Chapter 4
Effect of Temperature on Fruit Color Development

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Abstract Temperature is one of the most important factors affecting fruit coloration. Because of recent effects of global warming, inferior coloration has become a serious problem in many fruits, especially those for which coloration is important for the commercial appearance and value, such as grapes, apples, citrus fruits, and persimmons. Coloration in these fruit results from the synthesis and accumulation of pigments. The presence of anthocyanins or carotenoids is responsible for the color of fruit peels. The biosynthetic pathways of anthocyanins and carotenoids in these fruit have been characterized, and these studies have provided valuable information for understanding the occurrence of poor coloration in response to high temperature. In general, peel color development is enhanced by low temperatures and inhibited by high temperatures. Several techniques have been described to improve the peel color of fruit, and recent studies have identified the mechanisms underlying the effectiveness of these techniques.

Keywords Anthocyanin • Apple • Carotenoid • Citrus fruit • Global warming • Grape • Persimmon • Temperature

4.1 Introduction

Fruit development is influenced by many environmental conditions and the availability of nutrients. Although nutritional or soil conditions can be controlled by the application of fertilizers and soil management, environmental conditions, such as temperature, solar radiation, and humidity, are more difficult to control.

Recently, global warming has become a worldwide problem. For fruit cultivation, the ambient temperature during fruit development is an important factor that affects fruit quality. High temperatures during fruit development suppress fruit color development. For example, poor coloration caused by high temperature has been

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reported for grapes (Tomana et al. 1979; Naito et al. 1986), apples (Creasy 1968; Yamada et al. 1988; Arakawa 1991), Satsuma mandarin (Utsunomiya et al. 1982), and Japanese persimmon (Taira et al. 2000; Isobe and Kamada 2001). Efforts to reduce greenhouse gas levels in the atmosphere are underway; however, until such efforts are successful, fruit production must occur under undesirable conditions.

Poor fruit coloration often reduces the market price. Therefore, cultivation techniques that overcome high temperature-mediated color suppression are valuable to commercial producers. To facilitate the development of such cultivation methods, the relationship between temperature and color development, the molecular basis of pigment synthesis, and the mechanisms of color suppression at high temperature must be elucidated.

The aim of this chapter is to summarize the effect of high temperature on fruit color development and the cultivation technique to overcome poor coloration.

4.2 Effect of Temperature on the Fruit Coloration Process

Temperature affects fruit color development. For fruit production, most trees are grown in open fields, although some are cultivated under structures. Therefore, it is difficult to control atmospheric conditions such as temperature, solar radiation, or humidity. High temperatures cause poor fruit coloration in many types of fruit trees.

Fruit skin color is determined by secondary metabolites, such as phenolic compounds or terpenoids. For example, anthocyanin, a phenolic compound, is responsible for the pigmentation of apple and grape peels (Tsao et al. 2003; Shiraishi et al. 2007). Terpenoid compounds, including carotenoids, are present in the peel of the citrus fruits (Daito et al. 1975), persimmon (Veberic et al. 2010), and loquat fruit (Zhou et al. 2007). The quantities of anthocyanin or carotenoids present in fruit peels are determined by their biosynthesis, accumulation, and degradation. Temperature influences these processes, and high temperature can result in poor color development in certain types of fruit trees, particularly grape, apple, citrus, and persimmon.

4.2.1 Relationship Between Temperature and Grape Coloration and the Mechanism Underlying the Effects of Temperature

The grape is one of the most common fruit trees for which color development is suppressed by high temperature. Of all fruit under cultivation, grape production is the highest in the world, and the fruit are used for a variety of purposes, including wine production, table fruits, and for consumption of dry and fresh fruit. Poor coloration of the skin causes prices to decline, particularly with respect to sales for wine production and table fruit. Therefore, several investigations have explored the

Table 4.1 Research about temperature response of grape coloration under controlled temperature

Cultivar	Treated organ	Reference
Cardinal, Pinot Noir	Whole vine	Kliewer (1970)
Cardinal, Pinot Noir, Tokay Cabernet Sauvignon	Whole vine	Kliewer and Torres (1972)
Kyoho	Clusters, whole vine	Tomana et al. (1979)
Kyoho	Whole vine	Mori et al. (2004a)
Kokuo	Whole vine	Mori et al. (2004b)
Darkridge	Whole vine	Mori et al. (2005)
Aki Queen	Whole vine	Yamane et al. (2006), Yamane and Shibayama (2006b)
Pino Noir	Whole vine	Mori et al. (2007b)
Aki Queen	Clusters	Koshita et al. (2007)

