The role of environmental stress in fruit pigmentation

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Abstract

For many fruit crops, the colour of the fruit outwardly defines its eating quality. Fruit pigments provide reproductive advantage for the plant as well as providing protection against unfavourable environmental conditions and pathogens. For consumers these colours are considered attractive and provide many of the dietary benefits derived from fruits. In the majority of species, the main pigments are either carotenoids and/or anthocyanins. They are produced in the fruit as part of the ripening process, orchestrated by phytohormones and an ensuing transcriptional cascade, culminating in pigment biosynthesis. Whilst this is a controlled developmental process, the production of pigments is also attuned to environmental conditions such as light quantity and quality, availability of water and ambient temperature. If these factors intensify to stress levels, fruit tissues respond by increasing (or ceasing) pigment production. In many cases, if the stress is not severe, this can have a positive outcome for fruit quality. Here, we focus on the principal environmental factors (light, temperature and water) that can influence fruit colour.

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For many fruit crops, the colour of the fruit outwardly defines its eating quality. Fruit pigments provide reproductive advantage for the plant as well as providing protection against unfavourable environmental conditions and pathogens. For consumers these colours are considered attractive and provide many of the dietary benefits derived from fruits. In the majority of species, the main pigments are either carotenoids and/or anthocyanins. They are produced in the fruit as part of the ripening process, orchestrated by phytohormones and an ensuing transcriptional cascade, culminating in pigment biosynthesis. Whilst this is a controlled developmental process, the production of pigments is also attuned to environmental conditions such as light quantity and quality, availability of water and ambient temperature. If these factors intensify to stress levels, fruit tissues respond by increasing (or ceasing) pigment production. In many cases, if the stress is not severe, this can have a positive outcome for fruit quality. Here, we focus on the principal environmental factors (light, temperature and water) that can influence fruit colour.

1 BACKGROUND

The colour of fruit is generally associated with reproduction, specifically a means to promote seed dispersal by making the fruit visually attractive to herbivores/omnivores. Colour, therefore, is a key component of fruit development and intrinsically related to the ripening process. Fruit colours are derived from 'secondary (or specialised) metabolite' pathways. In evolutionary terms, these pathways in flowering plants and the breadth of their products have grown in number and complexity, in response to environmental and pathogenic stimuli and to adaptive changes for pollinator attraction. These colour pigments are largely derived from either the carotenoid and/or flavonoid pathways.

Colour helps to define the attractiveness and quality of fruits and strongly influences consumer demand. Hence, for many years, improvements or changes to fruit colour have been a major target of breeding programmes across a range of crops (Figure 1). Additionally, growers routinely implement a number of on-orchard management techniques to enhance fruit colour development (Wang et al., 2020). In this review, we will consider the impact of environmental stresses on fruit colour. While the term 'stress' usually conjures up negative connotations, moderate stress can enhance the concentration of numerous phytochemicals, including those that colour our fruits. The timing, duration and severity of any stress will determine the plant's response and consequent impact on colour.

Figure 1

A range of pigments, including anthocyanins and carotenoids, confer numerous health benefits to the consumer.

Fruit pigmentation is part of the programmed development that culminates in ripening. This orchestrated process is largely driven by phytohormones and mediated via transcription factors (TFs) (Allan & Espley 2018; Kumar, Khurana & Sharma 2013). This process, however, can be strongly influenced by environmental conditions such as light intensity and spectral quality as well as temperature. Knowledge of how the environment affects fruit colour will become increasingly important under changing climatic conditions globally. Increases in solar radiation and temperature as well as less predictable rainfall and a higher incidence of drought are predicted to affect crops (Challinor et al. 2014; Lobell & Gourdji 2012). Climate change is expected to require the breeding of new varieties adapted to different conditions to tackle the potential issues of compromised plant health, flowering, fruit set and fruit development.

Colours in fruit not only protect the fruit itself, but also have implications for human health. As such, they have been recognised as an integral component of a healthy diet (Martin & Li 2017). In fact, rather than simply maintain the amounts of these pigmented phytochemicals, many consider that they should be enhanced to promote greater potential health benefits (D'Amelia et al. 2018; Poiroux-Gonord et al. 2010).

2

2 Fruit pigments and their effects on human health

One of the key drivers for research into plant pigments is the association of these compounds with dietary health (Martin & Li 2017). Fruits are particularly rich sources of these phytochemicals and so changes in the composition or concentration are of interest. For carotenoids, one of the most abundant and important of these pigmented phytochemicals is β-carotene, which has provitamin A properties and is converted into retinol (vitamin A) in the body. Other carotenoid sources of provitamin A include α-carotene and β-cryptoxanthin (Rodriguez-Concepcion *et al.* 2018). Vitamin A is an essential part of our diet and deficiency is still a major problem in developing countries (West & Darnton-Hill 2008), which prompted the development of provitamin A-enriched crops (Giuliano 2017). Carotenoids also provide the macular pigments, xanthophylls including lutein and zeaxanthin, which have antioxidant and short-wavelength light absorption functions in the eye (Bernstein *et al.* 2016). These are associated with eye health, particularly the prevention of age-related macular degeneration (Carpentier, Knaus & Suh 2009). Consumption of carotenoids has also been associated with disease prevention, including a reduced incidence of cardiovascular disease and some cancers, as well as positive effects on cognitive function (Leermakers *et al.* 2016; Lindbergh *et al.* 2018; Mein, Lian & Wang 2008).

An increasing number of clinical trials have shown evidence for the health claims associated with anthocyanins. Many of these studies link anthocyanins to protection against human diseases, including cardiovascular and age-related degenerative diseases, obesity, metabolic syndrome and cancer (reviewed by Gonçalves *et al.* 2021; Kalt *et al.* 2020; Pojer *et al.* 2013). There was earlier speculation about the mechanism of action, as these compounds were not found in human circulatory systems at the site of the action, but it appears now that bioavailability is greater than originally thought (Kay *et al.* 2017; Lila *et al.* 2016). If the protection that pigments provide in fruit is due to their antioxidant activities, is this also the mechanism the major human health benefits associated with their dietary consumption? This is less certain, and further research is required to confirm the modes of action. However, it has recently been established that one key mechanism for the health effects is via the extensive impact of an anthocyanin-rich diet on the gut microflora, which further process the final functional compounds (Espley *et al.* 2014; Groh *et al.* 2020; Jucá *et al.* 2020; Liso *et al.* 2018; Ntemiri *et al.* 2020; Ou, Yang & Liu 2020).

