



Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Reprint of “Photoprotection from anthocyanins and thermal energy dissipation in senescing red and green *Sambucus canadensis* peduncles”

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ARTICLE INFO

Keywords:

Anthocyanin
Xanthophyll cycle
Photoprotection
Light-screening
Sambucus canadensis
Peduncle

ABSTRACT

Senescing photosynthetic tissues utilize a number of photoprotective mechanisms, including thermal energy dissipation involving the xanthophyll cycle, and often the screening of light energy by anthocyanins. The relative utilization of thermal energy dissipation when anthocyanins are present versus absent remains to be characterized. Using sun-acclimated *Sambucus canadensis* peduncles, which synthesize anthocyanins concomitant with fruit ripening, we compared pigment content (anthocyanins, carotenoids and chlorophylls) and chlorophyll fluorescence data (non-photochemical quenching [NPQ] and photochemical quantum yields of photosystem II, during and after prolonged light stress), before, during and after fruit ripening. Shade-acclimated peduncles, which remain green during senescence, were used for comparison. Additionally, we compared the xanthophyll cycle activity (i.e., constituents of the xanthophyll cycle) of sun- and shade-acclimated peduncles during fruit ripening. Before and during fruit ripening, when exposed to 1600 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ white light, shade-acclimated peduncles had higher NPQ values and, during fruit ripening, greater proportions of de-epoxidized xanthophyll cycle pigments than did the sun-acclimated peduncles, although both types incurred similar levels of photoinactivation (i.e., reduction in Φ_{PSII}). After the fruit had ripened and peduncles were at the later stages of senescence, the green peduncles were photoinactivated significantly more than were the red ones, following light stress. Collectively, our data indicate that green peduncles, at the early stages of senescence, compensate for their absence of anthocyanins by invoking higher levels of energy dissipation. However, at the later stages of senescence, the level of compensatory thermal energy dissipation in green peduncles was insufficient, and was associated with greater levels of photoinactivation, compared to red peduncles. We conclude that photoprotection by anthocyanins augments the protective functions of xanthophyll cycle pigments in *S. canadensis* peduncles, and is especially important for mitigating effects of light stress towards the later stages of senescence in high light environments.

1. Introduction

Anthocyanin pigments impart red, blue, purple and black hues to plants. They often occur in reproductive organs such as flowers and fruits, the structures that support them, peduncles, pedicels and rays, as well as vegetative organs, leaves, stems, hypocotyls and roots. Given the widespread occurrence of anthocyanins across the plant kingdom, it is not surprising that a variety of possible adaptive roles have been proposed for these pigments (Chalker-Scott, 1999; Gould, 2004; Landi et al., 2015). Anthocyanic colouration in reproductive structures is

thought to advertise the availability of nectar and ripe fleshy fruits to pollinators and frugivores (Davies, 2009; Steyn, 2009), while in vegetative structures may signal the presence of chemical or mechanical defenses (Lev-Yadun and Gould, 2009; Cooney et al., 2012; Menzies et al., 2016). Anthocyanins may also perform physiological functions, potentially acting as osmoregulators, ROS scavengers, heavy metal chelators and light screens in photosynthetic tissue (Chalker-Scott, 2002; Gould et al., 2002; Gould et al., 2010; Hughes et al., 2013; Landi et al., 2015).

In elderberry (*Sambucus* spp), anthocyanin production causes the

DOI of original article: <http://dx.doi.org/10.1016/j.envexpbot.2017.12.019>

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<https://doi.org/10.1016/j.envexpbot.2018.02.011>

Received 22 September 2017; Received in revised form 27 December 2017; Accepted 27 December 2017
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colour change from green to black in ripening fruits. It also causes a conspicuous reddening of the peduncles, rays and pedicels, which precedes fruit ripening and is arguably one of the most recognizable features of elderberry plants. The extent of peduncle reddening in some *Sambucus* species is greatly influenced by the light environment (Schaefer and Braun, 2009). Shaded peduncles, such as those in the forest understory, predominantly remain green, whereas sun-exposed peduncles usually turn red (Cooney et al., 2015). For *Sambucus nigra*, red peduncles are more chromatically contrasted against surrounding green foliage and bear fruits with higher sugar content than do green peduncles (Schaefer and Braun, 2009). Thus, reddening provides accurate information on fruit quality to approaching frugivores. It is unclear, however, if frugivore communication was the primary selective force driving the evolution of peduncle reddening (i.e., that the anthocyanins function as visual ‘signals’). While anthocyanin accumulation has been linked many times to sugar accumulation in foliar tissues (e.g., Schaberg et al., 2003), experimental manipulation of peduncle sugar content has previously been shown to have no effect on peduncle colour in *Sambucus nigra* (Cooney et al., 2015). It is at least possible that peduncle colouration evolved as an ameliorative response to one or more abiotic stressors, but that the visual information these red organs provided was subsequently co-opted by frugivores to assess fruit quality (i.e., the anthocyanins function as ‘cues’). Indeed, because the peduncles usually redden earlier than do the fruit, these reproductive structures do appear to be unnecessarily conspicuous prior to ripening. In addition, the requirement for light to initiate peduncle reddening means that ripe fruits on understory plants do not subtend red peduncles, yet they still need frugivores for seed dispersal. As neither the timing nor the distribution of reddening appears to be optimally suited to frugivore attraction, a function other than signaling might better explain anthocyanin accumulation in elderberry peduncles.