relationship between temperature and anthocyanin content in grapes; further, the coloration response to temperature under controlled conditions has been the focus of intense research (Table 4.1). Kliewer (1970) and Kliewer and Torres (1972) first examined the relationship between temperature and anthocyanin content. Kliewer (1970) demonstrated that the anthocyanin concentration of the Cardinal and Pinot Noir varieties grown at an ambient temperature (68 °F) was significantly higher than in grapes grown at 86 °F. They also investigated the difference in grape tolerance to elevated temperature (Kliewer and Torres 1972). Tomana et al. (1979) separately controlled the ambient temperature around grape clusters and the whole vine, showing that low temperature around clusters enhanced anthocyanin content in the “Kyoho” grape. Mori et al. (2004a, b, 2005, 2007a, b) investigated the relationship between temperature and anthocyanin content in many cultivars. They reported that high temperatures at night decreased anthocyanin content in “Kyoho” (Mori et al. 2004a), “Kokuo” (Mori et al. 2004b), and “Darkridge” (Mori et al. 2005) grapes, as determined using a phytotron, on whole vines.

In “Kyoho” and “Aki Queen” grapes, the effect of the temperature surrounding clusters from early maturation to the harvest stage was investigated. These studies demonstrated that high temperatures around clusters inhibit anthocyanin accumulation, whereas low temperatures accelerate anthocyanin accumulation (Tomana et al. 1979; Koshita et al. 2007).

The effect of temperature on grape coloration has been demonstrated in many reports, and these investigations have led to research on the regulatory mechanisms of anthocyanin biosynthesis in grape skin under different temperature conditions.

Coombe (1973) reported that abscisic acid (ABA) and sugar content increased concomitant with grape maturation, and they speculated that ABA participates in anthocyanin biosynthesis. Studies on the relationship between ABA content and coloration (Tomana et al. 1979; Yamane et al. 2006; Koshita et al. 2007) revealed that anthocyanin content and ABA content are higher in the skin when these cultivars are grown at lower temperatures compared with those grown at higher temperatures. ABA is an important phytohormone for regulating anthocyanin

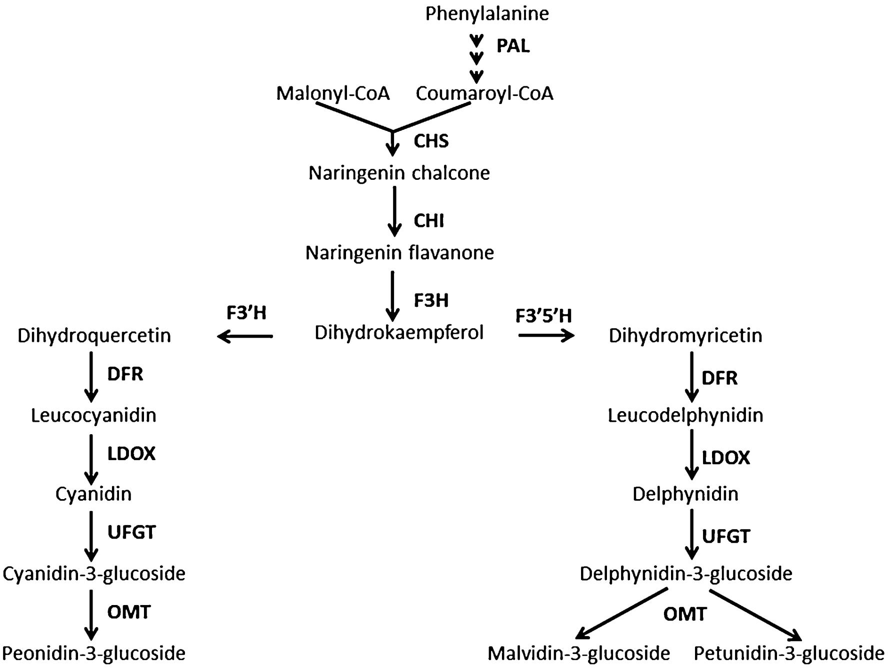

Fig. 4.1 Scheme of the anthocyanin biosynthetic pathway in grape skins. PAL phenylalanine ammonia lyase, CHS chalcone synthase, CHI chalcone isomerase, F3H flavanone 3-hydroxylase, F3′H flavonoid 3′-hydroxylase, F3′5′H flavonoid 3′-5′-hydroxylase, DFR dihydroflavonol 4-reductase, LDOX leucoanthocyanidin dioxygenase, UFGT UDP-glucose flavonoid 3-*O*-glucosyltransferase, OMT *O*-methyltransferase