3 THE STRESS Response: a brief overview

When plants are subjected to sufficient environmental stress, reduction-oxidation (redox) reactions occur (Figure 2). Under normal conditions, partially reduced or activated forms of oxygen, known as ROS, are generated, but at a rate that can be managed by the plant's ROS-scavenging machinery. Under highly stressful conditions, this redox homeostasis can become unbalanced, and these highly reactive molecules can cause cellular damage. As cellular ROS concentrations increase, for example with extreme temperature or drought, damage can afflict DNA, RNA, membranes and ultimately destroy the cell itself (Mittler 2002). As oxygen is produced during photosynthesis, the chloroplastic photosynthetic machinery, particularly in leaves, is the site of much of the ensuing ROS (Foyer 2018). In green developing fruit, where active photosynthesis is driving metabolism, this can still apply, but as the fruit ripens, ROS can be generated in other organelles, particularly mitochondria (Schertl & Braun 2014). This rise in respiratory sourced ROS, may occur when the common chloroplast/chromoplast shift removes the central mechanisms for coping with ROS: the xanthophyll (and other carotenoid) cycles embedded within the photosynthetic machinery.

Since these redox reactions are inevitable in an oxygenated world, plants have had to evolve coping mechanisms. One mechanism is enzymatic, with enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione peroxidase, monohydroascorbate (MDHAR) and dehydroascorbate reductase (DHAR)(Das & Roychoudhury 2014). The other major mechanism involves the non-enzymatic antioxidants such as ascorbic acid (AsA) and numerous polyphenols and terpenes (Decros *et al.* 2019). AsA is an important scavenger of reactive oxygen and in a scenario where stress leads to a reduction in photosynthesis and an increase in photooxidative damage and ROS production, AsA production may be enhanced. AsA production does not directly affect the colour of fruit and will not be covered in this review, but nevertheless it is interesting to consider that the same signals that mediate changes in the concentration of AsA in fruit,

may also mediate changes in polyphenol and terpene production. The polyphenols include flavonoids such as catechin, quercetin and anthocyanins, while terpenes include the pigmented carotenoids lycopene and β-carotene. It is clear then, that these plant pigments have a role in fruit beyond facilitating seed dispersal since there is good evidence for the induction of red pigmentation in vegetative tissues directly in response to ROS production. Plants have evolved this pigmentation to act as sunscreens and antioxidants and alleviate stresses from damaging environmental conditions (Davies *et al* . 2022).

The amount of ROS will also affect the concentrations of plant hormones, including abscisic acid (ABA), brassinosteroids (BRs), auxin and gibberellins (GAs). Phytohormones play a major role in ripening, with ethylene and ABA having key roles in climacteric and non-climacteric fruits, respectively (Fenn & Giovannoni 2021). Both ethylene and ABA play dual roles in the fruit, being not only linked with ripening, but also with the stress response (Husain *et al.* 2020; Leng, Yuan & Guo 2013). Several studies have shown a connection between increased content of fruit ABA, as a response to stress or at onset of fruit ripening, and the accumulation of anthocyanins (Jia *et al.* 2011; Karppinen *et al.* 2018; Wheeler *et al.* 2009; Zifkin*et al.* 2012). It has been suggested that accumulation of ABA inside the cell induces downstream signalling involving ROS and calcium as secondary messengers, resulting in activation of the TFs controlling the anthocyanin biosynthetic pathway (Vighi *et al.* 2019). Phytohormones can also interact, sometimes antagonistically such as has been shown for ABA and ethylene, but sometimes positively through providing an enhanced response to abiotic stresses (Müller 2021).

In this review, we concentrate on the major environmental stressors that influence pigment carotenoid and anthocyanin production in fruit crops. Chlorophyll accumulation and degradation also contribute to fruit colour, particularly before ripening occurs, but this falls outside the scope of this review. While betalains are also important plant pigments, they are most commonly found in leaves, flowers, tubers and only quite rarely found in fruit, such as in prickly pear (*Opuntia ficus-indica*) and dragon fruit/pitaya (*Hylocereus costaricensis*) (Cheok *et al* . 2022). They too are elevated in response to various environmental stresses: this has recently been well reviewed (Davies*et al.* 2018; Li *et al.* 2019) and will not be covered here.
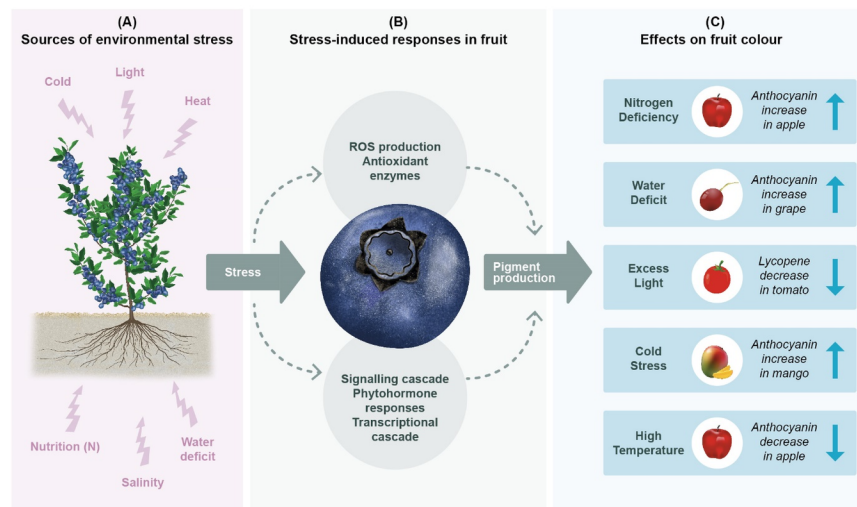
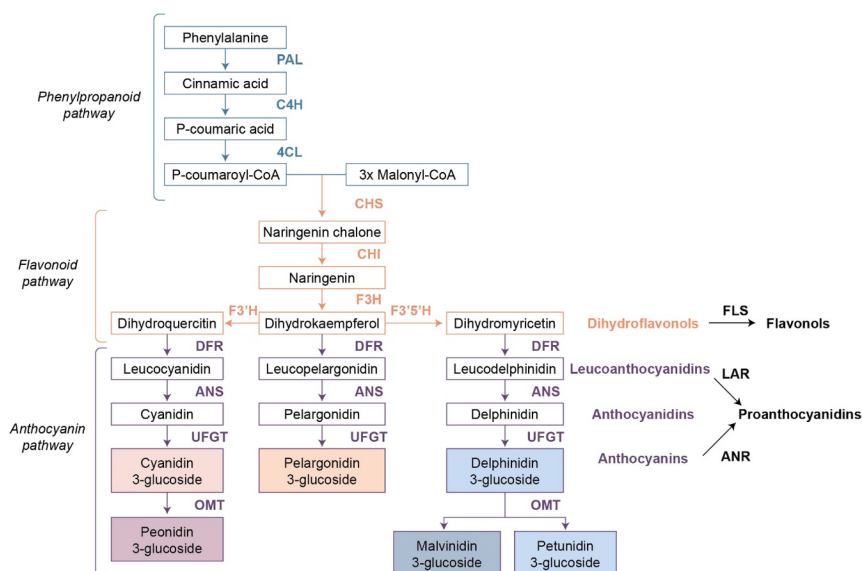**Figure 2**

