21 Postharvest Physiology

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21.1 Introduction

Successful postharvest handling of mangoes requires knowledge of the postharvest physiology of the fruit and how it determines the best handling practices to maintain and develop high fruit quality. For example, mango, like banana, tomato and avocado, is a climacteric fruit, which may be picked when it is physiologically mature but before ripening has commenced (termed the 'mature-green' stage of maturity). Mature-green mangoes can subsequently be ripened postharvest. Mangoes picked prior to the mature-green stage can be induced to ripen by treatment with ethylene, but the quality will be poor. As the mango fruit mature and ripen on the tree, their eating quality improves. Mango fruit that are allowed to begin to ripen on the tree generally represent the best eating quality, but their potential marketable life decreases as ripening progresses, due to the difficulty of controlling the ripening process once it has been initiated and because of increased susceptibility to bruising and decay.

The longer harvest is delayed past the mature-green stage, cultivars susceptible to internal physiological fruit disorders (internal breakdown, jelly seed, soft nose and stem-end cavity) tend to develop more fruit with symptoms (Raymond *et al.*, 1998; Brecht, 2018; see Chapter 13, this volume). As a tropical species, mangoes are very sensitive to chilling injury (CI), which limits the use of refrigeration to maintain postharvest quality. Mangoes are also subject to other physiological disorders, physical damage and decay, the symptoms of which can make the fruit unmarketable (Yahia *et al.*, 2006a; Yahia, 2011; Brecht, 2018).

Mature-green mangoes can be stored in the unripe state as long as the initiation of ethylene production and hence ripening is avoided. The initiation of ripening can be avoided by prompt cooling and storage at a low temperature at which ripening does not occur or, more effectively, by changing the composition of the storage atmosphere so that the O_2 level is reduced and CO_2 level is raised. This latter approach is called either modified atmosphere (MA) or controlled atmosphere (CA) storage, depending on the degree of control. These technologies slow fruit metabolism and specifically inhibit the initiation of ethylene production. With the use of MA or CA, mangoes can typically be maintained in a firm, green condition for significantly longer than with normal refrigerated air storage. However, there are limits to the levels of O_2 and CO_2 that can be tolerated by mangoes and these limits are affected by several factors, i.e., cultivar, maturity or ripeness stage, storage temperature and storage time (Yahia, 1998). Although much research has been conducted on mango CA storage (Brecht, 2020), the international nature of the mango trade, with fruit available from multiple countries every month of the year, attenuates much of the incentive for extended postharvest life beyond that which is required to meet shipping requirements. Recently, the global demand for tree-ripe mangoes has accelerated among consumers due to their superior quality compared with the mature-green harvested fruit. Research indicates that ripening of tree-ripe mangoes can be delayed sufficiently by CA/MA (Bender *et al.*, 2000b, 2022; Nakamura *et al.*, 2003; Singh and Zaharah, 2013; Ullah *et al.*, 2010), particularly with ethylene scrubbing (Brecht *et al.*, 2023) at the chilling threshold temperature to accommodate many international shipping routes.

Mango postharvest physiology and technology have been described in previous reports, book chapters and reviews (Subramanyam *et al.*, 1975; Lakshminarayana, 1980; Ledger, 1986; Peacock, 1986; Lizada, 1991; Coates and Johnson, 1993; Johnson and Coates, 1993; Lizada, 1993; Heather, 1994; Jacobi *et al.*, 1994; Johnson *et al.*, 1997; Mitra and Baldwin, 1997; Tharanathan *et al.*, 2006; Yahia *et al.*, 2006a; Yahia, 2011; Brecht and Yahia, 2017).

21.2 Contribution of Mango Fruit to Human Nutrition and Health

21.2.1 Vitamin content

Consumers are becoming aware of the nutritional and health benefits of fresh fruits and vegetables (Yahia *et al.*, 2019). Mango fruit are an excellent source of several nutritional and bioactive components known to be beneficial for human nutrition and health (Maldonado-Celis *et al.*, 2019; Yahia *et al.*,

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2023; Chapter 24 this volume). Mango fruit are a rich source of vitamin C (Thomas, 1975; Vinci *et al.*, 1995) (Table 21.1) with the highest concentrations (300 mg/100 g) in fresh 'Raspuri' fruit during the early stages of development and lower (39.1–69.5 mg/100 g) at maturity (Siddappa and Bhatia, 1954). The content of vitamin C was reported to range between 13 and 178 mg/100 g in the ripe fruit of 50 cultivars surveyed by Singh (1960). The vitamin C content in fully developed mango fruit of cultivars grown in Puerto Rico ranged between 6 and 63 mg/100 g (Iguina de George *et al.*, 1969). Vitamin C content was 105.2, 65.7 and 17.3 mg/100 g in 'Langra', 'Ashwini' and 'Fazli' mangoes, respectively (Gofur *et al.*, 1994) and decreased rapidly 5–7 weeks after fruit set, and when ripe fruit were stored at room temperature. Other vitamins are also present in mango. Stahl (1935) measured vitamin B1 (thiamine) between 35–60 µg/100 g in two cultivars and vitamin B2 (riboflavin) between 45–55 µg/100 g in three cultivars. Thiamine content of four Philippine cultivars was 57–600 µg/100 g and riboflavin content of three cultivars was 37–730 µ/100 g (Quinones *et al.*, 1944). Folic acid in green mangoes was 36 mg/100 g (Gosh, 1960).

21.2.2 Carotenoids

The mango fruit is a rich source of carotenoids, i.e., α-carotene, β-carotene (all-*trans*), β-cryptoxthanin (all-*trans* and *cis*), zeaxanthin (all-*trans*), luteoxanthin isomers, violaxanthin (all-*trans* and *cis*) and neoxanthin (all-*trans* and *cis*) function as pro-vitamin A (Mercadante *et al.*, 1997; Yahia *et al.*, 2006b; Ornelas-Paz *et al.*, 2007, 2008; Yahia *et al.*, 2023). The total carotenoid content reportedly increased from the mature-green to the ripe stage in 'Keitt' (2.3–38.0 µg/g) and 'Tommy Atkins' (7.0–51.2 µg/g) (Mercadante and Rodriguez-Amaya, 1998). Concentrations of the major carotenoids, violaxantin and β-carotene increased with ripening. In 'Keitt', concentrations of all-*trans*- β-carotene, all-*trans*-violaxanthin and 9-*cis*-violaxanthin increased from mature-green fruit to ripe fruit (1.7, 5.4 and 1.7 µg/g to 6.7, 18.0 and 7.2 µg/g), respectively (Mercadante and Rodriguez-Amaya, 1998). In 'Tommy Atkins' these carotenoids increased from 2.0, 6.9 and 3.3 µg/g to 5.8, 22.4 and 14.5 µg/g, respectively, during ripening. Geographical effects were reported to be substantial (Mercadante and Rodriguez-Amaya, 1998). Some of the *cis* and *trans* isomers of pro-vitamin A reported in 'Haden' and 'Tommy Atkins' mangoes include 13-*cis*-β-carotene (trace amounts), *trans*-β-carotene (12.5–15.5 µg/g) and *trans*-α-cryptoxanthin (0.3–0.4 µg/g) (Godoy and Rodriguez-Amaya, 1994). In processed mango juice, violaxanthin was not detected, auroxanthin appeared at an appreciable level, and β-carotene was the principal carotenoid (Mercadante and Rodriguez-Amaya, 1998). The major carotenoid in 'Bourbon', 'Haden', 'Extreme', 'Golden' and 'Tommy Atkins' mangoes was found to be β-carotene (48–84% of the total), while epoxycarotenoids (violaxanthin, luteoxanthin and mutatoxanthin) constituted 13–49% of the total (Godoy and Rodriguez-Amaya, 1989). Mean vitamin A in these mangoes (retinol equivalents per 100 g) ranged from 115.3 ('Haden') to 430.5 ('Extreme').