accumulation in the grape, and application of ABA treatments to grape clusters improves coloration (Matsushima et al. 1989). Sparvoli et al. (1994) and Boss et al. (1996) isolated grape genes related to the anthocyanin biosynthetic pathway, and they reported that UDP-glucose flavonoid 3-*O*-glucosyltransferase (UFGT) is a key enzyme for anthocyanin biosynthesis in the grape skin (Fig. 4.1). Transcriptional regulators of anthocyanin biosynthesis contain a MYB domain, a basic helix–loop–helix (bHLH) domain, or WD40 repeats, and these protein complexes determine the expression of the anthocyanin biosynthesis genes (Ramsay and Glover 2005). In grapes, *Myb*-related genes control the anthocyanin biosynthetic pathway (Kobayashi et al. 2005), (Kobayashi et al. 2002). Therefore, expression of the *Myb*-related genes and anthocyanin biosynthesis-related genes regulates anthocyanin content, and these pathways may have an important role in grape coloration. The expression of these genes is closely related to anthocyanin content. Mori et al. (2004b, 2005) demonstrated the importance of anthocyanin biosynthesis-related gene expression and enzyme activity, showing that activity was higher in cultivars grown under low night temperature conditions compared to those grown under high night temperatures. Tomana et al. (1979) and Koshita et al. (2007) reported that low temperatures around clusters increased both anthocyanin levels and ABA content.

Thus, ABA content is higher in the skin of grapes grown under lower temperature conditions, resulting in better coloration. Exogenously applied ABA also activates the expression of the anthocyanin biosynthetic genes and enhances grape coloring (Ban et al. 2003; Jeong et al. 2004). Therefore, ABA also is important in determining grape coloration.

4.2.2 Temperature During Maturation Affects Citrus Peel Coloration

The peel color of the yellow- or orange-colored citrus fruit primarily consists of carotenoids. In general, high ambient temperature during the citrus maturation period causes poor coloration of the citrus peel. The peel color of the "Redblush" grapefruit was a deeper hue of yellow when trees were exposed to cooler temperatures during development (Young et al. 1969). In Satsuma mandarin fruits, lower ambient temperatures during fruit development resulted in earlier accumulation of carotenoids (Utsunomiya et al. 1982). Manera et al. (2012) demonstrated that the autumnal temperature decline was associated with degreening of lemon peel. Sugiura et al. (2007) suggested that global warming may delay the onset of coloration or cause poor coloration of the Satsuma mandarin peel. The carotenoid biosynthetic pathway in citrus is well characterized (Ikoma et al. 2001; Kato et al. 2004, 2006) (Fig. 4.2). Ikoma et al. (2001) demonstrated that phytoene synthase has an important role in carotenoid accumulation in citrus fruits. Kato et al. (2004) showed that changes in the peel color from green to orange were accompanied by a decline in lycopene ε-cyclase and an increase in lycopene β-cyclase. Utsunomiya et al. (1982) quantified ABA content in the peels of Satsuma mandarin fruit grown at temperatures of 15 °C, 23 °C, and 30 °C; they observed higher ABA content and better coloration in the peels of fruit grown at the lowest temperature. These data suggest that ABA is involved in carotenoid synthesis in Satsuma mandarin fruits.

4.2.3 Relationship Between Temperature and Apple Coloration

The red skin color of an apple is the result of anthocyanin and many environmental factors, including light, temperature, and soil nutrition (reviewed by Saure 1990). The skin color of the apple fruit is an important factor for determining market prices, and it has been suggested that high temperature inhibits coloration. Yamada et al. (1988) controlled the ambient temperature around fruit during its development, and they demonstrated that the anthocyanin content of the skin was higher at 10 °C than at 17 °C in the "Fuji" apple; furthermore, anthocyanin accumulation was inhibited at 24 °C. Arakawa (1991) investigated the relationship between temperature and anthocyanin accumulation in several apple varieties, including "Jonathan," "Fuji,"