The major sources of environmental stress that affect fruit pigmentation. (a) Examples of sources of environmental stress, (b) responses to stress as initiated by ROS production, and (c) examples of the stresses that can increase or decrease concentration of fruit pigments in apple, grape, tomato and mango.

4 THE biosynthesis and transcriptional regulation of Fruit pigmentS

4

The biosynthesis of flavonoid pigments

Anthocyanins are key pigments in fruit, generating red, blue and purple hues. These compounds usually accumulate in the epidermal or sub-epidermal tissues of different plant organs, offering protection against variable environmental stress factors, especially excess of light. The biosynthesis of anthocyanins occurs in the cytosol via the phenylpropanoid and flavonoid pathways. The precursors for flavonoids, including the pigmented anthocyanins, are malonyl-CoA and p -coumaroyl-CoA. From these precursors the first committed enzyme, chalcone synthase (CHS), forms chalcone, establishing the C_{15} backbone (Figure 3). Chalcone is isomerised by chalcone isomerase (CHI) to produce chalcone naringenin, which is hydroxylated by flavanone 3β-hydroxylase (F3H), converting naringenin to dihydroflavonol. Further hydroxylation is carried out by flavonoid 3'-hydroxylase (F3'H) to form cyanidin, or flavonoid 3'5' -hydroxylase (F3'5'H) to form delphinidin. Dihydroflavonol is reduced by dihydroflavonol 4-reductase (DFR) to produce leucoanthocyanidin, which is converted into the pigmented compound anthocyanidin by anthocyanidin synthase (ANS), also sometimes referred to as leucoanthocyanidin dioxygenase (LDOX). Finally, glycosylation is carried out by uridine diphosphate (UDP)-glycosyl:flavonoid 3-θ -glycosyltransferase (UFGT). Further addition of sugars and acyl side groups may follow. After biosynthesis, anthocyanins are transported to vacuoles or, rarely, cell walls. The differences in anthocyanin colours result from various factors, including the number of hydroxyl groups on the B-ring, the sugars and acyl side groups, the vacuolar pH or the accumulation of specific metal ions. To date, more than 650 different anthocyanins have been identified, the most common ones being glucosides of six aglycons: cyanidin, delphinidin, pelargonidin, petunidin, peonidin and malvidin (Jaakola 2013; Zhang, Butelli & Martin 2014).

Figure 3

Simplified overview of the biosynthetic pathway leading to anthocyanin biosynthesis in fruit. Enzyme abbreviations as follows; PAL, phenylalanine ammonia lyase; C4H, cinnamate 4-hydroxylase; 4CL, 4-coumarate-CoA ligase; CHS, chalcone synthase; CHI, chalcone isomerase; F3H, flavanone 3-hydroxylase; F3'H, flavonoid 3' hydroxylase; F3'5'H, flavonoid 3',5' hydroxylase; FLS, flavonol synthase; OMT, O-methyltransferase; LAR, leucoanthocyanidin reductase; ANR, anthocyanidin reductase; DFR, dihydroflavonol 4-reductase; ANS, anthocyanidin synthase; UFGT, uridine diphosphate (UDP)-glucose:flavonoid 3-θ -glucosyltransferase.

