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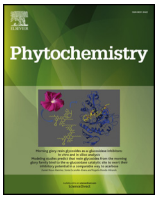

Review

Understanding the genetic regulation of anthocyanin biosynthesis in plants – Tools for breeding purple varieties of fruits and vegetables

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ABSTRACT

Anthocyanins are naturally occurring flavonoids derived from the phenylpropanoid pathway. There is increasing evidence of the preventative and protective roles of anthocyanins against a broad range of pathologies, including different cancer types and metabolic diseases. However, most of the fresh produce available to consumers typically contains only small amounts of anthocyanins, mostly limited to the epidermis of plant organs. Therefore, transgenic and non-transgenic approaches have been proposed to enhance the levels of this phytonutrient in vegetables, fruits, and cereals. Here, were review the current literature on the anthocyanin biosynthesis pathway in model and crop species, including the structural and regulatory genes involved in the differential pigmentation patterns of plant structures. Furthermore, we explore the genetic regulation of anthocyanin biosynthesis and the reasons why it is strongly repressed in specific cell types, in order to create more efficient breeding strategies to boost the biosynthesis and accumulation of anthocyanins in fresh fruits and vegetables.

1. Introduction

Anthocyanins are specialized metabolites of the phenylpropanoid pathway that are widely distributed in the plant kingdom. These glycosylated flavonoids are one of the most important water-soluble pigments in plants and provide the shades of blue, purple, red and pink to plant organs, including leaves, petals, fruits, and seeds (Mazza and Miniati, 2018; Onslow, 2014). Anthocyanins present in the epidermis of flowers and fruits provide visual cues to attract pollinators and seed dispersers (Rieseberg and Blackman, 2010; Tanaka et al., 2008). The fact that anthocyanins are induced under diverse biotic and abiotic stresses suggests a role in cell stress coping mechanisms (Ferreyra et al., 2012; Landi et al., 2015; Zhang et al., 2014a). Moreover, it is quite puzzling that different stresses induce distinct anthocyanin profiles (Kovinich et al., 2014), which further suggest that individual types might play distinct roles in the physiology of the plants.

Despite being a minor component of the human diet, many studies have highlighted the health benefits of anthocyanins and other phenolic compounds, thus potentially helping in the prevention of different chronic pathologies (Amiot et al., 2016; Hooper et al., 2008; Khoo et al., 2017; Toufektsian et al., 2008). Most importantly, these benefits are expected to be achieved only when a considerable amount of anthocyanins is regularly consumed in the diet (Butelli et al., 2008; Habanova et al., 2016; Petroni et al., 2014). However, most of the vegetables available in the market contain only small quantities of anthocyanins in their edible parts, with the pigment often restricted to the epidermal layers (peel/skin), such as leaf and petal epidermis, the seed coat (testa), and the epidermal cells of the fruit (exocarp or peel) (Butelli et al., 2008). Since the peel usually accounts for less than 5% of the total mass of edible parts of the plant (Sestari et al., 2014), the lack of anthocyanin accumulation in parenchymal cells of cortical tissues considerably limits the total amount of these compounds in most fresh foods available to the consumer. Even blueberry, which is popularly regarded as a “superfood” due to their anthocyanin content (Reque et al., 2014), the biosynthesis and accumulation of these pigments are exclusively restricted to the fruit skin, as seen in the white flesh of commercial varieties.

This differential pigmentation pattern of plant organs showing cyanic epidermis (colored skin/exocarp) and acyanic cortex (e.g., white flesh made of non-pigmented parenchymal cells) is commonly found in

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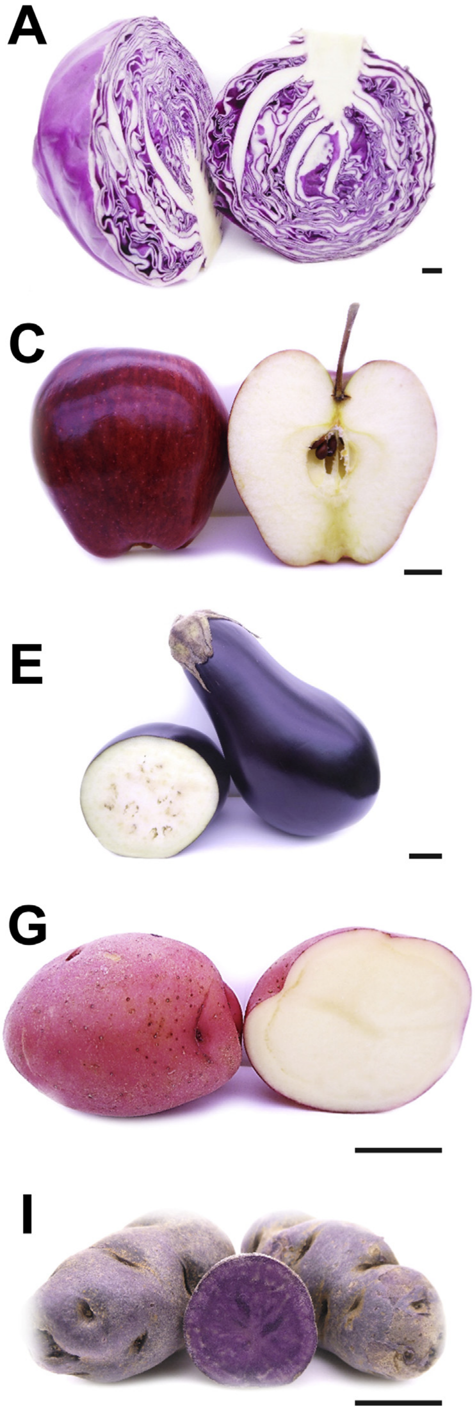

Fig. 1. Dietary sources of anthocyanins. (A) Purple cabbage. (B) Onion bulb. (C) Apple. (D) Grape. (E) Eggplant. (F) Blueberry. (G) Potato. (H) Purple tomato (*Aft/atv/hp2* triple mutant, cv. Micro-Tom). (I) Purple potato. (J) Red cherry. Except for H-J, all other examples accumulate anthocyanin in the epidermal tissue, while parenchymal cells remain acyanic. Scale: 20 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

eggplant, grape, plum, apple, radish, as well as purple varieties of tomato, onion, and cabbage (Fig. 1). Nonetheless, this is not a universal fact: there are remarkable examples of plant varieties bearing edible organs with cyanic parenchyma, such as purple potatoes, blood oranges, red-flesh apples, *teinturier* grapes, purple carrots, as well as dark-flesh stone fruits (e.g., cherries, peaches, and plums). Genetic engineering, as well as molecular and conventional breeding, have been employed to generate purple versions of some horticultural crops. The public interest in the transgenic purple tomato (Butelli et al., 2008) as well as the commercial success of many purple varieties of horticultural species derived from conventional breeding, such the cauliflower (Chiu and Li, 2012; Chiu et al., 2010), potato (Liu et al., 2015b), and carrot (Xu et al., 2017) attest to the demand for cyanic varieties with potentially higher nutritional value. On the other hand, whereas it is quite straightforward to use biotechnology to boost anthocyanin content in crops, the transgenic approach can severely limit product marketing. The reasons for that are due to legislation that forbids the commercialization of transgenic foods and the public perception and marketability, since the consumer niche most concerned with food nutrition tends to reject transgenic foods, even in countries where transgenic