Fruit Ripening and Characteristics Regulated by Physiologically Active Substances

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ABSTRACT

Fruit color and aroma volatile compounds are important factors that determine fruit quality. The effects of jasmonates (jasmonic acid and methyl jasmonate) on fruit color development differed between climacteric and nonclimacteric fruit. Jasmonates, and jasmonates combined with an ethylene action inhibitor stimulated greater anthocyanin accumulation in apples regardless of fruit growth stages. The expression of *UDP-glucose:flavonoid 3-O-glucosyltransferase* (*UFGluT*) anthocyanin biosynthetic gene was increased in the skin of fruits treated with jasmonates and these fruits also had much higher anthocyanin content than untreated controls. In contrast, jasmonates did not influence anthocyanin accumulation in sweet cherries. The impact of jasmonate application on volatile compound production was dependent on fruit ripening stage; jasmonates increased the volatiles in preclimacteric fruit, but decreased the volatiles in climacteric fruit. In addition, jasmonates influenced 1-aminocyclopropane-1-carboxylate (ACC) synthase (ACS) and ACC oxidase (ACO) gene transcription. In pears (*Pyrus communis* L.), jasmonate application at the preclimacteric stage stimulated ethylene production and the expression of the *ACS* and the *ACO* messenger RNA (mRNA) levels. In contrast, the accumulation of *ACS* mRNA levels in fruit treated with jasmonate at the climacteric stage was low and ethylene production also decreased. Some types of physiologically active substances may play a protective role against chilling injury. For example, endogenous polyamines were linked to the degree of chilling injury in mangosteens. Additionally, EC_{50} values of superoxide (O_2^-) and 1-diphenyl-2-picrylhydrazyl (DPPH)-radical scavenging activity were also associated with the degree of chilling injury.

CONTENTS

INTRODUCTION

The production of anthocyanins, carotenoids, and aroma volatiles reflects the developmental change that occurs to allow commercial harvest. The fruits show dramatic physiological changes at the ripening stage and physiologically active substances such as plant hormones play a role in these changes.

In general, jasmonates, ABA, and ethylene have been shown to promote leaf abscission, stomatal closure, leaf yellowing, and to inhibit plant growth. In addition, the presence of ABA, ethylene, and jasmonates stimulates anthocyanin biosynthesis (Franceschi and Grimes 1991; Abeles *et al*. 1992; Gaynor and Cowan 1995; Kondo *et al*. 2001b).

Physiologically active substances may also play a role in the protection against stress. For instance, jasmonate application reduced chilling injury in tomatoes (*Lycopersicon esculentum* L.) and papayas (*Carica papaya* L.) (Ding *et al*. 2001; Gonzalez-Aguilar *et al*. 2003). In general, freezing injury is caused by membrane lesions based on cellular dehydration (Thomashow 1999). The production of reactive oxygen species, which is induced by freezing, contributes to membrane damage (Mckersie and Bowley 1998) and is promoted by environmental factors such as ultraviolet light, salt and low temperature (Matsui and Li 2003). This review summarizes the effect of physiologically active substances on the regulation of fruit quality. A portion of the manuscript was arranged from previous reports written by the author.

Jasmonates and anthocyanin formation in apple fruit

Jasmonate application promoted anthocyanin formation in apple fruit on the tree (**Fig. 1**, Kondo 2007) and has also been reported to promote chlorophyll degradation in tomato peel (Saniewski *et al.* 1987). Thus, jasmonates play a role not only in the reduction of chlorophyll content but also in