The biosynthesis of carotenoid pigments

Carotenoids provide many of the red, orange and yellow pigments in fruit, as seen in citrus (*Citrus* spp.), tomato (*Solanum lycopersicon*), capsicum/pepper (*Capsicum* spp.) and papaya (*Carica papaya*). Carotenoids are essential for photoprotection and integral to the photosynthetic machinery and in green tissues are co-ordinately regulated with chlorophylls (Frank & Cogdell 1996). The pathway is located in plastids and derived from the mevalonate-independent pathway (MEP) pathway, which generates the C_{20} compound geranylgeranyl pyrophosphate (GGPP) (Cunningham & Gantt 1998). The condensation of two GGPP molecules provides the first carotenoids, the colourless phytoene, and is catalysed by phytoene synthase (PSY) (Figure 4). This is often seen as the rate-limiting step for carotenoid synthesis, regulating downstream pathway flux. A two-step desaturation of phytoene, by phytoene desaturase (PDS), catalyses phytoene into phytofluene and then zeta-carotene, which is converted to di-cis zeta-carotene by zeta-carotene isomerase (Z-ISO). Desaturation by zeta-carotene desaturase (ZDS) and isomerization by carotene isomerase (CRTISO) produces lycopene and from this the pathway branches, with lycopene beta cyclases (LCYB) producing alpha-carotene and the nutritional vitamin A precursor, β-carotene (Moise, Al-Babili & Wurtzel 2014). The conversion of alpha-carotene to lutein and beta-carotene to zeaxanthin is through the action of carotene hydroxylases. Beyond these steps, other carotenoids such as xanthophylls, including astaxanthin, are generated and finally, through the actions of nine-*cis*-epoxycarotenoid dioxygenases (NCEDs) and carotenoid cleavage dioxygenases (CCDs), the phytohormone abscisic acid (ABA) and a range of apocarotenoids are produced (Giuliano 2014). Carotenoid accumulation is further influenced by cell physiology, specifically the number of available carotenoid storage plastids (Cazzonelli & Pogson 2010).
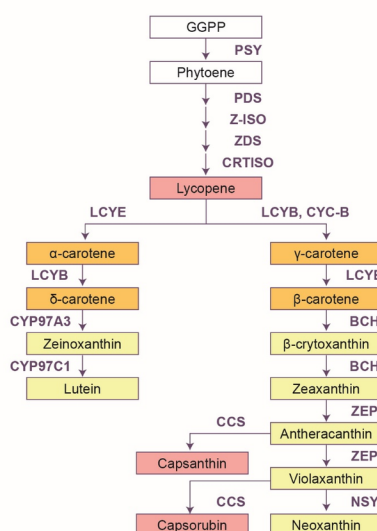

Figure 4

Simplified overview of the carotenoid biosynthetic pathway in fruit. Enzyme abbreviations as follows; PSY, phytoene synthase; PDS, phytoene desaturase; Z-ISO, ζ-carotene isomerase; ZDS, ζ-carotene desaturase; CRTISO, carotenoid isomerase; LCYE, lycopene ε-cyclase; LCYB, lycopene β-cyclase; BCH, β-carotene hydroxylase; CYP97, cytochrome P450-type monooxygenase 97; ZEP, zeaxanthin epoxidase; CCS, capsanthin-capsorubin synthase; NXS, neoxanthin synthase.

The transcriptional regulation of plant pigments

The transcriptional regulation of anthocyanins in fruit has been well documented: at its core is a TF complex, termed the MYB-bHLH-WD40 (MBW) complex (Allan, Hellens & Laing 2008). The MYB component is derived from the subgroup (SG) 6 class of MYBs (as defined by Stracke et al. (2001) as opposed to the SG5 MYBs, which control proanthocyanidins) and has been characterised in many fruit species (Albert *et al.*

2014; Jaakola 2013). The MYBs are expressed in ripening fruit and activate either the whole biosynthetic pathway or a subset of genes in the pathway. Examples of activators include FaMYB10 and FvMYB10 in strawberry (Lin-Wang *et al.* 2014; Medina-Puche *et al.* 2014), MYB10 in nectarine (*Prunus persica*) (Ravaglia *et al.* 2013), VmMYBA in bilberry (*Vaccinium myrtillus*) (Karppine *et al.* 2021), PpMYB10.1 in peach (*Prunus persica*) (Rahim, Busatto & Trainotti 2014), VcMYBA1 in blueberry (*Vaccinium* Section *Cyanococcus*) (Plunkett *et al.* 2018) and MYB114 in pear (*Pyrus bretschneideri*) (Yao *et al.* 2017). MYBs can also act as repressors of anthocyanin, such as the SG4 MYBs, FaMYB1 from strawberry (Aharoni *et al.* 2001) and MdMYB16 from apple (*Malus domestica*) (Xu *et al.* 2017), as recently reviewed by LaFountain & Yuan (2021). There is increasing evidence for the interactions of different types of MYBs on anthocyanin regulation, such as the co-ordinated actions of MYBA1 and MYBPA1.1 in blueberry (Lafferty *et al.* 2021). Transcriptional regulation of anthocyanin is not restricted to the MBW complex: other TFs, such as MADs VmTRD4 in bilberry (Jaakola *et al.* 2010) and PpNAC1 in peach (Zhou *et al.* 2015) have been shown to have regulatory control. This TF-mediated control of pigments occurs in response to both developmental cues, but also environmental stresses.

Carotenoid biosynthesis is stimulated by the presence of ROS (Pan *et al.* 2009). Stress perceived in the leaves can trigger responses in the fruit, for example, the incidence of high light in leaves of citrus leads to increases in carotenoids in the fruit (Poiroux-Gonord *et al.* 2013). Many TFs have been associated with carotenoid biosynthesis as part of the fruit ripening cascade, but the evidence for there being master transcriptional regulators of carotenoid pigments is less clear cut than for anthocyanins (Stanley & Yuan 2019). A number of TFs have recently been shown to control at least parts of the pathway. In citrus, the AGAMOUS-LIKE MADS TF, CsMADS6, was shown to activate the promoter of *LCYb1* and drive the expression of carotenoid pathway genes *PSY* , *PDS* and *CCD1,* while repressing transcription of LCYE and so increasing the flux towards β-carotene (Lu *et al.* 2018). Another TF in citrus, CrMYB68, negatively regulates the expression of beta-carotene hydroxylase (BCH), controlling the α- and β-branches of carotenoid biosynthesis (Zhu *et al.* 2017). A MYB from kiwifruit (*Actinidia chinensis var. deliciosa*), MYB7, was reported to activate the promoter of *LCYb* and in heterologous systems elevated expression of *PSY* , *PDS* and *ZDS* to drive carotenoid accumulation (Ampomah-Dwamena *et al.* 2019). In papaya, two other TF classes have been implicated in regulating carotenoids: CpbHLH1 and CpbHLH2 repress and activate respectively the promoters of CYCB and LCYB, while the NAC TFs, CpNAC1 and CpNAC2, bind the promoters of PDS (NAC1) and PDS, ZDS, LYCE and BCH (NAC2) (Fu *et al.* 2016; 2017). The greatest body of work on the transcriptional control of carotenoids has been carried out in tomato where the major ripening MADS TFs, Tomato AGAMOUS-LIKE (TAGL1, homologous to CsMADS6), Ripening Inhibitor (RIN), FRUITFULL1 (FUL1) and FUL2 exert largely positive effects on the carotenoid pathway, as reviewed in Stanley & Yuan (2019).