Children in Senegal with normal cytology were found to have higher serum retinol and β-carotene levels than those with abnormal cytology after massive oral doses of vitamin A and consumption of mangoes (Carlier *et al.*, 1992). Mango retinol is highly bioavailable (82% efficiency) by estimating vitamin A and carotene reserves in the liver and plasma of rats (Yuyama *et al.*, 1991). During mango fruit ripening, vitamin A increases, with ripe mangoes found to be tenfold richer in carotene than partially ripe fruit, while unripe green mangoes contained only trace amounts (Modi and Reddy, 1967). Mevalonic acid, a precursor of carotenoids, increases progressively during mango ripening (Modi and Reddy, 1967). Vitamin A equivalents in 100 g of mango fruit are 1000 to 6000 IU (Singh, 1960). The β-carotene content measured in fruit of 30 mango cultivars in Puerto Rico ranged from 400 to 800 IU/100 g fresh fruit (Iguina de George *et al.*, 1969). The development of β-carotene in mangoes held at 16–21°C was lower than that at 20–28°C (Vazquez-Salinas and Lakshminarayana, 1985). Jungalwala and Cama (1963) identified 16 different carotenoids in 'Alphonso' mangoes, and β–carotene accounted for 60% of the total. Of the oxycarotenoids, luteoxanthin, violaxanthin and *cis*-violaxanthin were present in significant amounts. All the oxycarotenoids were present as β-carotene derivatives, mostly as epoxides of zeaxanthin. Variation in carotenoid content, as in many other constituents, is due to several factors, i.e., cultivar, harvest maturity, geography, climate, storage/processing conditions and analytical procedures employed.

Several carotenoids occur in fruit of different mango cultivars (Cano and de Ancos, 1994; Ben-Amotz and Fishler, 1998; Chen *et al.*, 2004; Maldonado-Celis *et al.*, 2019), but only a few of them occur in significant concentrations (Ornelas-Paz *et al.*, 2007). Mercadante *et al.* (1997) quantified several carotenoids in ´Keitt´ mangoes; the most predominant ones were all-*trans*-β-carotene, all-*trans*-violaxanthin, and 9-*cis*-violaxanthin, accounting for 27, 38 and 18% of the total carotenoid content, respectively. Similar findings have been reported for crude extracts from other mango cultivars (Mercadante and Rodríguez-Amaya, 1998; Pott *et al.*, 2003a, b). Carotenoids are responsible for the yellow colour of the peel of several mango cultivars, and the yellow-orange colour of the mesocarp of all cultivars (Vázquez-Caicedo *et al.*, 2004). All-*trans*-β-carotene and the dibutyrates of all-*trans*-violaxanthin and 9-*cis*-violaxanthin are the main carotenoids in 'Ataulfo' and 'Manila' mangoes (Yahia *et al.*, 2006b; Ornelas-Paz *et al.*, 2008; Fig. 21.1). The content of these carotenoids during fruit ripening increased exponentially in 'Ataulfo' and exponentially or in a second order polynomial manner in 'Manila', and the highest correlation coefficients were obtained for the relationships between the internal and external a* and hue° colour values and the content of the evaluated carotenoids in both mango cultivars (R = 0.81–0.94). Equations to predict the content of the most important carotenoids in 'Manila' and 'Ataulfo' mangoes on the basis of their internal and external colour values were obtained by Ornelas-Paz *et al.* (2008).

Tocopherol

The content of α-tocopherol (a type of vitamin E) was ca. 0.5 mg/100 g in an unidentified mango cultivar from Costa Rica (Burns *et al.*, 2003), while the USDA Nutrient Database (2018) indicated an α-tocopherol content of 0.9 mg/100 g. Ornelas-Paz *et al.* (2007) found that α-tocopherol was the only detectable

Table 21.1. Composition per 100 g of the edible portion of mango fruit.

Nutrient	Value per 100 g edible portion
Water g	83.5
Energy kcal	60
Energy kj	250
Protein g	0.82
Total lipid (fat) g	0.38
Ash g	0.36
Carbohydrate, by difference g	15.00
Fibre, total dietary g	1.6
Sugars, total g	13.7
Minerals	
Calcium mg	11
Iron mg	0.16
Magnesium mg	10
Phosphorus mg	14
Potassium mg	168
Sodium mg	1
Zinc mg	0.09
Copper mg	0.111
Manganese mg	0.063
Selenium μg	0.6
Vitamins	
Vitamin C (total ascorbic acid) mg	36.4
Thiamin mg	0.028
Riboflavin mg	0.038
Niacin mg	0.669
Pantothenic acid mg	0.197
Vitamin B6 mg	0.119
Folate, total μg	43
Folic acid μg	0
Folate, food μg	43
Vitamin B12 μg	0
Vitamin A RAE	54
Retinol μg	0
Vitamin E (alpha-tocopherol) mg	0.9
Vitamin K (phylloquinone) μg	4.2
Lipids	
Fatty acids, total saturated g	0.092
4:0 g	0.000
6:0 g	0.000
8:0 g	0.000
10:0 g	0.000
12:0 g	0.001
14:0 g	0.013
16:0 g	0.072
18:0 g	0.004
Fatty acids, total monounsaturated, g	0.140
16:1 undifferentiated g	0.067
18:1 undifferentiated g	0.075
20:1 g	0.000
22:1 undifferentiated g	0.000
Fatty acids, total polyunsaturated g	0.071
18:2 undifferentiated g	0.019
18:3 undifferentiated g	0.051
18:4 g	0.000

Continued

Table 21.1. Continued.

Nutrient	Value per 100 g edible portion
20:4 undifferentiated g	0.000
20:5 n-3 g	0.000
22:5 n-3 g	0.000
22:6 n-3 g	0.000
Cholesterol mg	0
Amino acids	
Tryptophan g	0.013
Threonine g	0.031
Isoleucine g	0.029
Leucine g	0.005
Lysine g	0.066
Methionine g	0.008
Phenylalanine g	0.027
Tyrosine g	0.016
Valine g	0.042
Arginine g	0.031
Histidine g	0.019
Alanine g	0.082
Aspartic acid g	0.068
Glutamic acid g	0.096
Glycine g	0.034
Proline g	0.029
Serine g	0.035
Other	
Ethanol g	0
Caffeine mg	0
Theobromine mg	0
β-Carotene µg	640
α-Carotene µg	9
Cryptoxanthin, beta µg	10
Lycopene µg	3
Lutein + zeaxanthin µg	23

Data from USDA Food Data Central (2024)
https://fdc.nal.usda.gov/fdc-app.html#/food-details/169910/nutrients

tocopherol in seven mango cultivars (Fig. 21.2); 'Haden' and 'Tommy Atkins' mangoes had the highest amounts at 380 and 470 µg/100 g, respectively, with ca. 200–250 µg/100 g found in the other cultivars.

21.2.3 Antioxidants and carcinogenesis

Mango fruit are rich in several types of antioxidant phytochemicals such as carotenoids and phenolics (Ornelas-Paz et al., 2007; Rocha-Ribeiro *et al.*, 2007; Maldonado-Celis *et al.*, 2019). Botting *et al.* (1999) showed that mango fruit contain antimutagens and the heterocyclic amine 2-amino-3-methylimidazo[4,5-*f*]quinoline. Percival *et al.* (2006) observed that whole mango juice inhibited cell proliferation in the leukaemic cell line HL-60 and also inhibited the neoplastic transformation of BALB/3T3 cells. Garcia-Solis *et al.* (2008) studied the effect of 'Ataulfo' mango consumption on chemically induced mammary carcinogenesis and plasma antioxidant capacity in rats treated with *N*-methyl-*N*-nitrosourea (MNU). Mango was administered in the drinking water (0.02–0.06 g/ml) during both short-term and long-term (LT) periods to rats treated or not with MNU. Rats treated with MNU showed no differences in mammary carcinogenesis or in plasma antioxidant capacity measured by both ferric reducing/antioxidant power (FRAP) and total oxyradical scavenging capacity assays. However, in animals not treated with MNU, but with an LT intake of mango, the plasma antioxidant capacity as measured by the FRAP assay tended to increase in a dose-dependent manner. This suggests that mango consumption by healthy subjects may increase antioxidants in plasma.

