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Review Article

New Opinion of Sugar and Light Crosstalk in the Induction of Anthocyanins Biosynthesis in Fruits

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Abstract

Anthocyanins have antioxidant properties, protective cardiovascular diseases, cancer, diabetes, visual disturbances, liver damage, or UV-B radiation, plant development that make a major contribution to the quality of fruits. The crosstalk amongst light, sugar, DELLAs and UV RESISTANCE LOCUS8 (UVR8) for anthocyanins accumulation was investigated. The UV-B irradiation significantly increased UVR8 and COP1 with the contribution of monomeric UVR8 to form a complex (UVR8-COP1-SPA) that regulates the transcription of specific anthocyanins biosynthesis genes. Sucrose increases the stabilization of DELLAs and degradation of gibberellins and activates the structural genes of anthocyanins biosynthesis. In this opinion article, DELLAs and *HY5* transcription factors have emerged as hubs under the sugar and light regulation networks in anthocyanins biosynthesis. A better understanding of these regulatory networks is able to beneficial for breeding programs directing to modify the anthocyanins. © 2018 Friends Science Publishers

Keywords: Anthocyanins; Flavonoid pathway; Light; Sucrose; DELLA

Introduction

Flavonoids characterize a large class of secondary plant metabolites in which anthocyanins are important health-promoting pigments (Kang *et al*., 2003; Kelebek and Selli, 2011; Wei *et al*., 2015; Li *et al*., 2016) defend against pathogens and ultraviolet radiation. Flavonoids also have an important role in the agronomic and nutritive significance of a plant and quality of fruits (Jaakola, 2013; Zhang *et al*., 2014a; Xu *et al*., 2015). Anthocyanins structurally comprises an anthocyanidin aglycon bound to one or more sugar moieties. Six anthocyanidins, namely petunidin (Pt), delphinidin (Dp), cyanidin (Cy), peonidin (Pn), pelargonidin (Pg), petunidin (Pt), and malvidin (Mv), occur mostly in fruits (Fig. 1).

Among anthocyanidins, most common in leaves is cyanindin. Names of compounds generally reflect species from which they were first obtained. Thus pelargonidin is from Pelargonium or geranium. It often exists in pink, scarlet, and orange-red flowers. Delphinidin was named after Delphinium, and generally mauve or blue flowers have this compound (Fig. 1). In particular, delphinidin and its methylated derivatives, malvidins, and petunidins are sources of purple and dark bluish colors, while pelargonidins and cyanidins are vital pigments in red colored fruits. Cyanidin usually is found in over 82% of fruits and berries studied. Anthocyanins give photo-protection during the senescing leaves and critical period of foliar nutrient resorption. Anthocyanins defend senescing foliage from photo-inhibitory irradiances, permitting the resorption of basic foliar supplements to happen during the time of photosynthetic instability and deteriorating photo-protective capacity (Holton and Cornish, 1995). Anthocyanins provide protection against various abiotic and biotic stresses of plants (Pourcel *et al*., 2007). Anthocyanins production is prompted during pathogen infection or stress and assist to plant protect against oxidative harm, for example, oxidative damage occurred with high irradiation when the capacity for carbon fixation is low (Zhang *et al*., 2014b). Many key regulatory genes controlling anthocyanins biosynthesis pathway enzymes and transcriptional factor have been identified in many species (Wei *et al*., 2015). Recently, a significant amount of new information has been gathered on regulatory proteins that control the expression of different essential genes of anthocyanins biosynthesis on the transcriptional and post-transcriptional stages. These genes are differentially controlled via biological and environmental factors such as sugar, hormones, light, and temperature. New findings have begun to expose the links between the developmental regulatory network and the regulator's network of anthocyanins biosynthesis during fruit ripening (Fang *et al*., 2016). The DELLA proteins have appeared as nuclei in sugar hormone, crosstalk in anthocyanins biosynthesis regulation networks (Das *et al*., 2012b).