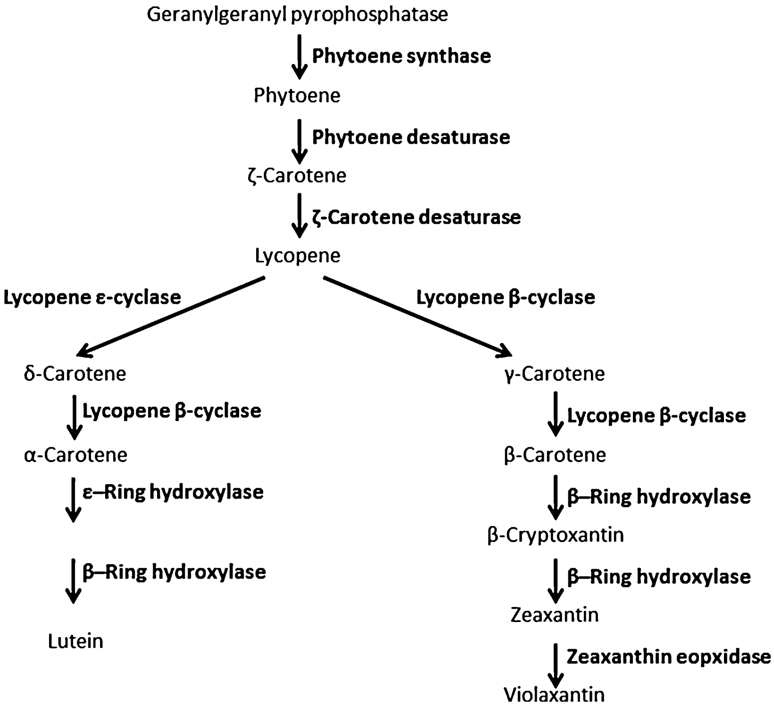

Fig. 4.2 Scheme of the main carotenoid biosynthetic pathway in the peels of citrus and persimmon

"Jonagold," and "Tsugaru" and reported the coloring response to temperature varied among cultivars. In apple skin, anthocyanin biosynthetic genes are responsible for the synthesis of anthocyanin, and the predominant anthocyanin in the apple skins is cyanidin-3-galactoside (Kondo et al. 2002). The expression of anthocyanin biosynthetic genes during red color development in apples was first reported by Honda et al. (2002). They isolated genes related to anthocyanin biosynthesis, including chalcone synthase (CHS), flavanone 3-hydroxylase (F3H), dihydroflavonol 4-reductase (DFR), anthocyanidin synthase (ANS), and UFGT (Fig. 4.3), and demonstrated that these genes are expressed coordinately during fruit development; there is a positive correlation between anthocyanin content and the expression of these genes. Subsequently, the effects of temperature on the expression of anthocyanin biosynthetic genes were investigated. Ubi et al. (2006) reported that low-temperature treatment during exposure to UV-B light enhanced both the expression of anthocyanin biosynthetic genes and the anthocyanin content of apple skin. Ban et al. (2007) suggested that the MYB transcription factor gene, *MdMYBA*, is a key regulatory gene in anthocyanin biosynthesis in apples, and they also proposed the importance of the bHLH transcription factor gene. Indeed, increased expression of the MdbHLH3 was confirmed at 17 °C, whereas lower transcription was detected under 27 °C (Xie et al. 2012).

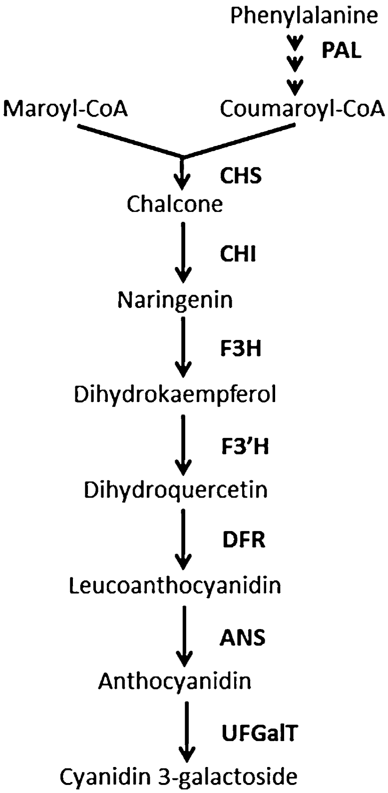

Fig. 4.3 Scheme of the main anthocyanin biosynthetic pathway in apple skins. Abbreviations of the pathway (CHS, CHI, F3H, F3′H, DFR) are defined in the legend of Fig. 4.1. ANS anthocyanin synthase, UFGalT UDP galactose flavonoid 3-*O*-galactosyltransferase

