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Review

A review for the molecular research of russet/semi-russet of sand pear exocarp and their genetic characters

Yue-zhi Wang*, Mei-song Dai, Dan-ying Cai, Shujun Zhang, Ze-bin Shi*

Institute of Horticulture, Zhejiang Academy of Agricultural Sciences, Hangzhou, Zhejiang Province 310021, China

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ABSTRACT

Exocarp protects the fruit against external stresses by means of its special physical and biochemical properties. It is also a commercially important quality for fruits characterized with certain color and structure. The color of sand pear exocarp can be divided into three types of russet, semi-russet and green. The green of exocarp is formed by accumulation of chlorophyll in epidermal cells. Russeting is a disorder of the fruit skin that results from microscopic cracks caused by growth stresses and several additional factors and the subsequent formation of higher plasticity periderm membranes by the accumulation of suberin on the inner part of the cell wall of the outer epidermal cell layers. Genes and pathways that are specific to exocarp russet formation have been identified in sand pear and its genetically related apple. The cuticle biosynthetic genes were repressed while stress response genes and suberin deposition genes were enhanced underlying the exocarp russeting. One major 'QTL' associated with russet of exocarp was identified at the top of LG 8. However, despite these advances, important aspects of russet and semi-russet inheritance remain obscure. Central questions include whether russet and semi-russet are belong to one type of quantitative trait or not, and their genetic characters. These issues are reviewed. Greater emphasis on gene mapping and cloning, biochemical characterization of metabolic intermediates and putative enzymes identified to put together correct and detailed pathways will be required to solve these unknowns of the mechanisms underlying the exocarp russet and semi-russet formation.

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1. Introduction

Exocarp color is a commercially important appearance quality for fruits. The fruit skin color of sand pear can be classified into three types of russet, semi-russet (partially russet/intermediate) and green, and the russet exocarp consists of a cork layer. For some varieties, anthoxanthin accumulated in the exocarp even causes the

* Corresponding author.
E-mail addresses: yzwang2010@mail.zaas.ac.cn (Y.-z. Wang), shizb@126.com (Z.-b. Shi).

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fruit surface with dyed red. For russet or green exocarp, the color depth is usually vulnerable to environmental impact with obviously difference between varieties. Some researchers have conducted testcross and proposed one or two loci control the fruit skin color (Kikuti, 1924; Mori, 1953; Shen et al., 1979; Inoue et al., 2006; Song et al., 2010). But Kim et al. (2005) reported that the trait of exocarp color showed normal distribution in the F1 population of P. *pyrifolia* Nakai'Niitaka' × P. *ussuriensis* Maxim. Yamamoto et al. (2014) also analyzed the exocarp color as quantitative trait using an F1 population. To date, no unified understanding has been issued for the classification of sand pear exocarp color, which directly hinders the trait genetic analysis and breeding selection. In past few years, new progresses have been made in the physiological and biochemical characterization, and molecular processes for the exocarp color of sand pear. So it is necessary to summarize these progresses, to clarify the existing problems, and provide a reference for the next studies.

2. Structure and biochemical basis for sand pear russet/semi-russet exocarp

The primary exocarp of sand pear is covered by cuticle layer, epidermis cell layer and cork meristem with outside-in order, and the number of epidermal cells layers may have a slight difference between varieties (Yan et al., 2009). The green of exocarp is formed by accumulation of chlorophyll in epidermal cells. Russeting in pears (*Pyrus communis* L.) is a disorder of the fruit skin that results from microscopic cracks in the cuticle and the subsequent formation of a periderm (Khanal et al., 2013). Studies on the aetiology of russeting identify the formation of microscopic cracks caused by growth stresses and several additional factors in the primary fruit skin as the first visible sign of russeting (for reviews see Faust and Shear 1972; and Shi 2011). The periderm membranes was revealed to have higher plasticity than the cuticular membranes (Khanal et al., 2013), which can effectively alleviate the pressure of the growth stresses in certain varieties.

Periderm membranes represented successive layers packed by suberized cells (Graça, 2015). Suberin was revealed to be a ubiquitous insoluble biopolyester composed of two poly-phenolic and one poly-aliphatic domain (SPPD, for Suberin Poly-Phenolic Domain, and SPAD, for Suberin Poly-Aliphatic Domain, respectively, Bernards 2002). In suberized cell walls, suberin is also associated with significant amounts of soluble lipids, the "waxes", which in potato can amount to 20% of the periderm weight and be mostly responsible for its low permeability (Schreiber et al., 2005). Comparison of the biochemical substances between russet exocarp and their green exocarp mutants also indicated that the content of lignin, cellulose and hemicellulose in the russet exocarp could be higher than in the green exocarp (Heng et al., 2014; Wang et al., 2014b).