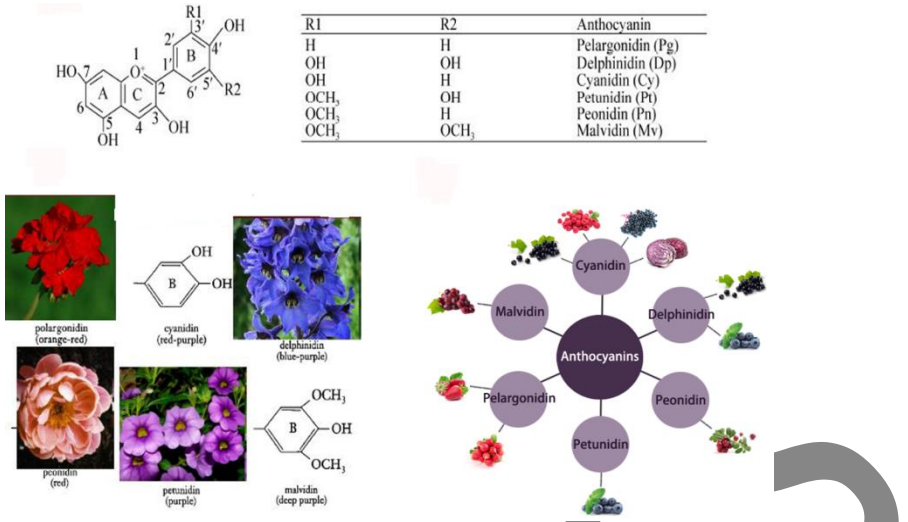

Fig. 1: Anthocyanin skeleton and six common anthocyanins

Recently, numerous molecular mechanisms have been suggested to elucidate the interaction of sugar signaling and light with anthocyanins biosynthesis pathway.

Anthocyanins is one of the best regulatory and metabolic pathway studied in plants and a convenient model for the analysis of many cellular, genetic, epigenetic, evolutionary processes (Koes *et al*., 2005; Albert *et al*., 2014; Xu *et al*., 2015). The accumulation of anthocyanins are directed through metabolic complexes that are synchronized through genetic, hormones and environmental factors, they are intensely interrelated by the expression of important structural controlling genes (Zoratti *et al*., 2014b; Wei *et al*., 2015). In *Arabidopsis*, all tissues have flavonols, but anthocyanins and PAs precisely store in seed coat or somatic tissues. In vegetative tissues, flavonoid biosynthesis pathway is commonly induced due to environmental fluxes and physiological changes as a defending tool to oxidative stresses in response to high-light, UV, temperature, salt, drought, pathogen infections, and hormones (Zhou *et al*., 2012; Xu *et al*., 2015). The particular flavonoid biosynthesis pathway starts with the association of three molecules of malonyl-CoA and one molecule of 4-coumaroyl-coenzyme A (CoA), which results in naringenin chalcone. This reaction is directed by chalcone synthase (*CHS*), before starting the pathway, separates into many divisions leading to diverse classes of flavonoids, including anthocyanins. Flavonoid 30-hydroxylase (*F30H*), Flavanone 3-hydroxylase (*F3H*) and flavonoid 30, 50-hydroxylase (*F3050H*) can then direct the route towards delphinidin anthocyanidins and cyanidin. Anthocyanidins are converted from leucoanthocyanins by anthocyanidin synthase/leucoanthocyanidin dioxygenase (*ANS/LDOX*) and further glycosylated by uridine-diphosphate (*UDP*)-glucose through the enzyme flavonoid-O-glycosyltransferase (*UFGT*). O-methyltransferases (*OMTs*) catalyze the realization of O-methylated anthocyanins, for example, malvidin, peonidin, and petunidin (Koes *et al*., 2005; Hichri *et al*., 2011; Jaakola, 2013).

The enzymes involved in the flavonoid pathway are enclosed in the cytosol that regulates the flavonoids biosynthesis after transferred into cell walls and/or vacuoles (Koes *et al*., 2005). The enzymes have an important role in the stability of the biosynthetic pathway because of the silencing, overexpression and heterologous expression of the single enzyme genes often prime to large changes in the flavonoid composition of the objective tissue (Griesser *et al*., 2008; Han *et al*., 2012). Transcription factors are responsible to increase the expression of structural genes of anthocyanins biosynthesis pathways that are identified in different species like *Arabidopsis*, *apple*, and *grapes* etc. anthocyanins pathway occurred as a result of transcription factors interaction including DNA-binding *R2R3-MYB* transcription factors and basic *bHLH* like *MYC*, *MADS-box*, and *WD40*-repeat proteins (Marles *et al*., 2003; Allan *et al*., 2008; Matus *et al*., 2008). Many secondary plant metabolite pathways are controlled by a different kind of MYB proteins, responding to biotic and abiotic stresses, signal transduction, developmental changes, plant resistance against wounding and osmotic stress and disease resistance (He *et al*., 2016). The expression of MYB and *bHLH* proteins regulate the subgroup of genes and the regulatory complex is mainly affected by *WD40* proteins. In fruits, mostly in grapes, the anthocyanins pathway regulation has been deeply studied and the fourteen anthocyanins pathway associated *R2R3-MYB* family member has been identified (Matus *et al*., 2008; Fournier-Level *et al*., 2010).

Plant hormones have a vital role in the regulation of fruit development, ripening, and expression of anthocyanins biosynthesis genes. In non-climacteric fruits showed that the ABA participated in the expression of ripening linked with anthocyanins biosynthesis (Koyama *et al*., 2010; Jia *et al*., 2011; Jia *et al*., 2016). The ABA has a central role in regulating the ripening of non-climacteric fruit and accumulation of anthocyanins was confirmed in strawberry.