Influence of Gene x Environment

Whilst the general biosynthesis and regulation of colour pathways has been elucidated, the final colour of the fruit is determined by both genetic and environmental factors. The genetic background determines the ability of fruit to produce certain pigments, whilst environmental factors affect the final composition and amounts of pigments in a ripe fruit. The fruit skin, which acts as a barrier protecting the internal tissues of developing fruit, including the photosynthetic machinery, is where the greatest effects of environmental factors on fruit pigment production are normally detected. Both controlled and field studies with cultivated and wild ecotypes have provided a better understanding of gene x environment (GxE) interaction in fruit pigment production (Jaakola & Hohtola 2010). Such studies have identified variation in anthocyanin content between fruit ecotypes or cultivars growing in different geographical locations (Fredes *et al.* 2014; González-de-Peredo *et al.* 2019; Sikuten *et al.* 2021). With wild *Vaccinium* berries, field studies have often shown high variation in the anthocyanin composition between growth location and seasons (Connor *et al.* 2002; Rohloff *et al.* 2015). However, specific geographical trends also have been observed, such as higher total anthocyanin contents and a higher proportion of delphinidin branch anthocyanins towards northern latitudes (Åkerstrom *et al.* 2010; Latti *et al.* 2010; Lätti, Riihinen & Kainulainen 2008) and at higher altitudes (Zoratti *et al.* 2015). A controlled study with southern and northern bilberry ecotypes indicated that ecotypes from higher altitudes produced a higher concentration of anthocyanins irrespective of day length and temperature conditions

(Uleberg *et al.* 2012). Geographical variation has also been detected in the carotenoid contents of different fruit species and cultivars (Dias*et al.* 2021). In some cases, climatic factors have been found to have greater impacts on carotenoid biosynthesis than cultivar differences, for instance in papaya (Kimura, Rodriguez-Amaya & Yokoyama 1991), mango (*Mangifera indica*) (Mercadante & Rodriguez-Amaya 1998), and West Indian cherry (*Malpighia glabra*) (Rodriguez-Amaya 2001). A comprehensive analysis of the carotenoid content in Portuguese fruit showed variation between the same apple and orange (*Citrus sinensis*) cultivars grown in different geographical regions (Dias, Camões & Oliveira 2009). High variation in carotenoid content was detected between wild Seabuckthorn (*Hippophae rhamnoides*) populations growing at different altitudes trans-Himalaya in India (Korekar *et al.* 2014). The major stressors are considered in the following sections, with the proviso that GxE can have additional and compounding effects.

5 The major environmental stress factors that affect fruit colour

Light stress

Light is one of the most important environmental factors affecting the accumulation of pigments during fruit ripening. Light effects can be categorised by duration (photoperiod), intensity (quantity), and quality (wavelength), all of which have been shown to affect pigment production. Both excess and inadequate light intensities and their fluctuations are collectively known as light stress. In addition, fluctuations in light wavelengths, especially excess of UV-light, can also cause light stress. Stress from non-optimal light conditions can cause alterations in pigment production (Zoratti *et al* . 2014). Plants convert photons of light through photosynthetic fixation of carbon dioxide into sugars. Light quality affects both photosynthetic rate and assimilation. Exquisite mechanisms have been developed to tolerate light stress, accumulation of pigments being one of the most important (Yang *et al.* 2019).

Little or moderate light stress can actually be beneficial for fruit quality by enhancing pigment concentration. On-tree apple experiments have shown that light stress induces anthocyanin production: these anthocyanins may reduce the amount of excess light as well as reducing the damage from the increased ROS produced to protect chlorophylls and carotenoids as part of the photooxidative machinery (Merzlyak & Chivkunova 2000). On-tree experiments have also shown that full spectra, including UV light, are essential for anthocyanin production (Henry-Kirk*et al.* 2018). Fruit bagging and shading experiments confirm the importance of direct exposure to light for biosynthesis of anthocyanins and carotenoids. Light exclusion results in transcriptional suppression of biosynthetic pathway genes and reduced accumulation of pigments (Downey, Dokoozlian & Krstic 2006; Saini & Keum 2018; Zhu *et al.* 2021; Zoratti *et al.* 2014). Whereas many fruits, like apples, have an absolute light requirement for anthocyanin biosynthesis (An *et al.* 2020a), there are species and cultivars that show no change in anthocyanin accumulation when in shaded conditions or any degradation of anthocyanins under high irradiation (Downey *et al.*2006; Zoratti *et al.* 2014). This indicates that there are different genetic regulation mechanisms for anthocyanin biosynthesis in some fruits, which are not fully understood.

Anthocyanins intercept and absorb light energy to avoid photodamage caused by excess light energy, directly scavenge free radicals and indirectly remove ROS by interacting with molecules in other signalling pathways (Li *et al.* 2019). In extreme high light conditions, anthocyanins play an important role in mitigating photoinhibition and photodamage. Naturally red-skinned pear species have been shown to maintain better photosynthetic capacity under high light and high temperature conditions, while some green-skinned pear cultivars increase skin anthocyanins in response to high light stress (Thomson, Turpin & Goodwin 2018).

In tomato, the accumulation of carotenoids during ripening is significantly influenced by light. Phytochrome induces degradation of phytochrome-interacting factor 1 (PIF1), a bHLH-type TF. In mature green tomato, PIF1 directly binds to the PIF-binding E-box PBE box of the PSY1 promoter of the carotenoid biosynthetic pathway, to repress carotenogenesis. During ripening, developmentally controlled degradation of chlorophylls reduces the self-shading effect, allowing phytochrome-mediated degradation of PIF1, which leads to depression of PSY1. This accelerates carotenoid biosynthesis and shifts the profile from xanthophyll, which is typical for leaves, to carotenes, mainly lycopene and β-carotene (Saini & Keum 2018). Exposure of tomato

8

to excessive sunlight has been reported to inhibit the synthesis of lycopene (Brandt *et al.* 2006; Ilić & Fallik 2017). It has been proposed that ROS and redox status, combined with sugar and carbon status, integrate the stress response and photosynthetic metabolism, and so influencing the synthesis of carotenoids (Fanciullino, Bidel & Urban 2014). In Clementine (*Citrus clementina*), accumulation of high amounts of soluble sugars through photosynthesis during the early stages of fruit development negatively influenced plastid development, which affected carotenoid accumulation, although later in fruit development, greater sugar accumulation increased carotenoid production (Fanciullino*et al.* 2014; Saini & Keum 2018).