In leaves, anthocyanins have been most commonly reported to exert a photoprotective function. When chloroplasts receive more light than can be used for photosynthesis, they are vulnerable to molecular damage leading to a sustained decline in photosynthetic efficiency referred to as photoinactivation (as reviewed in Melis, 1999; Logan, 2006). By attenuating light intensities reaching the chloroplast, it has been hypothesized that anthocyanins minimize photoinactivation (Gould et al., 1995; Gould, 2010). Consistent with this, numerous studies have reported that red leaves are photoinactivated less than are green leaves (Gould et al., 1995; Dodd et al., 1998; Feild et al., 2001; Manetas et al., 2002; Hughes et al., 2005; Nielsen and Simonsen, 2011; Hughes et al., 2012; Tattini et al., 2014). However, the photoprotection hypothesis is not restricted to foliar anthocyanins; similar photoprotective effects have been described for other photosynthetic organs, such as stems (Gould et al., 2010), fruit (Steyn et al., 2009) and pods (Smillie and Hetherington, 1999). Peduncles, too, can be photosynthetic and therefore susceptible to photoinactivation. Cooney et al. (2015) examined whether a photoprotective function might similarly explain anthocyanin accumulation in elderberry peduncles. They showed that anthocyanins in sub-epidermal parenchyma significantly reduced the transmission of green light to chloroplasts in the peduncle cortex and that, compared with green peduncles, the red peduncles maintained higher quantum efficiencies of photosystem II (PSII) under saturating light intensities. Following light stress, red peduncles also displayed lower levels of photoinactivation compared to green peduncles.

Experimental support for a photoprotective function of anthocyanins is not universal; several studies failed to find any advantage to a leaf of being red under strong light (Burger and Edwards, 1996; Kyparissis et al., 2007; Zeliou et al., 2009; Nikiforou and Manetas, 2010; Liakopoulos and Spanorigas, 2012). There are, of course, a variety of mechanisms in addition to anthocyanins that might serve to minimize photoinactivation. Leaf angle and reflectivity, as well as chloroplast position, can moderate light capture, and chloroplast ultrastructure and biochemistry can affect the partitioning of excitation

energy and thus the fate of excess absorbed light (reviewed in Logan, 2006). Thermal energy dissipation via the xanthophyll cycle and lutein is a prevailing photoprotective mechanism across the plant kingdom (Demmig-Adams et al., 2012, and references therein). Anthocyanins might, therefore, be regarded a component part of an integrated suite of mechanisms that function in concert to protect leaves from excess light. However, the possible interactions between light screening by anthocyanins and other mechanisms, such as thermal energy dissipation, has received scant attention. In one such study, red- and green-leaved varieties of coleus (*Solenostemon scutellarioides*) exhibited comparable reductions in both PSII quantum efficiency and photoinactivation resulting from light stress (Logan et al., 2015). During light stress, the green coleus maintained higher levels of thermal energy dissipation, supported by larger xanthophyll cycle pools and greater xanthophyll cycle conversion states (Logan et al., 2015). Thus, the benefits obtained by the red leaves from light screening were compensated in the green-leaved coleus through greater engagement of thermal energy dissipation. That study highlights the importance of quantifying other photoprotective mechanisms when evaluating the relative contribution of light screening by anthocyanins. However, inter-variety comparisons, such as that described by Logan et al. (2015), or inter-specific comparisons, such as that described by Hughes et al. (2012) are unable to control for other anatomical, ultrastructural, and biochemical features which, along with anthocyanin accumulation and xanthophyll cycle activity, may influence overall protection against excess-light.

Peduncle reddening in elderberry is for a number of reasons an excellent system to compare the photoprotective roles of anthocyanin accumulation and thermal energy dissipation while controlling for those other anatomical, ultrastructural, and biochemical photoprotective features. First, a photoprotective role for anthocyanins has already been established in *Sambucus* (Cooney et al., 2015) although the contribution of xanthophyll cycle activity to peduncle photoprotection remains largely ignored. Second, reddening among *Sambucus* peduncles displays both temporal and spatial variability. Thus, we can compare xanthophyll cycle activity and anthocyanic photoprotection either (i) for a single ecotype before, during and after anthocyanin biosynthesis or (ii) between ecotypes that vary in levels of anthocyanin accumulation. We can therefore control for possible anatomical, ultrastructural, and biochemical photoprotective features by examining the partitioning of light energy within sun-acclimated peduncles, before and after reddening, of the same ecotype, and then compare these to shade-acclimated peduncles, which remain green throughout their development.

Here, using chlorophyll fluorescence analyses and measurements of pigment content (chlorophylls, anthocyanins and constituents of the xanthophyll cycle), we report the responses of sun- and shade-acclimated peduncles of *Sambucus canadensis* (i.e., those that turn red as they mature vs. those that remain green, respectively) to strong light before, during, and after fruit ripening. We hypothesized that the requirement for xanthophyll cycle activity during light stress would be less in the red, sun-acclimated peduncles than in the green, shade-acclimated ones, and that following light stress, the red peduncles would be less photoinactivated.

2. Material and methods

2.1. Study site and plant material

Peduncles represent the main stalk of an infructescence (Fig. 1) and were the tissue of interest in this study. Rays, the secondary branches of an infructescence, and pedicels, the stalks of each individual fruit within an infructescence, similarly turn red prior to fruit ripening. However, rays and pedicels were not considered further in this study. All plant material was collected from a natural population on a private rural property in Brunswick, Maine, U.S.A. (43°55′31″N, 70°04′47″W) in the summer/fall of 2013. There, *S. canadensis* forms a small tree up to

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