Fig. 1 Effect of jasmonate application on anthocyanin formation in 'Tsugaru' apples. Jasmonates were applied 20 days before harvest.
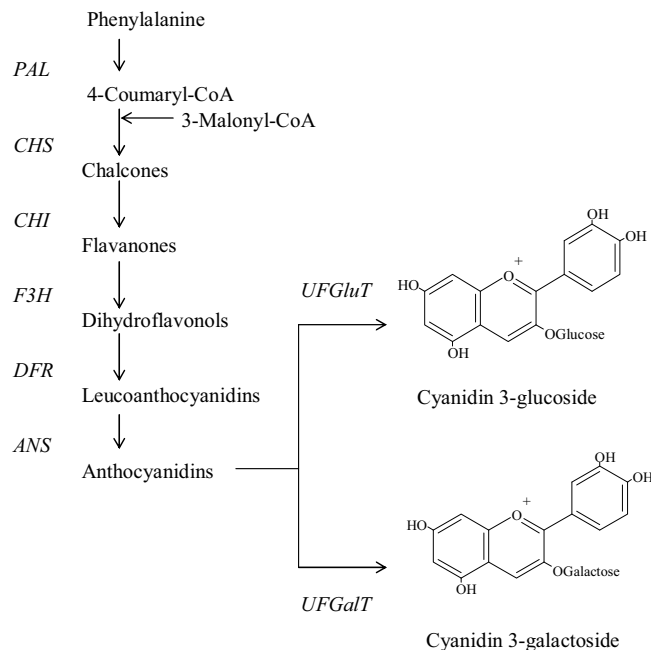

Fig. 2 Anthocyanin synthesis in apples. PAL: Phenylalanine ammonia-lyase, CHS: Chalcone synthase, CHI: Chalcone isomerase, F3H: Flavanone 3-hydroxylase, DFR: Dihydroflavonol 4-reductase, ANS: Anthocyanidin synthase, UFGluT: UDP glucose flavonoid 3-*O*-glucosyltransferase, UFGalT: UDP galactose flavonoid 3-*O*-galactosyltransferase.

anthocyanin accumulation. Plant growth regulators have been used to improve fruit coloration (Kondo and Hayata 1995), and jasmonates may be involved via their stimulation of anthocyanin formation. In general, ethylene is closely related to anthocyanin formation in apple fruit; the inhibition of endogenous ethylene production in the fruit retards anthocyanin formation (Kondo and Hayata 1995). The combination of jasmonates and AVG, an inhibitor of ACS activity, decreased anthocyanin accumulation compared to jasmonate treatment alone (Kondo *et al.* 2001b), but did not greatly inhibit it, suggesting that jasmonates may have an effect on anthocyanin formation independent of ethylene.

In contrast to the formation of anthocyanin in apples through the use of jasmonate treatment, the same treatment failed to promote anthocyanin accumulation in sweet cherries (Kondo *et al.* 2002c). However, ABA did stimulate anthocyanin production in sweet cherries. Moreover, anthocyanin formation by jasmonates has been reported in the stems and leaves of tulip bulbs (Saniewski *et al.* 1998). The promotion of anthocyanin accumulation in apple fruit by jasmonates can be attributed to the fact that endogenous jasmonates increase during the maturation period, but the increase of jasmonates during the maturation period was not observed in sweet cherry fruit or in grape berries (*Vitis* spp.) (Kondo and Fukuda 2001). In sweet cherry, a non-climacteric fruit, ethylene does not rise at harvest, but ABA does. However, the addition of fluridone, an inhibitor of ABA biosynthesis with jasmonates, decreased anthocyanin accumulation (Kondo *et al.* 2002c). These results suggest that jasmonates may not have a role in anthocyanin formation in sweet cherry fruit.

Chlorophyll, flavonols and carotenoids construct the skin color of non-red apples (Lancaster 1992). Flavonols and flavonoid concentration in the skin of non-red apples were constant throughout fruit growth (Ju *et al.* 1995). CHS is the first enzyme in the anthocyanin biosynthetic pathway, and the first specific flavonoid frame precursor (Terahara *et al.* 2000). Flavanon is converted to dihydroflavonol through the action of F3H and then to leucoanthocyanidin by DFR (**Fig. 2**). Therefore, the expression of *CHS*, *F3H* and *DFR* may result in the appearance of flavonol and leucocyanidin in the skin throughout fruit growth. The enzyme ANS converts leucoanthocyanidin to anthocyanidin and UFGluT subsequently catalyzes the transition from anthocyanidin to anthocyanidin glycosides. Proanthocyanidins such as catechin or epicatechin are found in the skin of both red and non-red apples (Kondo *et al.* 2002a). Proanthocyanidin is derived from leucoanthocyanidin (Gantet *et al.* 1993) which suggests that the reddening of apple fruit may be regulated by an enzyme that acts subsequent to leucoanthocyanidin (Lancaster 1992).