The quality of the light spectrum has been shown to affect fruit pigments. Treatments with UV-B and UV-C light during ripening or postharvest resulted in increased anthocyanin concentrations in many fruit species, including apple, peach, wine grape (*Vitis* spp.), and blueberry (Chen *et al.* 2021; Henry-Kirk *et al.* 2018; Zoratti *et al.* 2014). Changes in carotenoid content following exposure to UV-light have also been reported in tomato (Giuntini*et al.* 2005) and wine grape berries (*Vitis vinifera*) (Joubert *et al.* 2016).

Solar UV-B radiation has extensive photobiological effects on plants: stress caused by UV-B is known to enhance the production of ROS, leading to damage of DNA, proteins and the photosynthetic apparatus. In plants, UV-B light is absorbed by tryptophan amino acid residues in the dimeric form of UV8 photoreceptor, leading to UVR8 monomerization and formation of a complex with CONSTITUTIVE PHOTOMOR-PHOGENIC1 (COP1), a known mediator of diverse light signals in plants interacting with regulators of both anthocyanin and carotenoid biosynthesis (Stanley & Yuan 2019; Zoratti *et al.* 2014). Plant pigments have an important role in protection of tissues against UV-radiation. For instance, anthocyanins and flavonols have been shown to accumulate in the epidermal tissues, such as fruit skin, to shield against excess UV-light (Zoratti *et al.* 2014). During photosynthesis, carotenoids harvest light energy and transfer this energy to chlorophylls through singlet-singlet excitation transfer, a lower energy state transfer. Excessive energy from chlorophylls is absorbed by carotenoids through triplet-triplet transfer, which is a higher energy state transfer essential for photo-protection. Carotenoids with more than eleven conjugated double bonds have a high capacity for quenching singlet oxygen produced under light stress (Maoka 2020).

Other light spectrum wavelengths have also been shown to influence the accumulation of fruit pigments and particularly red and blue wavelengths affect the biosynthesis of anthocyanins and carotenoids. Red or blue light treatment has resulted in a detectable increase in anthocyanin content in several fruit crops, including strawberries, grape, pear, apple, and cherry (*Prunus avium*) (Kokalj *et al.* 2019a; Kokalj *et al.* 2019b; Koyama *et al.* 2012; Miao *et al.* 2016; Tao *et al.* 2018). Recently, both red and blue light were shown to increase anthocyanin biosynthesis during bilberry ripening (Samkumar *et al.* 2021; Samkumar *et al.* 2022). Interestingly, differences in the perception of red and blue light were detected between berries ripening whilst remaining attached to the mother plant, or when detached in Petri dishes. Transcriptomic analysis revealed differences in red and blue light signalling, leading to altered anthocyanin content in the ripe, treated berries, with red light increasing the anthocyanin content 12-fold compared with the control (Samkumar *et al.* 2021).

Many studies have shown that red light typically increases carotenoid biosynthesis in fruits, while blue light has less effect, although there are differences between species, cultivars and ripening stages. Spectral light quality experiments monitoring carotenoid biosynthesis in ripening*Capsicum annuum* showed that red radiation was the most effective in increasing carotenoid accumulation, whereas green and blue radiation inhibited the formation of capsanthin, the major carotenoid influencing fruit colour (Lopez, Candela & Sabater 1986; Pola, Sugaya & Photchanachai 2019). Similar results have been shown in *Citrus*(Gong *et al.* 2021; Ma *et al.* 2012). In kumquat (*Fortunella crassifolia*) fruit, a NAC family TF, FrCNAC22, was shown to mediate red light-induced carotenoid accumulation (Gong*et al.* 2021). Moreover, PIF1 regulation, following blue light perception, has been shown to act as a negative regulator of carotenoid biosynthesis (Gong *et al.* 2021).

Temperature stress

Temperature stresses, both below and above optimal growth temperatures, have been shown to affect plant pigment accumulation during fruit ripening. Although there is broad variation in what is the optimal

9

temperature depending on species, cultivar and ecotype, heat stress can inhibit pigment biosynthesis in ripening fruits. Studies demonstrate that this is the case for both carotenoid and anthocyanin pigments (Gashu *et al.* 2022; Kliewer 1977; Lin-Wang *et al.* 2011; Tomes 1963). When heat stress is moderate, the changes can be reversible, whereas severe episodes can cause irreversible changes to metabolites, resulting in crop failure.

Heat stress has been shown to inhibit anthocyanin biosynthesis in grape berry skin in controlled studies with temperatures higher than 30°C (Ryu*et al.* 2020; Yamane *et al.* 2006). Active inhibition and degradation of anthocyanin biosynthesis under high temperature conditions have also been reported in other fruits such as *Malus profusion* (Rehman *et al.* 2017) as well as in grape (Mohaved*et al.* 2016). Changes in ABA contents and in ABA/GA ratio have been associated with changes in anthocyanin concentrations under different temperature conditions (Ryu *et al.* 2020). Hot conditions during the growing season can dramatically reduce anthocyanin production in numerous apple cultivars, with an associated reduction in the transcription of the biosynthesis genes (Ubi *et al* . 2006) and the pathway regulating MYB TF, MYB10 (Lin-Wang *et al* . 2011). This appeared to be repression of anthocyanin activation, rather than an increase in transcription of known anthocyanin MYB repressors.