21.3 Mango Ripening Physiology

Ripening is part of the natural senescence of mango fruit. It is an irreversible process that contributes to organelle disruption

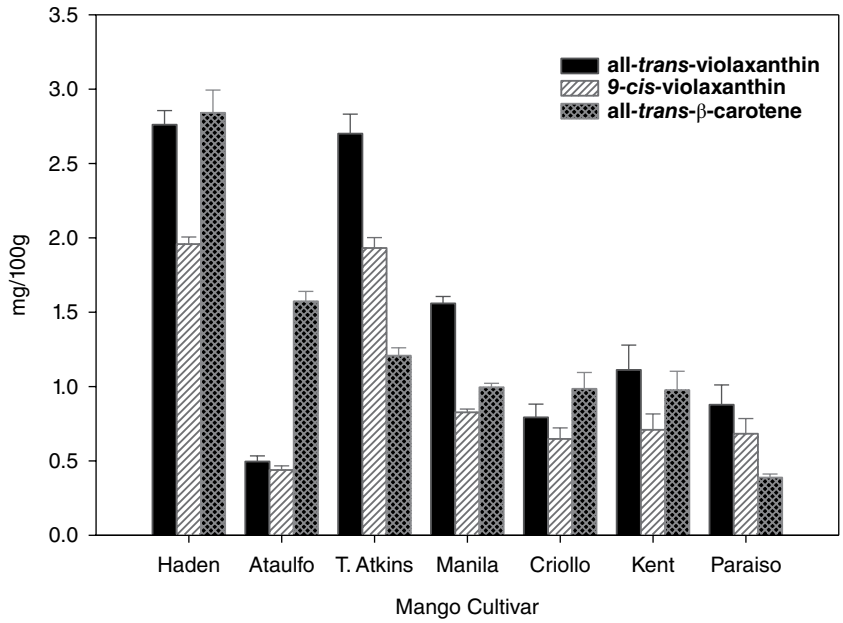

Fig. 21.1. Content of selected carotenoids in flesh of several mango cultivars. Data represent the mean of eight individual observations for each cultivar ± SE (Ornelas-Paz *et al.*, 2007).

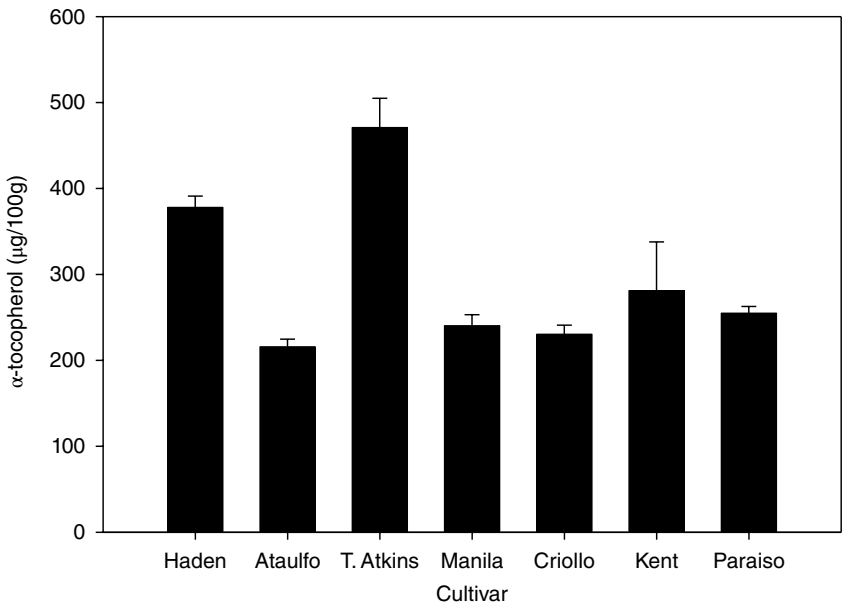

Fig. 21.2. The content of α-tocopherol in the flesh of several mango cultivars. Data represent the mean of eight individual observations for each cultivar ± SE (Ornelas-Paz *et al.*, 2008).

and changes in chemical constituents, flavour and texture. While ripening improves the eating quality of mango fruit, the postharvest life of the fruit is reduced. Natural senescence, and thus ripening, is aggravated and promoted by ethylene, mechanical injury and high temperature. This process can be delayed by lower temperature, elimination of mechanical damage and reducing ethylene production (Yahia *et al.*, 2006a). Ripening of mango has been reported to be inhibited while fruit are attached to the tree, and respiration and ripening are stimulated upon detachment (Lakshminarayana, 1973). Burg and Burg (1962) reported that ethylene levels in the tissues of mature-green, attached mango fruit were relatively high (1.87 µl/l) and suggested that ethylene was ineffective for promoting ripening, due to a ripening inhibitor supplied by the tree. Beaudry (2024) has recently reported the same behaviour with 'Pusa Manohari' and 'Amrapali' mangoes from India. However, those observations

are contradicted by the common commercial practice of harvesting mango fruit when internal flesh colour development has occurred adjacent to the stone.

Physicochemical ripening changes

Changes associated with mango fruit ripening include: (1) flesh colour from greenish yellow to yellow to orange in all cultivars, beginning near the stone and progressing outward (Table 21.2); (2) peel colour from green to yellow in some cultivars; (3) chlorophyll decreases and carotenoid content increases; (4) flesh firmness decreases (Table 21.2) and juiciness increases; (5) starch is converted into sugars, resulting in: (6) total soluble solids (TSS) content increases (Table 21.2); (7) titratable acidity (TA) decreases; (8) characteristic aroma volatiles increase; (9) CO_2 production rate increases from 40–50 to 160–200 mg/kg/h at 20°C; and (10) ethylene production rate increases from 0.1–0.2 to 1–3 µl/kg/h at 20°C. Gowda and Huddar (2000) found that the changes in eight mango selections during ripening included reductions in fruit weight, volume, length, thickness, firmness, flesh content, flesh to peel ratio, starch and vitamin C, and increases in TSS, pH, total sugars, sugar:acid ratio, flesh carotenoid content and peel colour. Farina *et al.* (2020) determined sensory quality (marketable traits) and qualitative responses of tree-ripe 'Keitt', 'Glenn', 'Osteen', 'Maya', 'Kensington Pride' and 'Tommy Atkins' mango fruit. There exist differences in a cultivar-dependent manner about fresh market requirements. Overall, 'Keitt' exhibited higher vitamins and protein content and better sensory appeal. 'Glenn' had higher firmness, vitamins, polyphenolics and antioxidants. 'Maya' achieved higher TSS and lower TA. 'Tommy Atkins' had better peel colour, total antioxidants, vitamin B2 and vitamin C contents.

21.3.1 Climacteric behaviour

Mango is a climacteric fruit, exhibiting a climacteric pattern of respiration and an increase in ethylene production during ripening (Cua and Lizada, 1990; Reddy and Srivastava, 1999; Lalel *et al.*, 2003; Fig. 21.3). The initiation of ethylene production within the fruit triggers and coordinates the changes that occur during ripening. These changes include colour changes in the peel and flesh, softening of the flesh and development of sweet flavour and aroma. Mangoes can be ripened after harvest when picked at physiological maturity (mature-green), that is, when they are fully sized, but before ripening has been initiated. Maturity indices, such as fruit development period, dry matter content, peel colour break and flesh firmness, are chosen to predict fruit quality potential and postharvest behaviour (Peacock *et al.*, 1986; Medlicott *et al.*, 1988). After harvest, the fruit are then cooled and isolated from possible sources of ethylene (other ripening fruit, engine exhaust, smoke, etc.) during storage or shipping. This is the primary strategy used to control ripening and thus extend shelf life. Respiration patterns and ripening behaviour vary among cultivars, with different climatic conditions and growing locations (Krishnamurthy and Subramanyam, 1970). Respiration is very high after fruit set and then declines and is maintained at a low rate until fruit ripening begins.

The rise in respiration and ethylene production during the climacteric is related to fruit ripening. The respiratory peak in 'Alphonso' harvested mature-green was reported to occur 5 days after harvest and the fruit ripened within 7 or 8 days (Karmarkar and Joshi, 1941), while in 'Kent' and 'Haden' the peak reportedly occurred on days 9 and 11, respectively (Burg and Burg, 1962), and in 'Pairi' on day 9 (Krishnamurthy and Subramanyam, 1970). These differences are normal, due to differences in location, climatic conditions, orchard and tree conditions, harvest maturity and postharvest temperature. The rise in the climacteric respiration in 'Dashehari', 'Amrapali' and 'Rataul' mangoes coincided with the highest level of sucrose and polygalacturonase (EC 3.2.1.15; PG) activity in ripening fruit (Kalra and Tandon, 1983). Respiration and ethylene production are excellent maturity indices, but require considerable expense to measure.