Cytokines increase light and sucrose induction anthocyanins pathway in *Arabidopsis* (Das *et al*., 2012c), while scarce knowledge of cytokinins role in fruit ripening-related anthocyanins biosynthesis. Jasmonates (JAs) have a role in color formation in grapevine and apples, through the interaction with ethylene biosynthesis (Ziosi *et al*., 2008; Zapata *et al*., 2014). Gibberellins also can hinder the ripening process and anthocyanins accumulation linked with ripening in fruits (Zapata *et al*., 2014). In *Arabidopsis*, ethylene has a negative effect on sugar and photosynthesis-induced anthocyanins accumulation by suppressing the positive regulation of the *MYB– bHLH–WD40* complex and encouraging the expression of the negative R3-MYB regulator MYBL2 (Jeong *et al*., 2010; Broeckling *et al*., 2016). While ethylene has found to be the regulator, the *UFGT* (The UDP glucose-flavonoid 3-O-glucosyltransferase) is a key enzyme for biosynthesis and by the stability of anthocyanin pigments of red *grapes* (Chervin *et al*., 2009). Anthocyanins biosynthesis signaling pathways promoted through sugars, plant hormones, light and relations among these signals. Sugar triggered the anthocyanins biosynthesis through the heterotrimeric M(L2) BW complexes that are under the regulation of hormones (Jeong *et al*., 2010; Das *et al*., 2012a, c). This review reports new findings for more understanding the role of light and sugar in the annotation of the anthocyanins biosynthesis pathway with DELLA proteins and the corresponding regulation of the transcriptional MBW complex.

Environment Frame in Anthocyanins

Light and temperature isa very important environmental factor affecting the biosynthesis of flavonoid in the plant (Zoratti *et al*., 2014a). Light exposure has a positive effect on the concentration of anthocyanins, especially in fruit skin and shading of fruit have the opposite effect (Jeong *et al*., 2004; Fujita *et al*., 2006; Matus *et al*., 2008; Azuma *et al*., 2012). Zhang *et al*. (2013) reported anthocyanins accumulation reduction when the berries were not under the light. Light exclusion increased the ratio of dihydroxylated/ trihydroxylated anthocyanins in accordance with the transcriptional abundance of *F30H/F3050H*, as a result of lower expression of structural (*CHS, CHI, F3H, DFR, LDOX, UFGT*) and regulatory genes (*MybA1*) in berry skin (Azuma *et al*., 2012; Guan *et al*., 2014).

Different temperatures are induced the quantitative and qualitative changes in the anthocyanins profile of apple, grapevine, bilberries and berries (Azuma *et al*., 2012; Uleberg *et al*., 2012), while high temperatures (30–35ºC) have been shown to decrease anthocyanins content in the skin of apple, grapevine and berries (Lin-Wang *et al*., 2011; Azuma *et al*., 2012). Flavonoid glycoside transferases and flavonoid methyltransferases are regulated by the light quality through different regulation mechanisms (Fu *et al*., 2016). The combination of low temperature and light treatment induce the anthocyanins biosynthesis in plant leaves and astimulating rapid anthocyanins accumulation in the skin of apple and pear. Previous literature perceived that higher concentration of flavonoids, particularly anthocyanins accumulation in plants under long duration photoperiods. Subsequently, the accumulation of anthocyanins is positively linked to light intensity. Anthocyanins accumulation in postharvest strawberry could be increased under the blue light that is produced from LED (light-emitting diode) (Kondo *et al*., 2014; Xu *et al*., 2014). The light treatment increasesthe enzymatic activity of flavonoid biosynthesis containing, *C4H,PAL 4CL, CHS, CHI* and *ANS* (Zoratti *et al*., 2015).

In addition, Wei *et al*. (2011) found that non climacteric litchi fruit (*Litchi chinensis*) reduced the anthocyanins accumulation with bagging treatments due to down-regulation of the structural gene of anthocyanins, for example: chalcone is omerase (*LcCHI*), chal cone synthase (*LcCHS*), anthocyanidin synthase (*LcANS*), dihydroflavonol 4-reductase (*LcDFR*), flavanone 3-hydroxylase (*LcF3H*), and UDP-glucose: flavonoid 3-*O*-glucosyltransferase (*LcUFGT*) (Wei *et al*., 2011). These genes showed upregulation with higher accumulation of anthocyanins after debagging treatment. Affirmative light effects on the flavonoid biosynthesis pathway has been identified in numerous fruit species and ornamental plants like, *tomato* (Løvdal *et al*., 2010), raspberry (Wang *et al*., 2009), cranberry (Zhou and Singh, 2004), bilberry (Uleberg *et al*., 2012) and Chinese bayberry (Fu *et al*., 2016). Some fruit, light has a less synergetic effect on flavonoid biosynthesis. In some cases, light has no/decrease anthocyanins accumulation, for example, the accumulation of anthocyanins was not affected by light and even higher light hinder the anthocyanins pathway in *pears* and tropical mangosteen (*Garcinia mangostana*) fruit. Carbone *et al*. (2009) observed the anthocyanins levels are depended on different developmental stages of fruit while PA_S and flavonols are affected by environmental factors (Carbone *et al*., 2009). In grapefruits light induced the expression of *R2R3-MYB* transcription factors, which play a positive role in there gulation of flavonoid biosynthesis (*VvMYB5a*), PA (*VvMYBPA2* and *VvMYBPA1*), flavonols (*VvMYB12* and *VvMYBF1*), and anthocyanins (*VvMYBA2* and VvMYBA1). As shown in Table 1 almost all the fruits *R2R3-MYB* transcription factors potential role for flavonoid biosynthesis have been studied, for example, litchi, Chinese bayberry, pear, nectarine, strawberry, apple, and grapes.

