the wax was removed from the cuticle of several tissues and tomato fruit [20]. In contrast, studies carried out in tomato wild type and a mutant lacking the enzyme beta-ketoacyl-coenzyme A synthase, which has low amount of wax in the cuticle, showed that cuticle from normal tomato showed a lower elastic modulus. Further, this characteristic was only observed in mature green tomatoes because in red ripe tomatoes, both the mutant and the wild type showed the same level of stiffness [21]. Studies focused on the changes of the cuticle biomechanical characteristics during tomato fruit ripening allowed the authors to suggest that the cuticle can be controlling the fruit growth rate during ripening, which in turn suggests that the cuticle can control the initiation of fruit growth to start the fruit development and ripening phenomena [22].

Studies in tomato fruit in which the invertase gene was inhibited found large changes in cuticular components and an increase in the cuticle thickness. Further, the data mentioned above suggest that the cell metabolism is closely related to the cuticle biosynthesis, which in turn suggests an active communication mechanism between cells and cuticle behavior. The growth behavior for the transgenic and wild type was similar, which rules out the fact that there was an alteration in the cell expansion, which could have had effects on cuticle accumulation. In turn, this clearly suggests that even though the cuticle is outside the cell, there is a mechanism of data exchange with the plant epidermal cell [23].

From the data included in this section of the chapter, the different components of the fruit cuticle give the particular biomechanical properties of the cuticle. In this regard, it is possible to put forward a hypothetical question about a signal created by changes in the cuticle biomechanics to induce the onset of the fruit ripening. Maybe there is a receptor that can sense these biomechanical cuticle changes, similar to the Arabidopsis receptor located at the cell membrane, known as THESEUS1, which can sense the integrity of the cell wall [24].

3. Involvement of cuticle in the onset of fruit ripening

Experimental evidence supporting the physiological function of ethylene in the initiation of fruit ripening is vast, and several excellent reviews are available on the subject [10, 11, 25]. However, until now, another suggestion about what the first signal initiating fruit ripening is has not been elaborated, to our knowledge.

The cuticle is the outermost layer that covers the fruit. Further, it is made of large molecules of lipophilic nature such as waxes, fatty alcohols, alkanes, and fatty acids [2].

Analysis carried out in several fruits clearly shows that the cuticle changes in amount and composition during fruit growth and development. This had been recorded in tomato [26], pitahaya [27], peach [28], olive [29], mango [30], and many other fruits. The molecular mechanism of cuticle biosynthesis had been studied in tomato [31], mango [30], and sweet cherry [32]. Further, important advances in that

mechanism in pitaya fruit (*Stenocereus thurberi*) have been achieved in our laboratory (García-Coronado, unpublished). The studies mentioned above clearly show that there is rather substantial information about the genes playing a role in cuticle biosynthesis. Besides that, there are several transcriptomes of fruits generated by the utilization of the next generation sequencing technology, including chili pepper [33], strawberry fruit [34], avocado [35], litchi [36], and many others. With all this information, an interesting review had been published about the changes in fruit cuticle composition and the molecular biology of cuticle biosynthesis in fleshy fruits [2]. All the scientific information mentioned above clearly shows that there is enough data to test experimentally the present hypothesis.

There are many differences in the cuticle composition in a tomato mutant designated as delayed fruit deterioration, which shows a large postharvest shelf life, as compared with a tomato fruit with a normal shelf life [37]. These data suggest that the fruit cuticle plays a role in the postharvest shelf life of fruits as it had been suggested by other authors [38]. Also, fruit softening is a characteristic associated with the fruit ripening phenomena. In this regard, it had been found that the cuticle plays an important role in tomato fruit softening [39], in contrast with earlier hypotheses stating that it is the plant cell wall that plays the main role during the fruit softening phenomena.

Evidence generated by studying rapidly expanding stems of *Arabidopsis* demonstrated that the amount and composition of the cuticle are maintained during these phenomena by synchronization between area expansion and the biosynthesis and exportation of cuticle components. Further, it was shown that the rate of expansion in the apical meristem was 10 times faster than in the middle stem section, and still, the cuticle amount and composition did not change [40]. These observations suggest that it is possible for the epidermal cell to detect the demand for cuticle components during the expansion of the plant stem. Likewise, it can be suggested that the fruit epidermis can also perceive when the fruit stops growing by cell expansion, which is the moment when the fruit starts the ripening phenomena [41].