Almeida *et al.* (2021) found that ripe tomato fruit had better plasticity to restore carotenoids following a heat wave compared with tomatoes that experienced excessive heat during the breaker stage (when pink colour is just starting to develop). They concluded that heat-related transcriptional and posttranscriptional mis-regulation during early carotenogenesis affected the carotenoid composition in the ripe tomatoes. Moreover, upstream ripening regulators, such as*CNR* and *NOR* , were also affected by the heat treatments. The results also suggested that epigenetic mechanisms were mediating heat-induced transcriptional changes.

It is not only high temperatures that can be problematic for fruit colour. Low temperature conditions at around 4–10°C can cause stress in developing fruits because of ROS production and generation of malondial-dehyde (MDA) in the cell, which can lead to severe membrane lipid peroxidation. Cold stress also promotes the accumulation of anthocyanin- and carotenoid-regulating phytohormones, ABA, jasmonates (JA), ethylene (ETH) and salicylic acid (SA) (He *et al.* 2022). ABA, JA and polyamines have been reported to be associated with low-temperature stress tolerance in apple fruitlets (Yoshikawa, Honda & Kondo 2007).

Lower temperatures have been observed to increase anthocyanin biosynthesis in many fruits, such as apples, table grapes, black currants (*Ribes nigrum*), cloudberries *(Rubus chamaemorus*), while anthocyanin accumulation is inhibited during heat stress (Chen*et al.* 2021; Downey *et al.* 2006; Martinussen *et al.*2010; Wang *et al* . 2018; Woznicki *et al.* 2015). The subsequent increase in anthocyanin concentration in fruit skin provides some tolerance to cold stress, for instance in mango (Sivankalyani*et al.* 2016; Sudheeran *et al.* 2018). This production of anthocyanin at these lower temperatures is providing an alternative means to other ROS coping mechanisms which are compromised by cold. However, for other fruits such as strawberry, temperatures below 10°C have been shown to inhibit anthocyanin biosynthesis, a process mediated by MITOGEN-ACTIVATED PROTEIN KINASE$_3$(FvMAPK$_3$) (Mao *et al.* 2022).

Whereas high temperature clearly represses transcription of MYB10 in apple, the opposite is seen with low temperature in crabapple. In this case, the transcription of the MBW activation complex, including MYB10, bHLH3/33 and TTG1, is elevated, leading to increased anthocyanin production (Tian *et al* . 2015). Other TFs are involved in this response and Fang et al. (2019) showed that the zinc finger TF, MdBBX20, responds to low temperature via MdbHLH3 interaction, to drive anthocyanin production in a HY5-dependent manner.

Cold stress has been shown to affect carotenoid contents in fruits as a response to the production of ROS, in a species-specific manner. For example, higher lycopene contents have been shown to offer tolerance against cold stress in grapefruit (*Citrus paradisi*) (Lado*et al.* 2015), whereas in mango, carotenoid contents decreased under cold stress (Rosalie *et al* , 2018). In pepper (*C. annuum*) fruit, Zhang et al. (2020) showed that *CaATHB-12* , a member of the HD-ZIP I gene family, is one of the key regulators of fruit carotenoid content.

Diurnal temperature, with cool nights and warm days, is critical to optimal fruit colour in some species and

a reduction in diurnal temperature range, as may become more evident with climate change, will impact anthocyanin in fruit peel, such as in apple (Qu & Zhou 2016). Clearly, optimal day and night temperatures help to produce high quality coloured fruit, while temperatures outside of this range often positively (cold) or negatively (excess heat) effect the concentration of colour.

Water stress

Water shortages are already a serious problem for much of the world's agriculture and horticulture (Lobell & Gourdji 2012). The predicted increase in severe climate events due to climate change, including drought, is likely to present even greater challenges for growers. Of particular concern is the potential impact on global food supply chains of reduced yield of major grain crops (Araus *et al.* 2002). Predicting the outcomes of different water deficiency scenarios and how these will affect crops is complex (Tramblay *et al.* 2020). For essential photosynthetic pigments in leaves (carotenoids and chlorophylls), water deficiency can result in reduced growth and yield (Jaleel *et al.* 2009) and in some fruits, water deficiency can reduce both anthocyanin and carotenoid concentrations, reducing fruit colour (Jiang *et al.* 2020). However, for other fruits, water deficiency outcomes are not necessarily deleterious. This may seem counter-intuitive since drought is likely to decrease leaf photosynthesis and, therefore, the distribution of primary metabolites to the fruit. These primary metabolites provide the precursors for all secondary/specialised metabolites and so, logically, may reduce the pool of substrates for pigmented compounds. However, since both the carotenoid and phenylpropanoid pathways are partly regulated by stress-induced ROS production, there are also likely to be positive effects of water deficiency on fruit pigments. The outcomes can be species-dependent and, given this tension between pathways, highly variable owing to the timing of fruit development at which the water deficiency occurs (cell division, cell expansion or ripening phases), and the severity and duration of the deficit. In terms of overall fruit quality, there are possible effects on other major sensory attributes such as aromas, the sugar/acid balance and texture (Ripoll *et al.* 2014).

In some cropping situations, water deficiency is intentionally used to improve colour. In red grape, anthocyanin is an important determinant of wine quality. When water is deficient, grape berry size is reduced, creating a higher skin:flesh ratio which, when coupled with increased anthocyanin production, can improve wine quality (Gambetta *et al.* 2020). Increases in grape berry anthocyanin concentrations following exposure to water deficit have been reported in Cabernet Sauvignon (Deluc *et al.* 2009), Merlot (Bucchetti *et al.* 2011) and Tempranillo (Santesteban, Miranda & Royo 2011). Anthocyanin composition can also change in a cultivar-specific manner, such as the drought-induced increase in acylated anthocyanins in Cabernet Sauvignon, while the same conditions led to a reduction in these compounds in Syrah (Hochberg *et al.* 2015). Further compositional changes can be created by a shift towards more tri-hydroxylated anthocyanins (darker purples and blues) via the up-regulation of flavonoid 3'5' hydroxylases (Castellarin *et al.* 2007).