The *CHS*, *F3H*, *DFR*, *ANS*, and *UFGluT* gene expression was detected in the colored portion of the apple fruit (Kondo *et al.* 2002b). In contrast, in the shaded portion where anthocyanin was not observed, *ANS* was detected,

but *UFGluT* was barely found. The application of jasmonates on disc samples significantly increased the concentration of cyanidin 3-galactoside (Kondo 2006). The expressions of *F3H*, *DFR*, and *ANS* were similar between the jasmonate-treated samples and the untreated control. F3H is the enzyme which catalyzes the conversion of flavanones to dihydroflavonols. DFR catalyzes the reduction of dihydroflavonols to leucoanthocyanidins, then ANS catalyzes leucoanthocyanidins to anthocyanidins. The expressions of *F3H*, *DFR*, and *ANS* were similar between jasmonate-treated and untreated controls, despite higher jasmonate-induced anthocyanin concentrations. This indicates that these enzymes may not be solely responsible for anthocyanin formation. Changes in anthocyanidins differed from those in anthocyanin, although *ANS* transcription was affected by the actual light intensity (Kondo *et al.* 2002a). Therefore, ANS transcription may not be a limiting factor in anthocyanin formation. In contrast, the expression of *UFGluT* had increased in the skin which was treated with jasmonates and also contained higher anthocyanin concentrations. This result suggests that the anthocyanin formation promoted by jasmo-
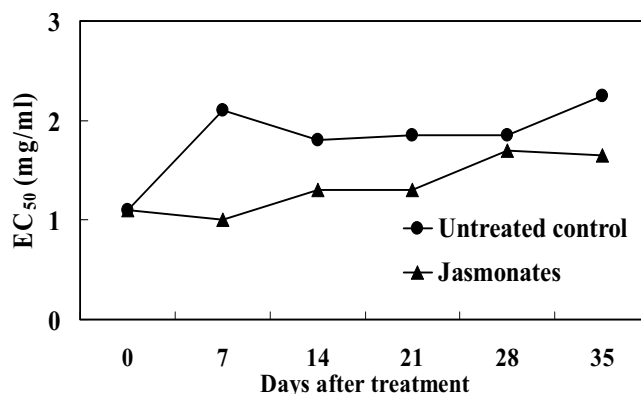

Fig. 3 Effect of jasmonate application on superoxide anion radical scavenging activity in apples. EC_{50} value shows the weight of the sample in a 1 ml reaction mixture. Jasmonates were applied 20 days before harvest.

nate treatment might have caused the stimulation of UFGluT, which is a downstream enzyme in the anthocyanin synthesis pathway.

EC_{50} values of O_2^- scavenging activity in the skin of jasmonate-treated fruit were lower than those in the skin of untreated control fruit (**Fig. 3**). This is consistent with the increase of anthocyanin in jasmonate-treated fruit being the cause of the increase of antioxidant activity (Kondo et al. 2002d).