The expression of alternative oxidase (Aox) and uncoupling proteins (Ucp) has been investigated during mango ripening and compared with the expression of peroxisomal thiolase (EC 2.3.1.176), a ripening marker in mango (Considine *et al.*, 2001). The multigene family for Aox in mango is expressed differentially during mango fruit ripening. Abundance of Aox message and protein peaks at the ripe stage, while expression of the single gene for the Ucp peaks at the turning or half-ripe stage, and the protein abundance peaks at the ripe stage. Proteins of the cytochrome chain peak at the mature-green stage, suggesting that increases in cytochrome chain components are important for facilitating the climacteric burst of respiration and that Aox and Ucp are important in postclimacteric senescence processes (Considine *et al.*, 2001). Because both message and protein for the Aox and Ucp increase in a similar pattern, their expression is not controlled in a reciprocal manner but may be active simultaneously.

Fruit slicing affects respiration rate (Allong *et al.*, 2001). Slicing of mature-green 'Julia' and 'Graham' mangoes increased respiration rate immediately after cutting, but it decreased significantly within the first 12 h of storage at 5 or 10°C, yet still remained at levels above that of the intact fruit throughout the storage period. The effect of slicing on half-ripe and firm-ripe fruit was an initial increase in respiration followed by a decline to levels of the intact fruit.

21.3.2 Ethylene production and responses

Mangoes have a moderate ethylene production peak of 1 to 3 µl/kg/h during ripening at 20°C. Ethylene, applied directly or as ethrel, induces faster and more uniform fruit softening (Lakshminarayana, 1973; Barmore, 1974; Lakshminarayana *et al.*, 1974; Sornsrivichai and Waru-Aswapti, 1989). Ethylene treatment can be prior to shipping (Barmore and Mitchell, 1975). There is disagreement regarding the effect of ethylene treatment on quality (Chaplin, 1988) and this may be related to maturity when treated, since treatment of immature fruit leads to softening, but the fruit have poor flavour.

Mango fruit ripening is accompanied by increased ethylene production, which coordinates the ripening process. Mango expresses an autocatalytic increase in ethylene production during ripening (Mattoo and Modi, 1969b). Ethylene pro-

Table 21.2. Flesh colour, firmness and soluble solids content during ripening of mangoes from Stage 1 to Stage 5 based on internal flesh colour advancement from centre to periphery. Adapted from Mango Maturity and Ripeness Guide, National Mango Board (NMB). Based on NMB-funded research in Florida and California, USA; Culiacan and Nayarit, Mexico; Ecuador; Peru; and Brazil (Authors' own table).

Cultivar and maturity stage	Flesh colour[a] (Hue°)	Firmness[b] (kg-force)	Soluble solids content (°Brix)
Tommy Atkins			
Stage 1	81.0	21.3–13.6	5–7
Stage 2	81.5	15.9–6.8	6–10
Stage 3	84.5	9.5–4.1	9–12
Stage 4	77.5	4.5–2.7	10–14
Stage 5	71.0	2.7–1.4	13–16
Honey (Ataulfo)			
Stage 1	91.0	21.3–10.0	5–7
Stage 2	76.0	13.2–5.4	7–11
Stage 3	76.5	8.2–2.7	11–14
Stage 4	78.5	2.3–0.9	13–16
Stage 5	68.5	1.4–0.45	13–18
Kent			
Stage 1	93.5	21.8–10.0	6–8
Stage 2	82.0	13.2–6.3	7–12
Stage 3	79.5	9.5–5.0	11–15
Stage 4	78.0	5.0–2.3	12–17
Stage 5	65.5	2.7–0.45	16–20
Keitt			
Stage 1	93.0	29.5–22.2	5–7
Stage 2	74.0	21.3–8.2	7–12
Stage 3	73.0	11.8–6.3	9–13
Stage 4	70.5	5.0–2.7	12–15
Stage 5	63.0	2.7–0.45	13–17
Haden			
Stage 1	93.0	23.6–11.3	6–9
Stage 2	74.0	15.9–7.3	9–12
Stage 3	73.0	7.7–3.6	11–15
Stage 4	70.5	4.1–1.8	12–16
Stage 5	63.0	2.7–0.9	13–17
Francis			
Stage 1	77.5	11.3–7.3	6–8
Stage 2	62.5	8.6–5.4	10–13
Stage 3	56.0	5.0–3.6	12–16
Stage 4	62.0	4.1–2.3	13–18
Stage 5	51.0	2.3–1.4	14–18

[a]CIE L*a*b* scale, measured midway between the pit surface and the peel.
[b]Bioyield force measured using an 8 mm diameter Magness-Taylor type convex tip probe.

duction starts before full ripeness is reached (Burg and Burg, 1962; Cua and Lizada, 1990). Ethylene production in unripe mangoes is very low (<0.1 µl/kg/h) (Burdon *et al.*, 1996). Ethylene production decreases as the fruit matures, is then undetectable for a time and reappears upon initiation of ripening (Akamine and Goo, 1973). 'Kent' and 'Haden' fruit were reported to have internal ethylene concentrations of ca. 0.01 µl/l during the preclimacteric phase, increasing to ca. 0.08 µl/l at the initiation of the climacteric, and up to 3.0 µl/l at the climacteric peak. Burg and Burg (1962) reported that ethylene production rises when or before CO_2 production rises in ripening mangoes, while Biale and Young (1981) included mangoes among fruit in which ethylene rises after CO_2 production rises.

Only a small concentration of exogenous ethylene (≥0.005 µl/l) is needed to initiate mango ripening (Wills *et al.*, 2001). The small amount of ethylene in the fruit at harvest is sufficient to initiate ripening (Burg and Burg, 1962). While 'Amrapali' and 'Dashehari' mangoes were found to produce a measurable amount of ethylene during ripening (Reddy and Srivastava,

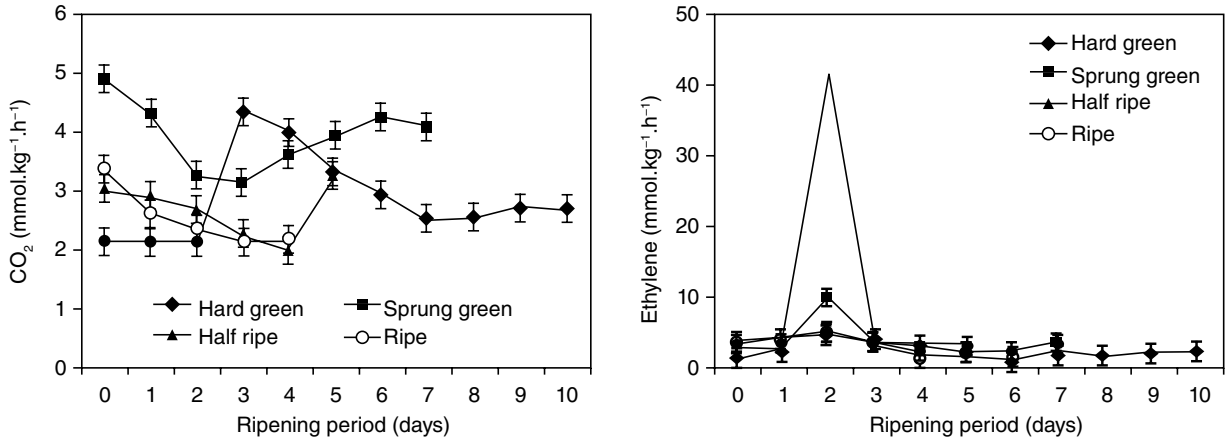

Fig. 21.3. The climacteric pattern of respiration and ethylene production during mango fruit ripening (Lalel *et al.*, 2003).