From the last years suggested that the role of the MYB transcription factors in MBW complex is more important and significantly involved in the light-induced expression of the flavonoid pathway as compare to *WD40* and *bHLH* partners that act as a helpful in this process (Matus *et al*., 2009). Surprisingly, *bHLH3* is the regulator of flavonoid biosynthesis in nectarine and *bHLH3* upregulation was observed after light treatment (Ravaglia *et al*., 2013).

Table 1: R2R3-MYB transcriptional factors role in anthocyanin biosynthesis

Species	R2R3 MYB	Function	References
Woodland strawberry (*Fragaria vesca*)	FvMYB10	Anthocyanin biosynthesis in flower petal	Miao *et al*., 2016; Lin-Wang *et al*., 2010
Litchi (*Litchi chinensis*)	LcMYB1	Anthocyanin biosynthesis in fruit pericarp	Lai *et al*., 2016; Lai *et al*., 2014
Pear (*Pyruspyrifolia*)	PyMYB10	Anthocyanin biosynthesis in fruit skin	Yang *et al*., 2015; Zhang *et al*., 2011
Nectarine (*Prunuspersica*)	PpMYB10	Anthocyanin biosynthesis in fruit skin	Ravaglia *et al*., 2013; Gonzalez *et al*., 2016
Chinese bayberry (*Myricarubra*)	MrMYB1	Anthocyanin biosynthesis in fruit	Niu *et al*., 2010
Grape (*Vitis vinifera, Vitis*× *labruscana*)	VvMYBF1	Flavonol biosynthesis in fruit skin	Guan *et al*., 2016; Liu *et al*., 2014; Azuma *et al*., 2012
	VvMYB12	Flavonol biosynthesis in fruit skin	Matus *et al*., 2010; Jeong *et al*., 2004; Matus *et al*., 2009
	VvMYBA1	Anthocyanin biosynthesis in fruit skin	Azuma *et al*., 2012; Koyama *et al*., 2012; Matus *et al*., 2009
	VlMYBA2	Anthocyanin biosynthesis in fruit skin	
	VvMYBPA1	Proanthocyanidin biosynthesis in fruit skin	Azuma *et al*., 2012
	VvMYBPA2	Proanthocyanidin biosynthesis in fruit skin	Koyama *et al*., 2012
	VvMYB5a	General flavonoid biosynthesis in fruit skin	
	VlMYB5b	General flavonoid biosynthesis in fruit skin	
Apple (*Malus*× *domestica*)	MdMYB1	Anthocyanin biosynthesis in fruit skin	Meng *et al*., 2016
	MdMYBA	Anthocyanin biosynthesis in fruit skin	Hu *et al*., 2016
	MdMYB10	Anthocyanin biosynthesis in fruit skin	Feng *et al*., 2013
	MdMYB9	Proanthocyanidin biosynthesis in leaves	Gesell *et al*., 2014
	MdMYB11	Proanthocyanidin biosynthesis in leaves	Gesell *et al*., 2014

The MRE (*R2R3-MYB* direct interaction through MYB) has been discovered to be important for light-regulated expression of flavonoid biosynthesis genes, like CHS. The MRE has played a significant role in the light regulatory unit (LRU) which is essential for the light induction expression of CHS. The light regulatory unit and additional light reactive elements have been stated not only helpful in promoters of flavonoid structural genes but also helpful in many anthocyanins biosynthetic structural genes (Zhou *et al*., 2013). In the darkness, COP1 is contained in the nucleus of the cell, it colloid with target transcription factors like *HY5* (ELONGATED HYPOCOTYL5) and mediates through ubiquitylation and degraded by the 26S proteasome pathway (Lau and Deng, 2012) (Fig. 3A).