ACS and ACO genes were influenced by physiologically active substances

Ethylene production is differentially influenced by other phytohormones. For instance, jasmonate treatment increased the ACC content, ACO activity, and ethylene production in sunflower seedlings (*Helianthus annuus* L.) (Emery and Reid 1996), but inhibited it in grain amaranth seeds (*Amaranthus caudatus* L.) (Kepczynski et al. 1999). On the other hand, auxin had an effect on ACS in the ethylene pathway; for example auxin application increased ACS2 mRNA levels in melons (*Cucumis melo* L.) (Ishiki et al. 2000) and ACS3 and ACS5 mRNA levels in tomatoes (*Lycopersicon esculentum* Mill.) (Coenen et al. 2003). The application of the synthetic auxin 2,4-dichlorophenoxypropionic acid (2,4-DP) increased ethylene production and the ripening activity of the 'La France' pear fruit on the tree (Kondo and Takano 2000), and the levels of ACS4 increased strongly in the 2, 4-DP-treated fruit (Kondo et al. 2006) as measured by mRNA hybridization. Therefore, ACS4 may be an ACS gene which is induced by auxin in pears. The ACS activity, ACC concentration, ACO activity and ethylene production increased in jasmonate-treated pear fruit at the preclimacteric stage (Kondo et al. 2007). The increase of the ACS1 and ACO1 mRNA levels were observed in jasmonate-treated fruit. In contrast to the preclimacteric stage, the ACS1 mRNA levels and ethylene production were decreased by jasmonate treatment at the climacteric stage (Kondo et al. 2007). ACC malonyltransferase is an enzyme which plays a role in the autoinhibition of the ethylene production of system 2 (Abeles et al. 1992). The results of jasmonate treatment at the preclimacteric and climacteric stages suggest that ACS1 may be influenced directly by jasmonates, resulting in the regulation of ethylene production.

Aroma volatile compounds were affected by physiologically active substances

The volatile compound production of apples is affected by various other substances. For example, AVG application slows the production of volatiles (Fan et al. 1998) while jasmonates also influence the aroma volatile production, but the effect can vary depending on the type of volatiles (Fan et al. 1997). Aroma volatiles are primarily synthesized in the skin (Knee and Hatfield 1981).

1-MCP, which blocks ethylene receptors and inhibits ethylene action, delays apple fruit ripening (Blankenship and Dole 2003). The levels of volatile compounds such as alcohols, esters, and ketones increase gradually toward ripening; however, their concentrations were the lowest in 1-MCP-treated fruit (Kondo et al. 2005). Furthermore, volatile compounds in 1-MCP-treated fruit did not increase greatly, even at ripening, suggesting that 1-MCP inhibits the production of volatile compounds. Volatile compounds in apples, produced by lipid and amino acid catabolism, are primarily synthesized in the skin (Fan et al. 1997; Rudell et al. 2002). Palmitic acid, stearic acid, oleic acid, linoleic acid, and triacontane were the predominant lipids detected in apple skin at harvest, but the levels of melissic acid, montanic acid, and heptacosan were greater in immature fruit skin (Noro et al. 1985). Thus, the late-forming lipids may be associated with aroma volatile synthesis during fruit ripening. According to Ranjan and Lewak (1995) the lipid catabolism enzyme lipase is associated with aroma volatile production and it is known that 1-MCP also influences the enzyme activity in the lipid catabolism pathway. Through suppression of its enzyme activity, 1-MCP may be difficult to recover from due to its ethylene inhibition properties.