1999), ethylene production did not follow a climacteric pattern and two ethylene peaks (at the mature-green and full-ripe stages) were recorded. This is probably due to the way that ethylene was measured in the different fruit, and the lack of control exerted on maturity stages of fruit. In 'Carabao' mangoes, the peak of ethylene production was reported to occur 110 days after flower initiation and decline as the fruit approached full maturity (Cua and Lizada, 1990). The content of 1-aminocyclopropane-1-carboxylic acid (ACC), the immediate precursor of ethylene, was found to increase in different tissues (peel, outer and inner mesocarp) during ripening in both the 'Amrapali' and 'Dashehari' mango cultivars, while ACC oxidase (EC 1.14.17.4; ACO), which catalyses the conversion of ACC to ethylene and ethylene production declined (Reddy and Srivastava, 1999). At the mature-green stage, fruit peel tissue has the highest levels of ethylene and ACO and less ACC accumulation compared with the outer and inner mesocarp. The inner mesocarp has less ACO activity and high ACC accumulation during ripening compared to peel; levels in the outer mesocarp are intermediate between those in the peel and inner mesocarp. Changes in the ability to convert ACC to ethylene in the peel are not related to changes in ripening parameters in the fruit flesh (Lederman *et al.*, 1997). Mango seed also produces ethylene (Reddy and Srivastava, 1999). Fruit slicing had no measurable effect on ethylene production in 'Julia' and 'Graham' mangoes (Allong *et al.*, 2001).

Treatment of mango fruit with acetaldehyde or ethanol (0.1, 0.5, or 1% ethanol or acetaldehyde vapour) was shown to have concentration-dependent inhibitory effects on ethylene production (Burdon *et al.*, 1996). It was found that application of ACC to acetaldehyde-treated fruit discs completely eliminated increased ACO activity, whereas application of ethanol did not; accordingly, it was suggested that acetaldehyde can either inhibit ACO activity directly or prevent the increase in the enzyme, thereby providing a possible mechanism for retarding fruit ripening.

Tree-ripe mangoes (i.e., those harvested at the onset of the climacteric and showing internal yellow-orange flesh colour development near the stone) are of prime quality due to improved texture, odour and flavour compared with mature-green mangoes. Bender *et al.* (2021) evaluated the postharvest storage life of tree-ripe 'Tommy Atkins' and 'Keitt' mangoes stored at lower temperatures (5 or 8°C) along with CA (5 kPa O_2 plus 10 or 25 kPa CO_2) to maintain fruit quality without exhibiting CI. Tree-ripe 'Tommy Atkins' and 'Keitt' mangoes were stored for 14 or 21 days, respectively. They reported that during CA storage, respiration rates were below 10 ml/kg/h and increased threefold on the third day of the shelf life period in air at 20°C. Ethanol concentration in mangoes stored in 25 kPa CO_2 increased during storage and remained elevated during shelf life, but no such pattern was seen in fruit stored in 10 kPa CO_2. Electrolyte leakage and ACC in 'Tommy Atkins' and 'Keitt' stored in 25 kPa CO_2 showed that mesocarp tissues are injured at higher CO_2 levels. No such CI symptoms were seen in CA (5 kPa O_2 plus 10 kPa CO_2) or air at 5 or 8°C. Overall, tree-ripe mangoes stored in 5 kPa O_2 plus 10 kPa CO_2 at 5 or 8°C maintained the quality of 'Tommy Atkins' and 'Keitt' mangoes for 14 or 21 days, respectively, without exhibiting CI symptoms.

21.4 Compositional Changes during Fruit Maturation and Ripening

Several important metabolic changes occur during the maturation and ripening of mangoes and some of these are useful as maturity indices (Ketsa *et al.*, 1991). The ripening changes are irreversible senescence processes that are related to degradation of organelles or changes in chemical constituents, and thus relate to the quality and postharvest life of the fruit. Natural senescence is aggravated and promoted by ethylene, mechanical injury and high temperature and can be delayed by low temperature, elimination of mechanical damage and reduction of ethylene production.

21.4.1 Organic acids

Organic acids are important for respiratory activity and as flavour constituents. During maturation and ripening, mango

fruit experience a substantial reduction of organic acids. The predominant acids in mature mango fruit are citric, succinic, malic and tartaric acids. Of these, citric acid is found in the highest concentration and tartaric acid in the lowest concentration (Shashirekha and Parwardhan, 1976; Sarker and Muhsi, 1981; Medlicott and Thompson, 1985). Ito *et al.* (1997) found that citric acid concentration in 'Irwin' mangoes steadily increased during fruit development, reaching a maximum at the beginning of the endocarp-hardening period, after which it steadily decreased. In 'Keitt', the predominant organic acids are citric and malic acids, but tartaric, oxalic, ascorbic and α–ketoglutaric acids are also present; the initial reduction in acidity is due to a substantial loss of citric acid and a small loss in malic acid (Medlicott and Thompson, 1985). In 'Badami' mangoes, citric acid was also the major organic acid, with malic and succinic acids also present (Shashirekha and Patwardhan, 1976). In 'Fazli' mangoes, oxalic, citric, malic, pyruvic and succinic acids have been detected and in 'Zardalu' tartaric acid has been detected (Kumar *et al.*, 1993). In general, citric and succinic acids decrease during ripening while malic acid shows different changes with different cultivars (Lizada, 1993).

Mango fruit contain organic acids involved in tricarboxylic acid cycle reactions, i.e., oxalic, succinic, pyruvic, oxaloacetic and α-ketoglutaric acids. In 'Pairi' mangoes, maximum concentration of α-oxoglutaric and pyruvic acids occurred before the climacteric peak. Aspartic and glutamic acid concentrations increased for about 3 days after harvest and then decreased as the climacteric maximum was reached (Krishnamurthy *et al.*, 1971). Malic enzyme (EC 1.1.1.40), which catalyses the oxidative decarboxylation of L-malic to pyruvic acid, occurred in the ¾-ripe and full-ripe stages and the activity pattern during ripening was found to be similar in 'Alphonso', 'Banganpalli', 'Dasheri', 'Fazli', 'Langra' and 'Suvarnarekha' (Selvaraj and Kumar, 1994). In 'Alfonso', the levels of malic dehydrogenase (EC 1.1.1.37) and succinic dehydrogenase (EC 1.3.5.1) increased with the onset of ripening; whereas the level of citrate synthase (EC 2.3.3.1) increased several-fold during maturation then decreased markedly during ripening (Baqui *et al.*, 1974). The activity of malic enzyme increases during ripening, reaching a maximum immediately after the climacteric peak, and then declines (Dubery *et al.*, 1984). The activity patterns of phosphoenol pyruvate carboxylase (EC 4.1.1.49; PEPC) and pyruvate decarboxylase (EC 4.1.1.1) during ripening were found to vary among cultivars, while malic enzyme activity increased during ripening. The PEPC activity during ripening was reported to be relatively high in 'Alphonso' and 'Langara', but low in 'Dashehari' and 'Totapuri' mangoes (Selvaraj and Kumar, 1994).

21.4.2 Soluble sugars

Soluble sugars undergo a major increase during mango fruit ripening, with increased sweetness the most important compositional change in flavour (Maldonado-Celis *et al.*, 2019). Starch increases in chloroplasts during fruit development, then is almost completely hydrolysed to simple sugars during ripening (Medlicott *et al.*, 1986; Selvaraj *et al.*, 1989; Kumar *et al.*, 1994; Ito *et al.*, 1997). Starch content in mango fruit mesocarp tissue can vary from 12% to 25% or higher (by weight) at physiological maturity and is essentially completely converted to sugars during ripening. In 'Alphonso' fruit, starch content was reported to be 14% in unripe fruit and ≈ 0.3% in the ripe fruit. Similarly, starch was almost undetectable in 'Irwin' after ripening, whereas sucrose increased significantly and fructose increased slightly (Ito *et al.*, 1997).