In the daytime during the light, COP1/SPA complex colloids with targeted photoreceptors that cause the inhibition the function of COP1/SPA complex through separation of COP1 and transportation from the nucleus to the cytoplasm (Fig. 3B). The small accumulation of COP1 in the cell nucleus permits nuclear localized the gene expression and transcriptional factors (Lau and Deng, 2012). During the removal of COP1 from the nucleus to the cytoplasm, *HY5* shows more stabilization in light (Fig. 3B). *HY5* significantly activate the *R2R3-MYBs* and the structural genes of the flavonoid biosynthesisin *Arabidopsis* and apple (Maier *et al*., 2013; Peng *et al*., 2013; Shin *et al*., 2013). As shown in Fig. 2, radiation of the UV-B light are absorbed through photoreceptor named UVR8 bring through COP1. COP1 preformed different role under visible light, *Arabidopsis* COP1 in UV-B light has a positive role through co-operating by UVR8 and regulate with the interaction of *HY5*. Subsequently, Tryptophan amino acid (Trp), especially in UVR8 photoreceptor (dimeric form), strongly absorbed UV-B radiation that converting to the monomerization of UVR8. COP1 and Monomeric form UVR8 that make a complex which gathers in the nucleus of the cell. The UVR8-SPA-COP1 complex that stabilizes the *HY5*, *bZIP* transcription factor and increasing the activity of *R2R3-MYBs* for the structural gene of flavonoid biosynthesis. Peng *et al.* (2013) reported the mechanism under the UV-B light radiation for improving the anthocyanins in apple (Peng *et al*., 2013). Near about 98% UV-light that is reaching to the ground surface act as UV-A radiation. Certain ideas of the presence of particular photoreceptor of the UV-A radiation that is different from the UVR8, however, it still uncertain (Li *et al*., 2014a) and we try to explain the new insights about this complex for the betterment of future research. After the Mutations in the SPA/COP1 complex exposed to an increase the accumulation in the anthocyanins of *Arabidopsis* and also the mutation in the signaling pathway of light have special effects on the flavonoid pathway in fruits (Maier *et al*., 2013). Anthocyanins biosynthesis reduction noticed by the proliferation regulation of photo-respiratory genes (Zhou *et al*., 2013). *Arabidopsis F3oH/CHI* mutant, under a higher expression of the photorespiratory gene, cannot accumulate the anthocyanins. From this *Arabidopsis* mutant result, we can propose that photorespiration linked genes involved in the reduction of anthocyanins accumulation.

HY5 is a *bZIP* transcription factor that has been linked to activation of the *CHS* gene and the flavonoid pathway in reaction to higher light and UV-B radiation in Arabidopsis (Lau and Deng, 2012). Shorter-wavelength lights UV-A, induced anthocyanins accumulation by up-regulated anthocyanins-related genes significantly in *turnip* (Wang *et al*., 2016). UV-B irradiation would induce the accumulation of anthocyanins via MdCOP1-mediated signaling, leading to activation and binding of *MdHY5* to the promoter regions of *MdMYB* genes (Peng *et al*., 2013).

R2R3-MYB genes related to flavonoid biosynthesis in fruits react to light or other environmental stimuli in a different manner (Azuma *et al*., 2012; Jaakola, 2013). It has not yet been fully understood how flavonoid biosynthesis pathway genes and *MYB*-related genes respond to various combinations of temperature and light.

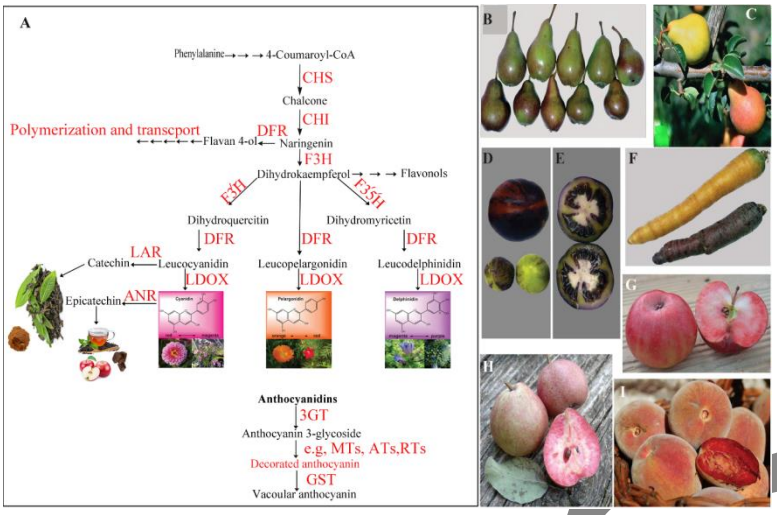

Fig. 2: (A) Scheme of the biosynthetic pathway of flavonoid pigments. **(B)** Staining of red shading (upper column) at the sun-uncovered side of pear fruits contrasted with the fruits accepting less extreme light (base line) which keep up more pigmentation (Passeri *et al*., 2016). **(C)** Pear fruit has lost its red shading and turned yellow on the tree. This phenomenon is accounted for pears fruits that observed after pinching the peduncle during the development process (Passeri *et al*., 2016). **(D)** Transgenic tomato fruits with plants expressing the *35S:SlANT1*construct. **(E)** green tomatoes from the same plants as in **(D)** showing purple flesh, locular cavities, and seeds (Kiferle *et al*., 2015). **(F)** Orange and purple carrots (De Jong *et al*., 2004). In **(G)**, **(H),** and **(I)** *Rosaceae* species ancient varieties with rich anthocyanin flesh (Passeri *et al*., 2016)