By doing a search in the Solgenomics database with the software Blastp using a cutinase orthologous gene from *Arabidopsis* AT4630140, it was possible to find genes that encodes for cutinases in the tomato genome (**Figure 1**). By analyzing **Figure 1**, it is clear that some of the cutinase-encoding genes are expressed before the initiation of fruit ripening. Furthermore, promoter analysis with the software plant promoter (PlantPAN; <http://PlantPAN.itps.ncku.edu.tw/>) of the first five genes, which shows the highest homology, the presence of the CREB response element in the genes Solyc02g071610, Solyc02g071720, Solyc03g005900 was found. Also, for the two first genes, the CREB element was found within 400 bp upstream of the translation start site. Furthermore, the gene Solyc02g071610 shows a large activity at 10 days post-anthesis (DPA), and it is still active at 15 DPA in the outer epidermis. Also, the gene Solyc02g071720 shows a low activity at 5 and 10 DPA. These stages of development are before the initiation of the tomato fruit ripening. Based on the above, it is possible to suggest that the release of the cuticle components can be carried out by any of these genes to initiate the signal to induce the active synthesis of ethylene.

The possible molecular mechanism explaining how a cuticle component can induce the activation of the fruit cutinases and in turn the release of cuticle components was generated with studies in fungi. In those studies, it was found that a component from the cuticle can activate a fungi transcription factor by phosphorylation, which in turn can induce the transcription of a gene encoding cutinase by binding to the CREB (cAMP response element binding) and Sp1 responsive elements