Ripe mangoes contain up to 10–20% total sugars (fresh weight; FW), depending on the cultivar and the stage of ripeness (Maldonado-Celis *et al.*, 2019; Table 21.2). At the beginning of ripening, reducing sugars make up most of the sugar content, while there are more non-reducing (ca. 17%) than reducing (3%) sugars in completely ripe fruit. Sucrose was shown to contribute 57% of the total sugar in ripe 'Keitt' mangoes, with fructose and glucose making up 28% and 15%, respectively (Medlicott and Thompson, 1985). Krishnamurthy *et al.* (1971), Lakshminarayana (1973, 1975) and Shashirekha and Patwardhan (1976) reported a simultaneous increase of glucose, fructose and sucrose during ripening, but Vazquez-Salinas and Lakshminarayana, (1985) observed a gradual reduction in glucose and fructose and a continuous increase of sucrose during ripening in 'Haden', 'Irwin', 'Kent' and 'Keitt'. Medlicott and Thompson (1985) and Vazquez-Salinas and Lakshminarayana (1985) identified the main reducing sugar as fructose, while Selvaraj *et al.* (1989) reported that glucose is predominant. Conflicting reports on the relative concentrations of individual sugars in mango fruit during ripening is cultivar-dependent and due to different storage and handling conditions (Medlicott and Thompson, 1985; Maldonado-Celis *et al.*, 2019).

Sucrose content increases during ripening as a result of starch hydrolysis from increased amylase (EC 3.2.1.1) activity (Mattoo and Modi, 1969a; Fuchs *et al.*, 1980; Tandon and Kalra, 1983). The high activities of sucrose synthase (EC 2.4.1.13) and invertase (EC 3.2.1.26) in the mesocarp during ripening indicate active sucrose metabolism (Kumar *et al.*, 1994). Hexoses and hexose phosphates can be formed from pyruvate by gluconeogenesis (Selvaraj and Kumar, 1994). The activity of glucose-6-phosphatase (EC 3.1.3.9) reportedly increases up to the ¾-ripe stage; whereas, fructose-1,6-diphosphatase (EC 3.1.3.11) activity increases as the fruit ripens from the ¾-ripe to full-ripe stage (Kumar and Selvaraj, 1990). The glycolytic enzyme hexokinase (6-phosphofructokinase; EC 2.7.1.11) has maximum activity at the ripe stage, while pyruvate kinase (EC 2.7.1.40) activity increases until the ¾-ripe stage and declines at ripening (Selvaraj and Kumar, 1994). The pattern of activity changes in hexokinase/phosphofructokinase and pyruvate kinase demonstrates that glycolysis is activated during mango fruit ripening.

Reducing sugars, mainly fructose, increase slightly during ripening, and sucrose synthase (EC 2.4.1.13) activity increases ≈10× during the phase of rapid sucrose accumulation (Castrillo *et al.*, 1992). This activity accounts for the maximum rate of sucrose synthesis. The proportion of sucrose phosphate synthase (EC 2.4.1.14) activity that is sensitive to inhibition by inorganic phosphate changes during ripening (Castrillo *et al.*, 1992). Maximum catalytic activity of sucrose synthase is constant throughout the ripening period and contributes significantly to sucrose metabolism. The activities of neutral and acid invertases (EC 3.2.1.26) are very low in comparison with the

other enzymes of sucrose synthesis. Acid invertase activity increases and later decreases during ripening.

21.4.3 Structural polysaccharides

Flesh firmness is important for the evaluation of fruit maturity, as softening indicates onset of ripening, thus affecting the potential for transport and storage; it is also an important sensory quality characteristic. Changes in fruit texture are due to changes in pectic substances in the middle lamella of cell walls and are cultivar-related (Selvaraj and Kumar, 1989; Maldonado-Celis *et al.*, 2019). Softening of mango fruit is characterized by increased solubility of cell wall pectins (Roe and Bruemmer, 1981; Tandon and Kalra, 1984; Lazan *et al.*, 1986; Nasrijal, 1993). In general, water-soluble polysaccharides increase during ripening (Lazan *et al.*, 1986; Brinson *et al.*, 1988), water- and alkali-soluble pectins decline and ammonium oxalate-soluble pectins increase as the fruit soften (Roe and Bruemmer, 1981). In mango, there is an overall loss of galactosyl and deoxyhexosyl residues during fruit ripening, the latter indicating degradation of the pectin component of the wall (Muda *et al.*, 1995). The loss of galactose appears to be restricted to the chelator soluble fraction of the wall pectin, while loss of deoxyhexose seems to be more evenly distributed among the pectin.

Pectinesterase (EC 3.1.1.11; PE), which catalyses the de-esterification of methyl groups from acidic pectins, has been detected in ripening mangoes (Tahir and Malik, 1977; Roe and Bruemmer, 1981; Ali *et al.*, 1990, 1995; Abu-Sarra and Abu-Goukh, 1992). Physiological maturity in mangoes is associated with lower PE activity (Van Lelyveld and Smith, 1979) and peel has higher PE activity than flesh (Ashraf *et al.*, 1981). Endo-polygalacturonase, which is responsible for degrading the 1-4-linked galacturonic acid residues, occurs in ripening fruit (Abu-Sarra and Abu-Goukh, 1992; Lazan *et al.*, 1986, 1993). Enzymatic and/or non-enzymatic processes, in addition to PG activity, are involved in the extensive softening of mango fruit (Mitcham and McDonald, 1992). Other cell wall hydrolases can be detected in ripening mango fruit, i.e., cellulases (EC 3.2.1.4; Lazan *et al.*, 1986; Abu-Sarra and Abu-Goukh, 1992), β-galactosidase (EC 3.2.1.23; Ali *et al.*, 1990, 1995; Lazan *et al.*, 1993), galactanase (EC 3.2.1.145; Ali *et al.*, 1990) and xylanase (EC 3.2.1.8; Ali *et al.*, 1990).

Ripening in mangoes, as characterized by decreased tissue firmness, is initiated in inner mesocarp tissue close to the seed and progresses outwards (Lazan *et al.*, 1993). Pectin solubilization of inner and outer mesocarp tissues is comparable, but begins earlier in the inner mesocarp (Lazan *et al.*, 1993). The outer mesocarp of 'Keitt' was found to remain firm for longer than in 'Tommy Atkins' and the inner mesocarp was softer than the outer mesocarp at each stage of ripening in both cultivars (Mitcham and McDonald, 1992). Cell wall neutral sugars, particularly arabinosyl, rhamnosyl and galactosyl residues, decreased with ripening in both cultivars. Ripe 'Keitt' fruit had higher concentrations of loosely associated, chelator-soluble pectin, soluble polyuronides and total pectin than 'Tommy Atkins'. Both cultivars had similar PG activity, which increased with ripening. The amount and molecular weight of cell wall hemicellulose decreased with ripening in both cultivars. Galactose was the only cell wall neutral sugar to show a significant decrease during ripening of 'Sensation' mangoes (Seymour *et al.*, 1990). Losses of neutral sugars can be due to hydrolysis of galactans and arabinogalactans by β-galactosidase having galactanase activity. β-Galactosidase activity shows a parallel increase with tissue softening during ripening.There are close correlations in mango fruit between the increases in β-galactosidase amount and activity and the progression of tissue softening and pectin solubilization and degradation during ripening (Ali *et al.*, 1995). This suggests that β-galactosidase has an important role in cell wall pectin modification and mango fruit softening during ripening.

Postharvest treatments, e.g., refrigeration, packaging, application of fruit coatings, etc., can retard mango fruit softening and activity of pectinases (Lazan *et al.*, 1990; Nasrijal, 1993; Yahia, 2011; Brecht and Yahia, 2017). Calcium (Ca) joins free carboxyl groups resulting from PE-catalysed hydrolysis of methyl ester bonds to form Ca-bridges between adjacent pectin molecules. When 'Haden' was dipped in or inflitrated with Ca, its storage life was extended by 1 week (Zambrano and Manzano, 1995). The technique of postharvest vacuum application of Ca to mango has also been reported by Tirmazi and Wills (1981), Wills *et al.* (1988), van Eeden (1992), and Yuen *et al.* (1993). Vacuum infiltration of 1–4% $CaCl_2$ at 300 mm Hg (40 kPa) into 'Amrapali' and 'Dashehari' mangoes ripened at 25°C, inhibited PG activity, while ethylene treatment at 1 µl/l markedly increased PG activity (Reddy and Srivastava, 1999). Pressure (115 kPa for 2 min) or vacuum infiltration (32 kPa) with 1-8% $CaCl_2$ delayed ripening of 'Kensington Pride' by 12 or 8 days, respectively; they also reported that vacuum infiltration of $CaCl_2$ caused some peel injury, which could be reduced by: (1) increasing the temperature of the fruit flesh or the $CaCl_2$ solution during pressure infiltration; (2) packaging the fruit in sealed polyethylene during pressure infiltration; and (3) packaging the fruit in sealed polyethylene bags or cling or shrink wraps after $CaCl_2$ treatment. Calcium chloride infiltration of 'Keitt' mangoes reduced ethylene production, respiration rate and the incidence of storage decay (van Eeden, 1992).