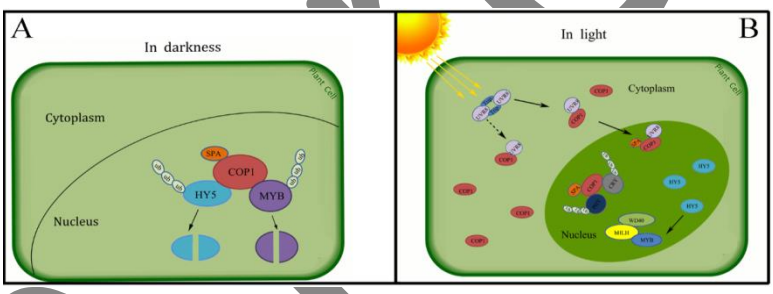

Fig. 3: (A) Signalling pathway mechanism model that effecting flavonoid biosynthesis under darkness**. (B)**Signaling pathway mechanism model that effecting flavonoid biosynthesis under UV-B radiation

Sugar Interaction with Transcriptional Factors for Induction of Anthocyanins

Sugar has an important role in photosynthesis, carbon metabolism that uses as a carbon/energy source, modulating the developmental and physiological process, survival in stress condition and regulation of genes (Broeckling *et al*., 2016). Sugar significant role in regulatory molecules has been already identified and driving nature of sugar for carbon metabolism (conversion of sucrose to glucose and fructose) and sugar interactions with plant hormone signaling (Ruan, 2012; Li *et al*., 2014b).

We describe here background and a current story about this interaction, Mita *et al*. (1997) first identified anthocyanins accumulation abundance in Arabidopsis leaves and cotyledons which are specifically grown on a sugar comprising medium (Mita *et al*., 1997). Similar results have also been identified in grape cells and radish hypocotyls (Hara *et al*., 2003). Teng *et al*. (2005) stated that sucrose triggers the anthocyanins biosynthesis through *PAP1/MYB75* transcription factor and *PAP1* knock-out mutant be deficient in this response (Teng *et al*., 2005). Solfaneli *et al*. (2006) further reported that expression of PAP1 was specific to sucrose and not for glucose or fructose (Solfanelli *et al*., 2006). Jeong *et al*. (2010) identified the effect of sucrose on regulatory genes of anthocyanins subsidized more than two-fold upregulation of transcriptional factors, for example, *TT8, TFs, GL3* and more than three-fold down regulation in a negative transcriptional factor like *MYBL2* (Jeong *et al*., 2010). Luo *et al*. (2012) reported higher PAP1 expression in glucose-treated seedlings as compared to sucrose treated seedlings (Luo *et al*., 2012). Sucrose induction expression of PAP1 has been shown to be modulated by hormones, mutations in AtSUC1 sucrose transporter. Li *et al*. (2014) defined sucrose increase gibberellin degradation through DELLA proteins, hindering growth and stimulating the

structural gene of anthocyanins *MYB75* in *Arabidopsis* (Li *et al*., 2014b). Although a more recent paper reported Sucrose treatment of Arabidopsis seedlings led to a 20-fold induction of PAP1 transcript, while represented a 6-fold increase over levels in glucose-treated seedlings (Broeckling *et al*., 2016).

However, very little studies reported the comprehensive molecular mechanisms elaborate the sucrose signaling in anthocyanins. Sucrose has a more additive effect for anthocyanins biosynthesis as compared to glucose in *Arabidopsis* (Teng *et al*., 2005). Exogenous sucrose regulates the lateral biosynthesis genes of anthocyanins like *LDOX, UF3GT,* and *DFR* by increasing more than a hundred folds, whereas the early biosynthesis genes substitute the upregulation of the *DFR* like *C4H, CHI* and *CHS* revealed lesser induction via Sucrose.