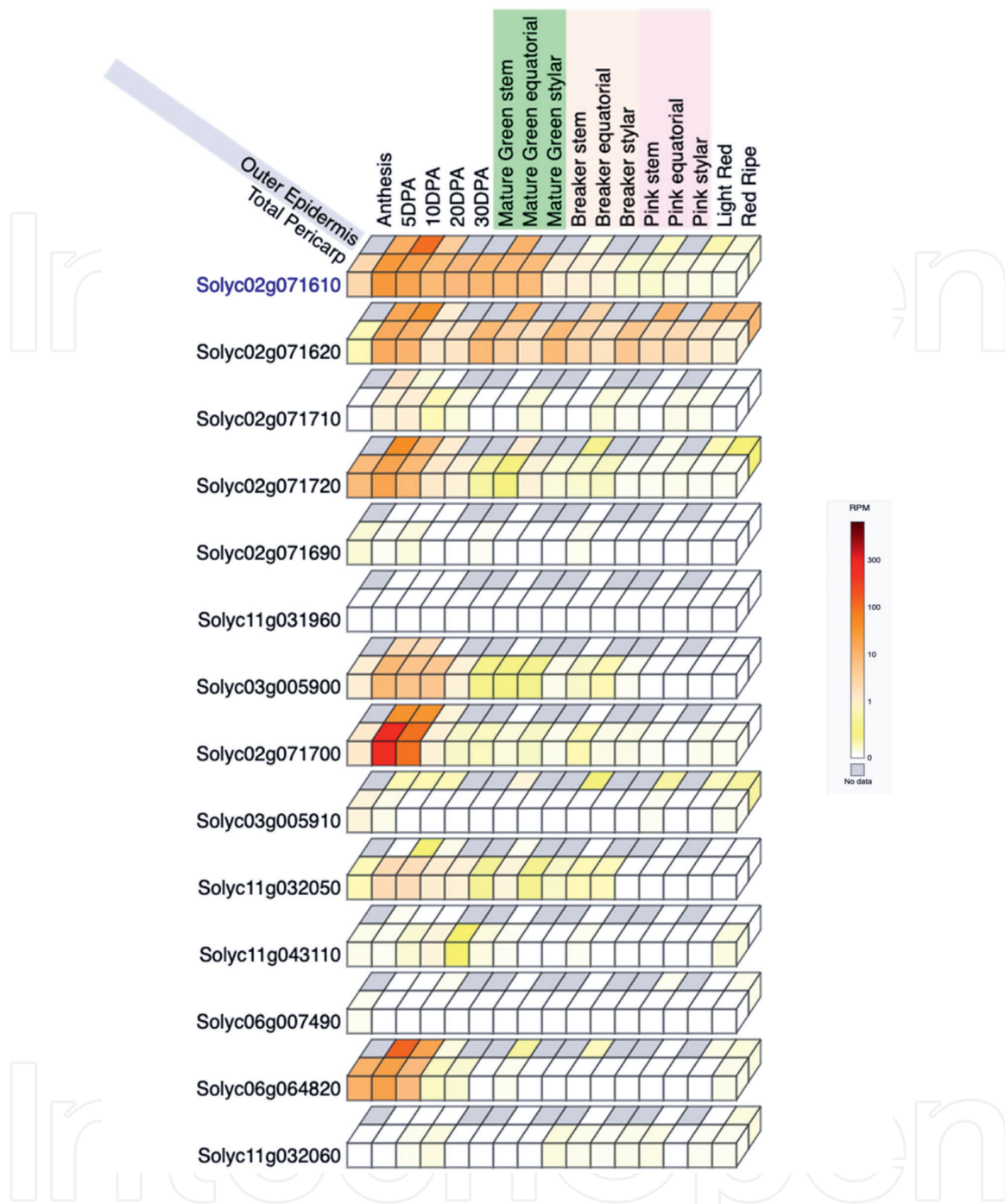


Figure 1. Changes in expression of tomato genes encoding for Cutinases during the tomato fruit growth and development phenomena. DPA stands for days post Anthesis.

present in the promoter of the gene. Further, the removal of the CREB responsive element eliminates the induction of the gene transcription activation [42]. Also, this responsive element had been found in the 5'-flanking region of the cutinase gene from *Colletotrichum gloeosporioides* and *Colletotrichum capsici* [43], suggesting that these responsive elements play an important role in the cutinase gene induction. Furthermore, it was found that cycloheximide inhibits the increase in cutinase activity, clearly demonstrating that protein synthesis is involved in the molecular mechanism [44]. Besides the above, it had been found that during ripening, the total number of cutin ester bonds is reduced, making easier the release of cuticle components [45].

On another side, it had been found that the fruit response mechanism in the presence of cuticle components during a pathogen attack includes the production of ethylene, suggesting that there is a mechanism underlying the induction of ethylene biosynthesis by cuticle components [46]. Unfortunately, the molecular mechanism by which a cuticle component can be recognized by the plant cell is not yet known [47], although the role of a receptor had been suggested [48]. It is important to mention that the hypothesis that a mechanism is able to sense a cuticle component by the plant cell is rather old.

Based on the above, our working hypothesis states that a similar mechanism found in fungi can exist in fruits. This in turn implies that a cuticle component released from the cuticle can induce the activation of a transcription factor, which can activate fruit cutinases in the nucleus, which will release cutin components to induce the synthesis of ethylene.

4. Main hypothesis drawbacks

It is important to mention that there are several statements in the hypothesis mentioned that need to be experimentally demonstrated, which are described next: the mechanism for the epidermal cell to detect the moment in which the fruit tissue stops growing by cell expansion; the mechanism explaining the ethylene synthesis induction by a cuticle component; and also, the mechanism by which the plant cell can recognize the cuticle component and the subsequent activation of the gene in the plant nucleus. However, as mentioned above, there is a big knowledge generated by the next-generation sequencing technology about the molecular biology of different fruit physiological phenomena as well as the molecular mechanism of cuticle biosynthesis. Therefore, it is quite possible to carry out experiments to help in the elucidation of the hypothesis elaborated in this document.

5. Conclusion

In this work, a hypothesis has been created as an alternative to explain the mechanism that controls the initiation of fruit ripening. This hypothesis sustains that the first signal to initiate fruit ripening is generated from a cuticle component and not by the hormone ethylene. The evidence supporting the hypothesis is experimental but was not generated by studying fruits. Further, this hypothesis still needs a great deal of experimental evidence to be demonstrated. Also, we believe it is important to challenge the actual paradigm about the fruit ripening phenomena with the recently generated scientific knowledge about the fruit cuticle, which plays roles in several plant physiological phenomena.

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