21.4.4 Pigments and colour

Mango peel colour is important for its role in the perception of overall quality (González-Aguilar *et al.*, 2001; Yahia, 2011; Brecht and Yahia, 2017) and can be important for determining the appropriate maturity for harvesting or processing and the stage or ripeness for consumption (Cocozza *et al.*, 2004; Mahayothee *et al.*, 2004; Jha *et al.*, 2007). The degreening of peel colour is a sign of fruit ripening in many mango cultivars and complete and uniform degreening is an indication of mango quality (Yahia, 2011; Brecht and Yahia, 2017). However, some mango cultivars retain green peel (e.g., 'Keitt', 'Tongdum', 'Dasheri', 'Langra', 'Fazli' and 'Katchamita') or flesh (e.g., 'Aromanis') in the ripe fruit. Depending on the cultivar, peel colour can change from dark to olive-green; sometimes reddish, orange-yellow or yellowish hues appear from the base colour. Some cultivars develop a reddish blush, which has been attributed to anthocyanins. Changes in mango peel colour

during ripening are due to the disappearance of chlorophyll and the appearance of other pigments (Fig. 21.4). In this process the well-arranged grana and osmiophilic globules in epidermal cell chloroplasts lose their integrity and the chloroplasts are transformed to chromoplasts containing yellow or red pigments (John *et al*., 1970; Lakshminarayana, 1980; Parikh *et al*., 1990; Lizada, 1993). In yellow peel cultivars, carotenoids and xanthophylls are the predominant pigments, but anthocyanin paenoidin-3-galactoside occurs in some cultivars (Proctor and Creasy, 1969). The chlorophyll concentration was shown to decrease in the green ripe cultivar 'Keitt' during ripening; however, carotenoid concentration increased and anthocyanin decreased gradually during ripening of the more typical cultivar, 'Tommy Atkins' (Medlicott *et al*., 1986). In 'Keitt', a substantial loss of chlorophyll in the peel occurs after the fruit begin to soften. Peel colour is not an adequate maturity index, however, since the fruit is already soft when the colour change occurs. 'Tommy Atkins' fruit develop more red and yellow pigmentation in the peel and mesocarp than 'Keitt' (Mitcham and McDonald, 1992).

In all mango cultivars the fruit flesh (mesocarp) contains high concentrations of carotenoids (up to 9 mg/100 g), producing an intense yellow to orange colour, which serves as an excellent maturity index as well as being a good source of vitamin A (Maldonado-Celis *et al*., 2019; Yahia *et al*., 2023). As for fruit softening, the development of yellow to orange flesh colour begins in inner mesocarp tissue close to the seed and progresses outwards, forming the basis for the common commercial maturity rating that ranges from 1 (zero progression) to 5 (100% progression) of the colour development across the mesocarp. The flesh carotenoid concentrations are cultivar-ependent. In 'Alphonso', 16 fractions of carotenoids have been reported: 50% of those are β-carotene (Jungalwala and Cama, 1963; John *et al*., 1970). No qualitative changes in carotenoid composition have been reported for 'Keitt' and 'Tommy Atkins' between the mature-green and ripe stages, although quantitative changes occur (Mercadante and Rodriguez-Amaya, 1998); however, John *et al*. (1970) detected 15, 14 and 17 carotenoids in 'Badami' mangoes at mature-green, partially ripe and fully ripe stages of fruit, respectively. Variation with respect to reported pigment types and their concentrations is likely due to differences in cultivar, geography and climate, maturity and postharvest treatments.

Mango peel colour can be used to estimate the content of all-*trans*-β-carotene (Vázquez-Caicedo *et al*., 2004), the most important provitamin A carotenoid (Wolf, 1984). Ornelas-Paz *et al*., (2007) demonstrated that external (peel) and internal (flesh) colours are similar in the non-blushed cultivars 'Manila' and 'Ataulfo' and contrasted with the blushed cultivars 'Criollo', 'Paraíso' and 'Kent'. The carotenoids in fruit peel of some mango cultivars can be correlated with some non-destructive colour measurements (Table 21.3; Figs 21.5 –21.7, Ornelas-Paz *et al*., 2008).

In mango the most abundant carotene is all-*trans*-β-carotene, while the most abundant xanthophylls are violaxanthin and its isomers (Wilberg and Rodriguez-Amaya, 1995; Chen *et al*., 2004; Maldonado-Celis *et al*., 2019). Mercadante *et al*. (1997) quantified many cartenoids in 'Keitt' and concluded that the most predominant xanthophylls were all-*trans*-violaxanthin and 9-*cis*-violaxanthin, accounting for 38% and 18% of total carotenoid content, respectively, although other xanthophylls are common in other cultivars (Ben-Amotz and Fishler, 1998; Setiawan *et al*., 2001).

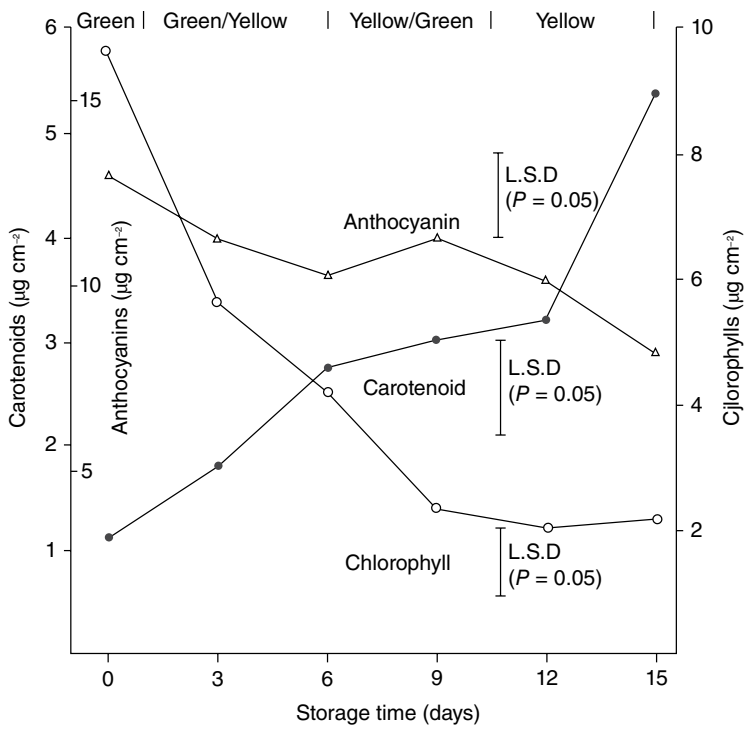

Fig. 21.4. Carotenoid, anthocyanin and chlorophyll concentrations in the peel of 'Tommy Atkins' mango during ripening at 22°C (Medlicott *et al*., 1986).