Phytohormones are intrinsically linked with drought perception and the resultant transcriptional cascade (Ullah *et al.* 2018), particularly ABA (Yamaguchi-Shinozaki & Shinozaki 2005). For example, in strawberry fruit, drought conditions increased ABA, which was correlated with elevated anthocyanin concentration (as well as AsA) without a reduction in fruit yield (Perin *et al.* 2019). A previous study in strawberry clearly demonstrated how the presence of ABA regulated the expression of the anthocyanin-regulating MYB TF,*FaMYB10,* which, in turn, elevated the anthocyanin biosynthetic genes and fruit colour (Medina-Puche *et al.* 2013). In apple, an alternative molecular model of drought-induced anthocyanin production has been proposed, whereby the ethylene response factor ERF38 partners with the homologous MYB1 to drive the anthocyanin biosynthetic pathway genes (An *et al.* 2020c).

For fruit colours derived from carotenoids the picture is less clear cut than for anthocyanins. In some cases, water deficit has been shown to reduce fruit carotenoid concentrations (De Pascale *et al.* 2007; Jiang *et al.* 2020). However, in tomato, there is strong evidence that concentrations of lycopene (and β-carotene) increase with water deficiency (Favati *et al.* 2009; Klunklin & Savage 2017; Patanè*et al.* 2021; Zushi & Matsuzoe 1998).

Nutrient stress

11

While fruit pigments are highly influenced by temperature, light and water, it is important to consider that they may also be altered by other environmental factors. For instance, salinity stress can either increase or reduce tomato anthocyanins depending on cultivar, while the pigmented carotenoids are reliably increased by as much as 2–3 fold across a range of cultivars (Borghesi *et al.* 2011). However, perhaps the most important consideration is nitrogen (N) status (Wang et al., 2018). In *Arabidopsis* , restricted N availability has been shown to shift metabolism towards flavonoid production, including anthocyanins, with evidence for increased transcription of the regulating TF (AtPAP1) and the biosynthetic pathway (Lillo, Lea & Ruoff 2008). If this is also true for fruits, it suggests that horticultural practices can elevate fruit anthocyanin concentrations, but that in planning nutrient applications, a balance is required to avoid detrimental yield effects on the overall crop (Jezek *et al.*2018). That the effects of N deficiency is not always so clear and in other crops, such as strawberry, and N application timing needs to be determined on a crop-by-crop basis (Jezek *et al.* 2018).

At the molecular level, studies in apple show a number of candidate genes linking N deficiency to an elevation in the anthocyanin pathway. Low N induces anthocyanin production, partly mediated by the mitogen-activated protein kinase (MAPK) signalling cascade, as shown for red-fleshed apples, where a MAPK family gene, *MdMKK9,* regulates the N status (Sun *et al.* 2022). Under low N conditions the autophagy nutrient recycling process can be activated, and studies in apple have demonstrated that the AuTophaGy (ATG) protein, MdATG18a, improves tolerance to nitrogen deficiency via upregulation of the anthocyanin pathway (Sun *et al.* 2018). In these cases, the increases in anthocyanin content are driven by an upregulation of the anthocyanin-regulating TF, MdMYB1/10. Conversely, the BTB/TAZ protein, BTB2, which is lowly expressed under low N but highly expressed under high N, negatively regulates the MYB, suppressing anthocyanin accumulation (An, Wang & Hao 2020b). It seems that fruit carotenoid contents, as shown in tomato, are either decreased or less affected by low nitrogen supply depending on the timing of the nitrogen supply reduction (Benard *et al.* 2009; Hernández *et al.* 2020).

6 Conclusions and perspectives

From research reviewed here, it is clear that some environmental stresses can enhance fruit colour: low temperature, high light (and UV) and a degree of water deficit can all be beneficial. Against this, the severity and timing of these stresses are critical in determining whether outcomes are positive or negative. Some of these stresses can be controlled horticulturally, such as limiting water supply, but climate change is outside grower control and thus likely to disrupt our current growing practices. Consumer desire for ever more healthy fruits is unlikely to dissipate — the pigments in fruits provide many of these health benefits, packaged with one of the strongest motivators for purchase — the attractiveness of colourful fruit. Of course, fruit cultivars, no matter how colourful, will also have to reach other key consumer expectations, such as texture, storability and flavour. As climate change creates less predictable temperatures across many fruit-growing regions, understanding how fruit pigmentation will be affected will become increasingly important if we are to maintain or improve fruit colour. For some fruit crops, indoor production may become a more attractive (and commercial) proposition to avoid crop losses due to damaging climatic events.

Various options are available to maintain fruit colour in this changing environment, including agronomic approaches (Poiroux-Gonord *et al.* 2010). Similarly, postharvest treatments can provide the potential to preserve and enhance fruit pigments (de Pascual-Teresa & Sanchez-Ballesta 2008). In the future, more substantive advances may be required to augment the incremental changes that can be made by in-field or postharvest management. In some circumstances, fruit breeding programmes have reduced the genetic and phenotypic diversity in breeding populations. To address production challenges associated with severe climate change, incorporating new genetic diversity is likely to become essential to maintain or improve fruit crops: the use of crop wild relatives that are better adapted to environmental stresses should be considered to introduce beneficial traits. Ideally, this would be in conjunction with deep bioinformatic resources (high quality genomes, transcriptomes and metabolomes), and an emphasis on mapping and molecular markers to help to target 'resilience' traits and rapidly incorporate these in new cultivars that are better adapted to our changing environment. Breeding varies markedly between species and varieties, and there will be an increasing need for developing crops suited to (and tested at) different geographic and environmental

locations. The complexity of GxE interactions on fruit pigmentation is complex, and more research into this area is required to understand the plant response and potential breeding strategies for fruit colour improvement.

'Traditional' genetic engineering has provided many examples of successfully increasing plant pigments (Martin & Li 2017). Sophisticated molecular engineering of fruit can provide platforms for elevated amounts of specific phytochemicals, including pigments (Li *et al.* 2018). The new breeding technologies such as CRISPR provide untapped potential for modifying our fruit crops both to improve their nutritional benefit (colour) and to tackle changing growing conditions (Wang, Zhang & Zhu 2019). It is likely that adoption of new breeding approaches will be required to maintain and enhance fruit pigments as we navigate environmental changes to fruit-growing regions across the globe.

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