In *Arabidopsis*, *R2R3-MYB* subfamily have 126 members in which 13 members are related to the regulation of flavonoid biosynthesis (Liao *et al*., 2016). Most of the *MYBs* are increased by expression of the structural genes in the flavonoid pathway e.g. transparent test a 2 (*TT2* and MYB123) involves the co-factors named *TTG1* (*WD40*) and *TT8* (*bHLH42*) to generate MBW complex which regulates the expression of the *ANR* and *DFR* genes, these are responsible for the production of proanthocyanidins that accumulate in the seed coat (Baudry *et al*., 2004; Das *et al*., 2012a). Likewise, *MYB90/PAP2* and *MYB75/PAP1* are involved for *bHLH* cofactor that is dependent on the stimulation of *PAL, CHS, DFR* and *GST* (glutathione S-transferase), these are main enzymes involved in the anthocyanins pathway (Hichri *et al*., 2011). But, some *MYBs* have also contrary to the positive, such as *VvMYB4* in the *grapes*, *FaMYB1* in *strawberry* and *MYBL2*, *R3-MYB* TFs protein, play a negative role during the higher light, nitrogen deficiency and different environmental cues.

Light has a critical role in sucrose induction anthocyanins accumulation and sugar signaling has a liaise role in the redox state of the photosynthetic electron transport. The sucrose role in the light signalling for anthocyanins biosynthesis clarified by using mutants *hy5*, *hy1* and *cry1/2* treated with the inhibitor of the photosynthetic electron transport [3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU)] that operate photosystem II on the QB binding site, however, not through 2,5-dibromo-3-methyl-6-isopropyl-benzoquinone [inhibitor of plastoquinone (PQ) oxidation (DBMIB)]. These results recommended that the PQ pool shows an important role in light and sugar association intended for anthocyanins accumulation, for example, DCMU retains the PQ pool oxidized but DBMIB decreases it (Das *et al*., 2011).

DEELAs Interference Role in Anthocyanins

Gibberellin (GA4) negatively affect the sucrose signaling pathway, proposing that GA and sucrose signaling pathways share mutual components or converge for the regulation of *PAP1* and *MYB75* gene expression. Gibberellin signaling show negatively correlates with DELLA proteins that are major facts of the integration complex of different hormone signals. Interestingly, *PAP1/MYB75* activated as a result of putative early DELLA target (Fig. 4) (Gallego-Bartolomé *et al*., 2011).

Recently reported, sucrose fixed/steadfast the DELLA proteins that make easy understanding of the negative effect of Gibberellin on the sucrose signaling role in the anthocyanins pathway.Gibberellin blocks the regulation of the sucrose related genes that increase the anthocyanins synthesis (Li *et al*., 2014b). The suppressive influence of GA was significantly controlled in *gai*-mutants through stabilization of DELLA protein, from these results finally suggesting that DELLAs have an ability to disruption of the Gibberellin-Sucrose interaction (Loreti *et al*., 2008). In *Arabidopsis* mutants, sucrose concentrations showed a positive correlation with anthocyanins accumulation and negatively correlate with seedling growth (Fig. 4). Remarkably, DELLA suppresses the protein of gibberellin (RGA) particularly showsin sucrose response, but for glucose shows very narrow effects (Li *et al*., 2014b).

Defective starch metabolism Mutants face starvation condition in night-time and this condition negatively effects on the growth of the plant in the night. DELLA level increased throughout the day would be due to more sucrose level at day-time. Interestingly, starchless mutants were showed higher growth in the day-time that point out a higher amount of sucrose in the light period (Phytologist *et al*., 2007). It would be an increased rate of growth in the day due to different levels of DELLAs. Starchless mutants are showed less growth in the night, might be due to the decrease level of starch, together with the variation in the gibberellin level due to the lack of sugars in night-time that is deriving the poor growth potential (Wiese *et al*., 2007; Paparelli *et al*., 2013). Gibberellin deficient mutants showed the dwarfism, that is disengaged from carbon availability, itmeans that gibberellin has some critical role in growth (Ribeiro *et al*., 2012). Mostly in higher plants *WD40*, *MYB* and *bHLH* combine together and make MBW complex that regulates the expression of many structural biosynthesis genes.

MBW complex action and some structural gene of anthocyanins are directly suppressed through JAZ family proteins and MYBL2, JAZ protein fixed the *MYB* and *bHLH*. Recently Xie *et al*. (2016) reported that JAZs and *MYBL2* mediate through gibberellic acid decreases the anthocyanins level in *Arabidopsis*. Dual luciferase assays showed that DELLAs openly isolate the JAZs and *MYBL2* repressor due to MBW complex activate that derive the anthocyanins. DELLAs interaction with JAZ and *MYBL2* show significant results in anthocyanins biosynthesis under abiotic stress. DELLA protein RGA accumulates under abiotic stresses, DELLA protein promoted anthocyanins biosynthesis with the coordinated in defense metabolic pathway and plant growth (Xie *et al*., 2016).