3. Gene expression characters underlying exocarp russeting of sand pear

Kim et al. (2005) reported that the trait of exocarp color showed normal distribution in the F1 population of *P. pyrifolia* Nakai'Niitaka' × *P. ssuriensis* Maxim, which indicates that the excarp russeting is controlled by a complex molecular mechanism. In the past few years, several sound studies reported the putative molecular regulation and a set of interesting pathways enriched by different expression genes conferring the exocarp russeting (Wang et al., 2014a,b Heng et al., 2014; Legay et al., 2015). With referenced to Legay et al. (2015), genes involved in exocarp russeting can be clustered in two groups of exocarp substances biosynthetic genes and stress responsive genes. The group of exocarp substances biosynthetic genes can be further classified into two functional subgroups of cuticle biosynthetic genes and suberin deposition genes. In the exocarp russeting, expression of the cuticle biosynthetic genes was repressed while the stress responsive genes and suberin deposition genes were elevated comparing with that in the green exocarp.

3.1. Repressed expression of cuticle biosynthesis genes

Cuticle consists of wax crystals with two different types, which are the epicuticular waxes consisting exclusively of very-long-chain aliphatics and the intracuticular waxes containing large quantities of pentacyclic triterpenoids, respectively (Vogg et al., 2004). Pathways of fatty acid elongation, biosynthesis of unsaturated fatty acids and biosynthesis of sesquiterpenoid/triterpenoid were all enriched in the gene expression comparison between the russet and green exocarp, and a set of genes were suggested to take significant role for the exocarp green/russet variation (Wang et al., 2014a,b). The 3-ketoacyl-CoA synthase (KCS), which catalyzes very long chain fatty acid (VLCFA) synthesis, showed repressed gene expression in the russet exocarp (Wang et al., 2014a,b; Legay et al., 2015). The similar regulation was also seen for the homologs of two types of fatty acid desaturase FAD2 and FAD8 (Wang et al., 2014a,b), which catalyze the synthesis of unsaturated fatty acids (Anai et al., 2003; Jung et al., 2011). AtGPAT6 homolog showed repressed expression in russet exocarp compared to the green exocarp (Wang et al., 2014a,b Legay et al., 2015), which was proved to be a crucial enzyme in the synthesis of palmitate-based cutin monomers in flowers (Li-Beisson et al., 2009).

3.2. Stress responsive genes

The decreased expression of cuticle biosynthetic genes leads to a stress response, which was suggested to be the cause for exocarp russeting, by not only affecting suberin deposition, but also the entire structure of the cell wall (Legay et al., 2015). It is normal for plants to form a cork layer as secondary protective tissue in the surface of organs under environmental stresses and/or mechanical hurts. A broad range of environmental factors that cause epidermal and cuticular defects have been identified as the most predominant cause of russeting (Reviewed by Shi 2011; Khanal et al., 2013). Epidermal and cuticular defects may directly affect the transpiration and resistance to pathogen invasion in corresponding tissues and consequently active the signal cascades of stress responses (Wang et al., 2014a; Heng et al., 2014; Legay et al., 2015). Those kinases proved as transmembrane pattern recognition receptors involved in biotic and abiotic stresses responses showed abundant transcripts in the russeting exocarps. Several genes involved in the metabolism of hormones (i.e. ABA, ethylene, jasmonic acid and auxin etc.) can also take role in the russeting regulation. The homolog of aquaporin-1 in sand pear showed decreased transcript abundance in the russeting exocarp which may hinder the fruit surface transpiration and reduce the organ water loss (Wang et al., 2014a). H_2O_2 can lead to hypersensitive cell death (Wang et al., 2013), which was found with high content in the exocarp of the russeted mutant (Heng et al., 2014). Combined with enhanced activity of POD enzymes and 12.2% increased lignin content in the exocarp of russeted mutant, H_2O_2 could directly contribute to the mutant formation (Heng et al., 2014). A large number of disease resistance response genes with higher expression indicate the activation of disease response mechanism in the russeting pericarps, which can act as the key protective barrier avoiding pathogen invasion before the full formation of periderm protection.