



Are betalain pigments the functional homologues of anthocyanins in plants?



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ABSTRACT

Betalains, a small group of alkaloid pigments restricted to certain families of the Caryophyllales, have comparable optical properties and share similar histological locations in vegetative tissues with those of the more abundant anthocyanins. It has long been speculated that the two pigments are functional homologues in plant-environment interactions. Recent empirical evidence indicates that anthocyanins and betacyanins are both effective photoprotectants, are associated with increased tolerance to drought and salinity stress, and are efficient scavengers of reactive oxygen species in plants facing a variety of abiotic stressors. Nevertheless, the capacity of betalains to maintain a red colour irrespective of changes in vacuolar pH, their enhanced absorptivity of visible wavelengths, and their strong association with vacuolar ATPase activity, suggest that they may confer adaptive benefits not found in those species that produce anthocyanins. There remains much to be learned about the functional significance of betalains.

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1. Introduction

Among the biochemically diverse groups of secondary metabolites in plants, the anthocyanins have arguably attracted the most scientific attention over recent decades. This large and disparate class of pigments found in the root and shoot systems of most angiosperms and some gymnosperms is especially notable for the range of reds and purples it confers to plant organs. Accordingly, a wide variety of functional hypotheses has been posited to explain the extraordinary evolutionary success of these compounds. There exists, however, another, much smaller group of pigments with comparable colours that has received considerably less attention. These are betalains, tyrosine-derived alkaloids that are restricted to certain fungi and one order of vascular plants. Because betalains and anthocyanins do not naturally co-exist in any extant species, and because of their similar optical and chemical properties, it has been suggested that the two may be functional homologues, the betalains substituting for anthocyanins in anthocyanin-free plants. Here, we compare recent evidence for putative roles of anthocyanins and betalains in vegetative organs to assess the degree to which the two pigment types might be functional equivalents in plant-environment interactions.

Betalains were originally called 'nitrogenous anthocyanins', which incorrectly implied structural similarities between the two pigment classes (Lawrence et al., 1939); indeed, it was not until the mid 20th century that the structural detail of betalain compounds was elucidated (Steglich and Strack, 1990). Mabry and Dreiding (1968) coined the term 'betalain', a derivative of betalamic acid which was originally identified from red beet (*Beta vulgaris*). We now know that two structurally different types of betalains exist (Fig. 1): the yellow/orange betaxanthins (λ_{\max} = approximately 470 nm) which are the condensation products of betalamic acid and assorted amino compounds, and the red betacyanins (λ_{\max} = approximately 536 nm) which are formed by glycosylation and acylation of cyclo-DOPA (Stintzing and Carle, 2004). To date, far fewer betalain compounds have been isolated from plants than have anthocyanins (Stintzing and Carle, 2007).

Like the anthocyanins, betalain pigments occur in the seeds, fruits, flowers, leaves, stems, and/or roots of plants from a wide range of natural environments (Gandía-Herrero and García-Carmona, 2013; Kugler et al., 2004; Strack et al., 2003; Svenson et al., 2008). The timing of betalain production varies across species; as with the anthocyanins, they may be present only in immature organs, only in senescing organs or else persist for the life of the organ (Fig. 2); (Hortensteiner and Lee, 2007; Lee and Collins, 2001); their synthesis may be restricted to reproductive organs, as in the flowers and fruit of many cacti (e.g., Kobayashi et al., 2000), or else occur in both vegetative and reproductive structures, such as the leaves and flowers of iceplants (Jain and Gould, 2015). Both betalains and anthocyanins are stored as

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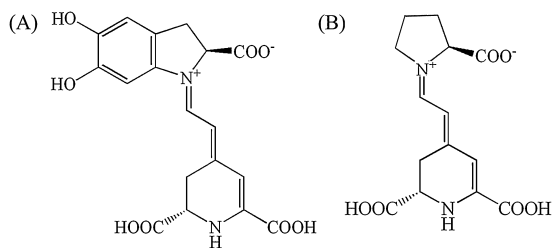


Fig. 1. Chemical structure of (A) betanidin, a common betacyanin and (B) indicaxanthin, a betaxanthin.

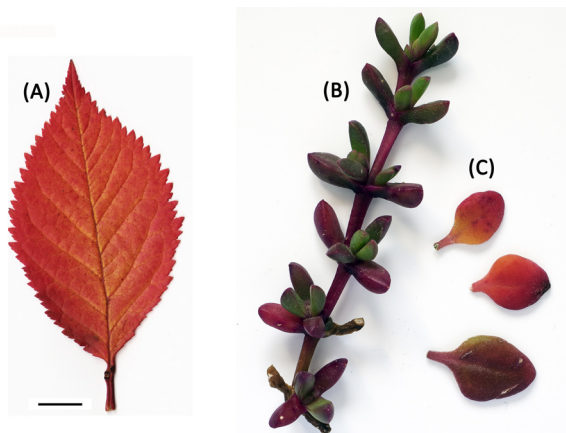


Fig. 2. Anthocyanins (A) and betacyanins (B,C) in vegetative shoots. (A) *Prunus avium*, (B) *Disphyma australe*, (C) *Tetragonia implexicoma*. Bar = 1 cm.

glycosides in the cell vacuole, and they share similar histological locations in dermal, ground, and vascular tissues of vegetative organs (Gould and Quinn, 1999; Jain and Gould, 2015; Kytridis and Manetas, 2006; Lee and Collins, 2001; Mosco, 2012; Tattini et al., 2014).