Jasmonate application also increased aroma volatiles in mangoes (Lalel et al. 2003). However, Kondo et al. (2005) demonstrated that the effect of jasmonates on volatile compound production was dependent on the developmental stage of the treated fruit. Jasmonates may decrease volatile compound production when applied at the climacteric stage. In contrast, jasmonate application at the preclimacteric stage may stimulate aroma volatile production, as shown by the correlative relationship between ethylene and aroma volatiles in alcohols and esters (**Fig. 4**).
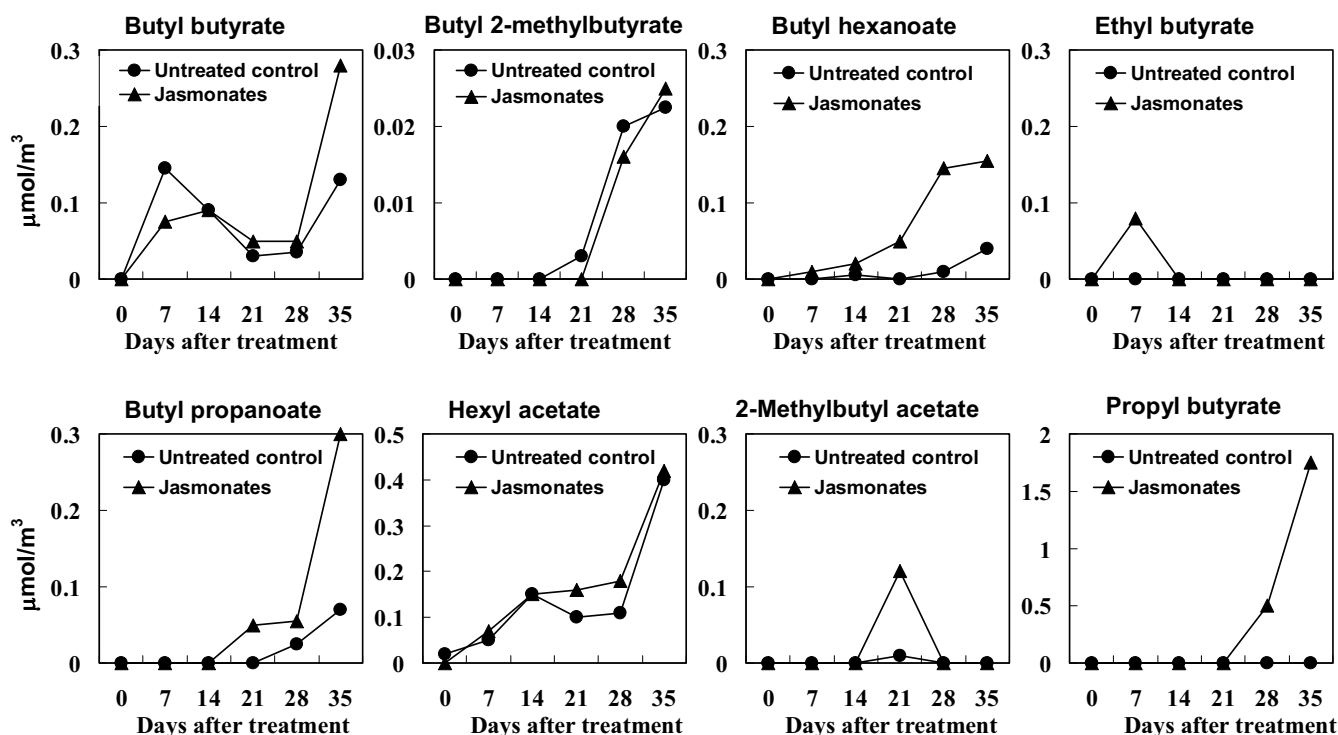

Fig. 4 Effect of jasmonate application on aroma volatiles in 'Tsugaru' apples. Jasmonates were applied 20 days before harvest.