4.2.4 Effect of High Temperatures in Autumn on the Coloration of the Japanese Persimmon

Previous reports documented a delay in the harvest season in the Japanese persimmon. Taira and Itamura (1989) noted that the timing and rate of peel coloration in the "Hiratanenashi" persimmon varied considerably on a yearly basis, and they suggested that this variation might be caused by temperature changes during color development. In the "Maekawa Jiro" persimmon, higher temperatures during the day or night were associated with slower rates of peel coloration during fruit development (Isobe and Kamada 2001). Sugiura et al. (2007) classified several fruit trees according to the response of fruit development to climate change, and the Japanese persimmon was categorized as having an accelerated flowering period but not an accelerated maturation period. Niikawa et al. (2014) investigated the relationship between coloration of the "Fuyu" persimmon at harvest time and the monthly mean temperature during the past 20 years. Their data suggested that skin coloration is influenced by temperature during the months of September and October. The peel color of the persimmon is derived from carotenoids (Veberic et al. 2010), and the red coloration is related to the lycopene content of the peel (Chujo 1982). Chujo and Ashizawa (1973a) investigated the relationship between temperature and the reddish color of the peel. They demonstrated that lycopene content in the peel of the detached “Fuyu” persimmon fruit was highest when temperatures were 25 °C during mid- to late October, and 15 °C from beginning to middle of November. They also compared the development of “Fuyu” persimmon peel color to the reddish-colored cultivars, “Beniemon” and “Nigorokonariba,” and they found that a gradual decrease in temperature was favorable for red color development as the fruit matured (Chujo and Ashizawa 1973b).

The biosynthetic pathway of carotenoids in the Japanese persimmon has been described, and the processes involved in carotenoid accumulation have been characterized (Fig. 4.2) through carotenoid biosynthetic gene expression and the quantification of carotenoids during maturation (Niikawa et al. 2007). Additional information obtained through molecular studies and gene expression experiments will be available in the future.

4.3 Techniques for Overcoming Poor Coloration Caused by High Temperature

Several cultivation techniques to overcome poor fruit coloration have been proposed. If these techniques are effective at high temperature, it will be possible to produce fruits with good coloration under warm conditions. In grapes, girdling treatment (Peacock et al. 1977; Yamamoto et al. 1992), low crop load (Kitamura et al. 2005), and water stress (Fukui et al. 2004) enhance coloring. Of these, the application of girdling treatment to the trunk is a popular technique for enhancing grape coloration. To make this approach feasible, many investigators have sought to identify the most effective treatment and the appropriate growth stage for its application to enhance color development. Yamamoto et al. (1992) investigated the application of girdling treatment during different growth stages and determined that girdling treatment applied 30 days after full bloom was most effective for color development in the “Kyoho” grape. Yamane and Shibayama (2007) determined that the application of girdling treatment 30 and 35 days after full bloom was most effective for enhancing anthocyanin accumulation in “Aki Queen” grapes. They suggested the concentration of total soluble solids present in the berry 30 days after full bloom is critical for anthocyanin accumulation. The effect of girdling treatment is also influenced by crop load, as higher crop loads reduced the effectiveness of girdling (Yamamoto et al. 1992; Yamane and Shibayama 2006a). These investigations indicate that determining the appropriate crop load and girdling stage are important for enhancing fruit color using this approach.

Grape cultivation under restricted rooting volume has the potential to produce better quality fruit. Imai et al. (1991) established an effective watering program for grapevines that are grown with restricted rooting volume. Fukui et al. (2004)

investigated the relationship between water-stressed and non-water-stressed conditions: the color index value was higher for grapes grown under water-stressed conditions than those grown under non-water-stressed conditions. Because of global warming, the production of grapes with good coloration will be challenging, even in areas where grapes have historically been produced. However, the integration of girdling treatment and the appropriate management of crop load and water stress may enable the production of grapes with good coloration, even in areas affected by global warming.

Apple coloration is enhanced by light (Arakawa et al. 1985; Ubi et al. 2006); therefore, improving light conditions by pruning or training is essential. In addition to these fundamental management techniques, leaf thinning, use of reflective mulch, and application of paper bags are often used to produce red-colored fruit. These strategies are performed to enhance the exposure of apple fruit to light. Soil nitrogen level is another important factor influencing apple coloration, although the effects are indirect. In "Golden Delicious" apples, the application of high levels of nitrogen increased the production of green-colored fruit (Williams and Billingsley 1974). Komamura et al. (2000) reported that excessive nitrogen application inhibited apple skin coloration and did not detect a relationship between fruit yield and nitrogen levels.

The peel color of citrus fruit is enhanced by water stress and nitrogen content. In navel oranges, peel coloration is improved in the fruits that received less water than fruits that were fully watered by an irrigation system (Kallsen et al. 2011). Tachibana and Yahata (1998) showed that the color indices of the "L," "a," and "b" decreased as nitrogen increased, and they also reported that lower nitrogen content in leaves was associated with better fruit quality. Takagi et al. (1989) suggested that reduced nitrogen levels in the peel improved the development of Satsuma mandarin peel color. Therefore, the nitrogen content of fruit peels is an important indicator of the nutritional condition of citrus fruits.

Fruit breeding programs have aided in the development of several new cultivars with enhanced color. The introduction of these cultivars into the current cultivation system will be beneficial for fruit producers.

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