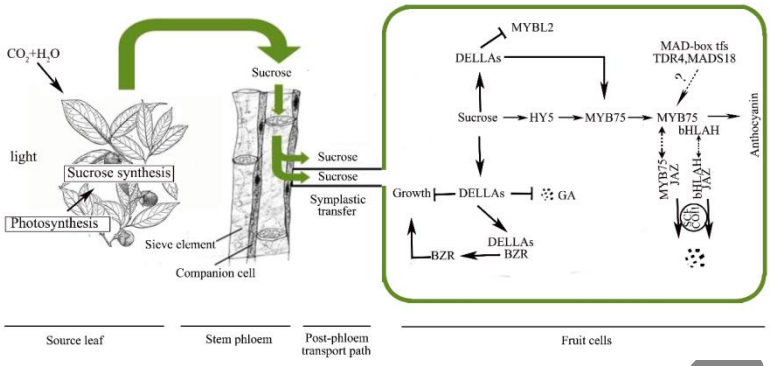

Fig. 4: A model depicting the role of sucrose in the regulation of anthocyanin biosynthesis in fruits. Sucrose stabilizes the DELLA protein and upregulates the transcription factor MYB75 via *HY5*. DELLA negatively affect the MYBL2 that are repressor the anthocyanin but positively regulate the *MYB75* that are an enhancer of anthocyanin biosynthesis. DELLAs also inhibiting growth through sequestering the BZR1 and degradation of Gibberellin. Jasmonates release the *MYB* and *bHLH* which are required the expression of anthocyanin

DELLAs also link the brassinosteroids (BR) to sucrose and gibberellin. The brassinosteroids and gibberellin pathways are closely interrelated through the direct interaction of DELLAs with BRASSI-NAZOLE-RESISTANT 1 (BZR1) transcriptional factor. DELLAs stabilization through sucrose due to DELLAs level increase, isolating BRZ1 and subsequently repressed the growth. This situation in vivo is more complex because DELLAs driving the contribution during growth changes under the development of plant (Stewart Lilley *et al*., 2013).

Jasmonates positively regulate anthocyanins biosynthesis and this regulation can be increased through more sucrose level. Jasmonates activate from releasing the *MYB* and *bHLH* from repression by JAZ proteins (Qi *et al*., 2011). The sucrose-specific induction of the anthocyanins synthesis and stabilization of the DELLA proteins by sucrose delivers a simple tool to link the sugars to others signaling pathway. The sucrose increases the transcriptional factors required for anthocyanins synthesis and DELLAs that trigger the activation of transcription of PAP1/MYB75 (Gallego-Bartolomé *et al*., 2011).

Conclusion

The composition of anthocyanins in ripe fruit is formed via the function of complicated metabolic networks regulated by genetic, developmental and environmental factors. In higher plants anthocyanins can be increased by sugar induction. Sugars are important carbohydrate sources of plants and also act as a signal molecule to activate/repress the many reactions of the cell. Sucrose, glucose, and fructose increase the accumulation of anthocyanins and a specific increase of anthocyanins are independent of osmotic effect but not dependent on the dose. Hexoses is a signal molecule in most plants and phosphorylation of hexose through hexokinase mandatory for starting the hexoses signal transduction pathway. Sucrose proceeds significant impact on the anthocyanins accumulation with the hormone interaction and triggered the transcript levels of many structural genes of anthocyanins biosynthesis e.g. *UF3GT*, *CHS*, *LDOX*, *DFR*, and *C4H*. The light critical role has recognized in the hormonal regulation for the accumulation of anthocyanins but the description of the light interactions with sugar and hormones still need to clarify e.g., epistatic interactions among the photoreceptor *HY5* and MBW complex need more study and LBGs under the light are regulated through mutually *HY5*and PAP1 that is also more increased via sugars. This review explains the understanding of the mechanism of the light-regulated anthocyanins biosynthesis in fruits that occurs via the COP1 signaling. Identification of additional factors that are influenced by sugar and other stimuli should be needed more clarification and might increase the regulation of transcriptional/posttranslational of PAP1. Additionally, interaction among the different hormones should be focused and need to explain the effect of different hormoneson anthocyanins accumulation via isolated genetic mutants that may be helpful to clarify. In sucrose signaling DELLAs an innovative element that is very helpful to clarification of the complex and a key sugar network and their interactions between the hormones in plants. DELLAs can also exploit growth arrest situations and anthocyanins biosynthesis linked by sucrose addition, and elucidate the effects of gibberellins degrade compounds (DELLA stabilizing) e.g triazole fungicide paclobutrazol (TFP) and daminozide (Alar) that endorse the colour of fruit (generally produced via sucrose accumulation) however, postponing maturation/ripening, retaining firmness of fruits and escaping early abscission. However, mechanisms related to other environmental factors need further clarification, but more in-depth studies are mandatory for an understanding the nature of the interaction as well as crosstalk between other factors in that control fruit development and ripening. The exact molecular mechanism of sugar sensing and signaling are not so clear and some confusion still remained, new genomic

and proteomic techniques might elucidate the sugar signaling interaction with anthocyanins accumulation. These studies will deepen our understanding of the role of interactions between these key players in the regulation of the anthocyanins biosynthesis pathway, which is likely to become one of the most interesting targets for future breeding work.

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