Chilling injury and physiologically active substances

Mangosteens (*Garcinia mangostana* L.) are cultivated in humid tropics. Low temperature may extend the postharvest shelf life of mangosteen during transportation, however, if held under 8°C they may suffer from chilling injury (Augustin and Azudin 1986). Polyamines may retard membrane damage in chilling injury by stabilizing membranes (Faust and Wang, 1993), as for example in zucchini squash where spermine treatments decreased chilling injury (*Cucurbita pepo* L.) (Kramer and Wang 1989). Chilling injury in rambutans was limited only to the skin and it was not observed in the aril (O'Hare 1995). The differences in polyamine concentrations are associated with the extent of chilling injury depending on the part of the fruit (Kondo *et al.* 2003). Although polyamines may inhibit chilling injury in mangosteens, their metabolic roles are unclear. The polyamine (putrescine, spermidine and spermine) concentrations decreased during early development of the skin and aril, but increased later in the skin development (Kondo *et al.* 2003). The high polyamine level in young fruit indicates that they may be involved in the process of cell division (Faust and Wang 1993). The putrescine concentration was the highest followed by spermidine and then spermine in the skin and aril, whereas spermidine concentration was the highest in the seed (Kondo *et al.* 2003). The composition of polyamines in mangosteens was similar to other fruits such as rambutans and tomatoes (Dibble *et al.* 1988; Faust and Wang 1993; Kondo *et al.* 2001a). Polyamine concentrations in the aril decreased toward harvest but those in the seed and the skin increased during the maturation period (Kondo *et al.* 2003). Although the relationship between polyamine concentrations and fruit growth has been reported in some fruits (Faust and Wang 1993), changes of polyamine levels and the weights of the skin, aril and seed in mangosteens were different. The increase of polyamines in the skin of the mangosteen toward maturation also occurred in cherimoyas (*Annona cherimola* Mill.). It has been demonstrated that high polyamine levels in cherimoyas act in a protective manner by keeping cellular structures highly acidic (Escribano and Merodio 1994). Thus, the role of polyamines during fruit development may vary depending on the part of fruit as the structures of the skin, aril and seed differ greatly (Nakasone and Paull 1998).

The symptoms of chilling injury in mangosteen skin are browning and hardening (Augustin and Azudin 1986) and this was observed in the skin of fruit stored at 7°C but not at 13°C (Kondo *et al.* 2003). Spermine treatment delayed the progress of chilling injury at 7°C and was attributed to its absorption by the skin and aril (Kondo *et al.* 2003). Putrescine and spermidine concentrations in the skin at 7°C were higher than those at 13°C, but their concentrations decreased as chilling injury progressed in storage. Putrescine concentrations in the undamaged aril were higher than those in the skin indicating that the difference in putrescine concentrations may be associated with the degree of chilling injury. Putrescine levels and chill-tolerance of rice cultivars were correlated when rice seedlings were chilled (Lee *et al.* 1995). Therefore, the accumulation of polyamines in the mangosteen skin at low temperature may be a natural self-defense mechanism against chilling injury.

A rise of ABA or putrescine concentrations was observed in chilling-tolerant rice cultivars but not in chilling-sensitive cultivars when they were held at -5°C (Lee *at al.* 1995). The chilling tolerance induced by the jasmonate application also coincided with a decrease in ion leakage in mango fruit (*Mangifera indica* L.) (Gonzalez-Aguilar *et al.* 2000). It has been shown that calcium is an important second messenger in a low-temperature signal transduction pathway; the levels of ABA increased rapidly with an influx of calcium from extracellular stores in *Arabidopsis* (Knight *et al.* 1996). The elevated cytoplasmic Ca^{2+} activates the release of an ABA precursor through environmental stress or imbalance from a stored form in cells (Netting 2000). An increase in ABA in jasmonate- or spermine-treated fruit suggests that these treatments may be effective as a means of improving chilling tolerance (Yoshikawa *et al.* 2007).

Polyphenolics and ascorbic acid are the major sources of antioxidants in apples (Kondo *et al.* 2002c; Tsao *et al.* 2005). The production of reactive oxygen can be promoted by environmental factors (Matsui and Li 2003). The EC_{50} values of O_2^--scavenging activity were lower in jasmonate- and spermine-treated fruit, and both the polyphenolic and ascorbic acid concentrations were higher in both types of treated apple fruit (Yoshikawa *et al.* 2007). These results suggest that ABA, jasmonates and polyamines may be associated with low-temperature stress tolerance in fruit.

CONCLUSIONS

Fruits are beneficial to our health as they contain vegetable fiber and antioxidants. In addition, the bright color and aroma volatiles are indicative of further healing effects. Thus, fruit is often in high demand and it is important to be able to maintain freshness for as long as possible after harvest. This paper outlines many ways in which physiologically active substances are essential to the regulation of fruit quality. In addition, these substances can contribute to the defense system of the fruit against environmental stress. A detailed outline on the function of plant hormones is currently being written.

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