Betacyanins and anthocyanins can produce a similar array of red colours (Lee and Collins, 2001; Tanaka et al., 2008). Both are also potent antioxidants, capable of scavenging a variety of reactive species (Hatier and Gould, 2009; Neill et al., 2002; Stintzing and Carle, 2004; Wang and Liu, 2007), and both have a relatively high osmotic potential, giving them the capacity to serve possible osmoregulatory roles (Chalker-Scott, 2002,1999; Stintzing and Carle, 2004). Although they are produced by very different biosynthetic pathways, the two pigment types are inducible by similar environmental cues, including light (Hatier and Gould, 2009; Hughes and Smith, 2007; Kishima et al., 1995; Vogt et al., 1999), UV radiation (Ibdah et al., 2002; Tsurunaga et al., 2013; Vogt et al., 1999; Wang et al., 2012), sucrose accumulation (Hughes et al., 2005; Oh et al., 2011; Solfanelli et al., 2006), and a host of abiotic stressors such as drought, low temperatures and salinity (Chaves et al., 2009; Duarte et al., 2013; Hayakawa and Agarie, 2010; Hughes, 2011; Jain and Gould, 2015; Nakashima et al., 2011; Pietrini et al., 2002; Sperdouli and Moustakas, 2012; Tahkokorpi et al., 2007; Wang and Liu, 2007). There are, therefore, compelling reasons to postulate that the two classes of pigments share common functional roles.

Notwithstanding these similarities, betalains are far less abundant than anthocyanins across the plant kingdom. The capacity to synthesise betalains has only been observed within one order of plants, the Caryophyllales, and even that has two families, the Caryophyllaceae and Molluginaceae, containing members that produce anthocyanins instead of betalains (Gandía-Herrero and García-Carmona, 2013). Aside from plants, the

only other organisms to synthesise betalains are certain genera of Basidiomycetes (Gill, 2003). No plant species studied to date has been found to accumulate both anthocyanins and betalains (Strack et al., 2003). This exclusivity remains unexplained, and is, perhaps, surprising given that gene homologues for a key enzyme in betalain biosynthesis are present in anthocyanic plants (Christinet et al., 2004) and that betanidin 6-O-glucosyltransferase, which catalyses the glucosylation of betacyanin, can also efficiently glucosylate the anthocyanidins (Vogt et al., 1997). There is, moreover, no apparent physiological barrier that prevents the two pigments from co-occurring; a recent study transferred part of the betalain biosynthetic pathway into cell cultures of potato, petals of *Antirrhinum* and shoots of *Arabidopsis*, and demonstrated that betalain production was possible in these normally anthocyanic plants when they were fed with a betalain intermediate, L-DOPA (Harris et al., 2012). Indeed, Clement and Mabry (1996) posited that the ancestor of the Caryophyllales could have held both types of pigments, but that one or the other was lost as species evolved. However, a recent phylogenetic analysis of the core Caryophyllales using *rbcl/matK* plastid gene markers has shown that the ancestral type was almost certainly anthocyanic (Brockington et al., 2011). Intriguingly, that study also indicated that the capacity to synthesise betalains may have arisen more than once, and that in the course of speciation, some lineages evidently switched from betalain production back to anthocyanin production. There seems, therefore, to be a 'cost' associated with betalain production, which preferentially drives the evolution of anthocyanic rather than betalainic plants. From a functional perspective, their mutual exclusivity indicates that betalains may substitute for, but do not complement the roles of anthocyanin pigments. There may also be unique properties of betalains that provide fitness benefits under certain environments.

Of the two betalain groups, the betacyanins have received far greater scientific attention from a plant-environment functional perspective. Nonetheless, the betaxanthins have also been implicated in vital functions such as pollinator attraction, desiccation tolerance and free-radical scavenging (Cai et al., 2005; Gandía-Herrero et al., 2005; Stintzing and Carle, 2004). However, there are as yet insufficient empirical data to afford useful comparisons between betaxanthins and anthocyanins; this review therefore focuses on the betacyanins in relation to key functional hypotheses proposed for the anthocyanins.

2. Photoprotection

Prolonged exposures to light energy in excess of the requirements for photosynthesis can lead to oxidative stress, damage to the manganese cluster in the oxygen-evolving complex of photosystem II (PSII), and inhibition of the repair of damaged PSII proteins (Takahashi and Badger, 2011). Anthocyanins in leaves and stems have long been proposed to contribute to the suite of photoprotective mechanisms that serve to mitigate photoinhibitory damage (Gould, 2010). According to the 'light screening hypothesis', anthocyanins in epidermal and/or palisade mesophyll cells would intercept quanta that might otherwise strike chloroplasts, thereby reducing excitation pressure on PSII. Consistent with the hypothesis, numerous studies have reported that red leaves and stems maintain higher quantum yields and recover from photoinactivation faster than do their green counterparts when exposed to saturating light (Boldt et al., 2014). However, the extent to which the photosynthetic machinery is apparently protected by anthocyanins seems to vary across species.

Although fewer studies have appraised a potential photoprotective role of foliar betalains, all report smaller declines in the quantum efficiency of PSII (Φ_{PSII} , as estimated by the ratio of variable to maximum chlorophyll fluorescence) in betacyanin than

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