Table 21.3. Correlation coefficients (*R*) for the relationships between the content of the main carotenoids in mesocarp and the internal/external colour values in 'Ataulfo' and 'Manila' mango fruit. The correlation analysis was performed using α= 0.5 (Ornelas-Paz *et al*., 2008)

'Ataulfo'			
Colour value	all-*trans*-violaxanthin	9-*cis*-violaxanthin	all-*trans*-β-carotene
a*	0.84/0.90	0.83/0.87	0.90/0.90
b*	-0.05/0.41	0.00/0.41	-0.05/0.45
L*	-0.75/0.19	-0.75/0.21	-0.80/0.27
C*	0.31/0.71	0.34/0.70	0.33/0.72
h°	-0.88/-0.89	-0.86/-0.87	-0.94/-0.90
'Manila'			
	all-*trans*-violaxanthin	9-*cis*-violaxanthin	all-*trans*-β-carotene
a*	0.92/0.87	0.93/0.89	0.86/0.81
b*	0.76/0.69	0.75/0.67	0.67/0.54
L*	-0.86/0.35	-0.86/0.32	-0.74/0.18
C*	0.81/0.74	0.81/0.73	0.73/0.61
h°	-0.90/-0.89	-0.92/-0.91	-0.82/-0.82

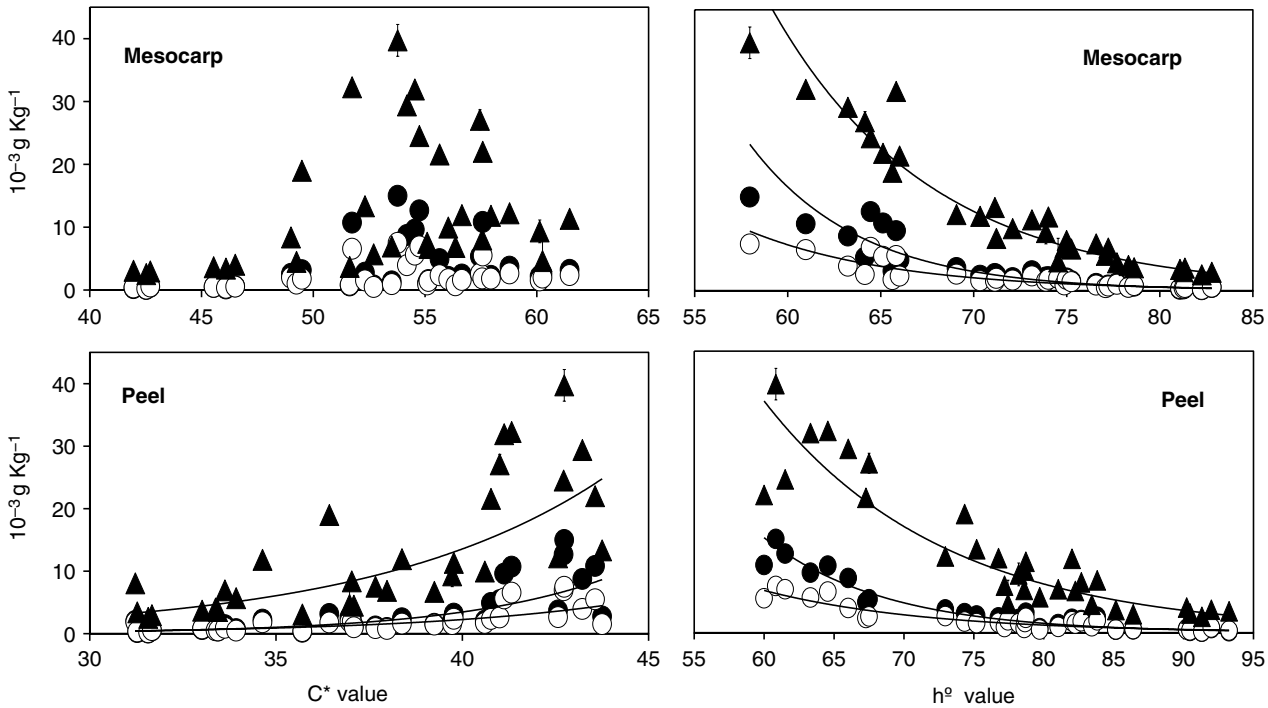

Fig. 21.5. Relationships between the content of all-*trans*-β-carotene (▲), all-*trans*-violaxanthin (as dibutyrate, ●), 9-*cis*-violaxanthin (as dibutyrate, ○) in mesocarp and the C* and h° values, measured in mesocarp or peel of 'Manila' mango fruit during ripening. Each point represents the mean of two independent measurements ± the standard error (vertical bars). The continuous line represents an exponential or second order polynomial regression (Ornelas-Paz *et al*., 2008).

Modi and Reddy (1967) reported an increase during mango ripening of the carotene precursors, mevalonic acid (MVA) and geraniol, with a concomitant increase in carotene content. The geraniol concentration of unripe 'Alphonso' mangoes varies from 0.5 to 3.0 µmol with 0.0 to 0.5 µmol MVA; in ripe mangoes the corresponding levels are 5–10 and 1–5 µmol, respectively. The increase in free geraniol and MVA indicates that these compounds are dephosphorylated during ripening. Acid phosphatase (EC 3.1.3.2) may regulate carotenogenesis in ripe mangoes (Mattoo *et al*., 1968). Mangoes stored at low temperatures and then ripened at room temperature fail to synthesize as many carotenoids as fruit stored at room temperature (Krishnamurthy and Subramanyam, 1973; Thomas, 1975). Hot water treatments increase the colour intensity of the flesh (Medlicott *et al*., 1986) and the peel (Esguerra and Lizada, 1990).

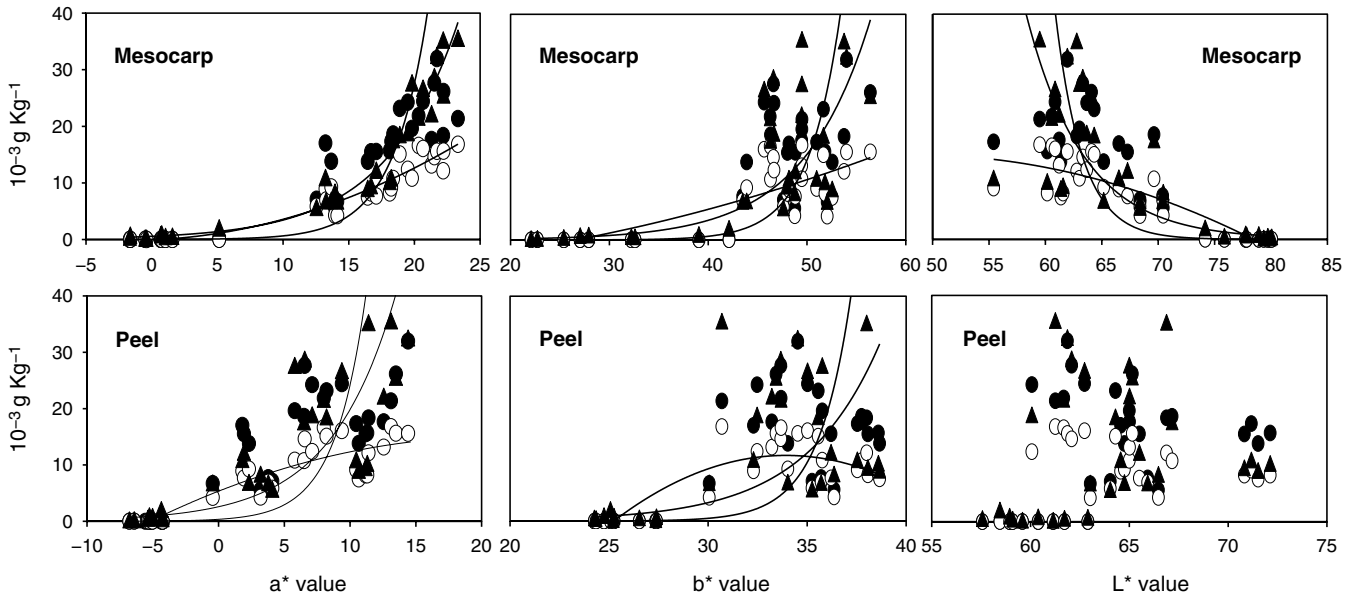

Fig. 21.6. Relationships between the content of all-*trans*-β-carotene (▲), all-*trans*-violaxanthin (as dibutyrate, ●), 9-*cis*-violaxanthin (as dibutyrate, ○) in mesocarp and the a*, b* and L* values, measured in mesocarp or peel of 'Manila' mango fruit during ripening. Each point represents the mean of two independent measurements ± the standard error (vertical bars). The continuous line represents an exponential or second order polynomial regression (Ornelas-Paz *et al.*, 2008).

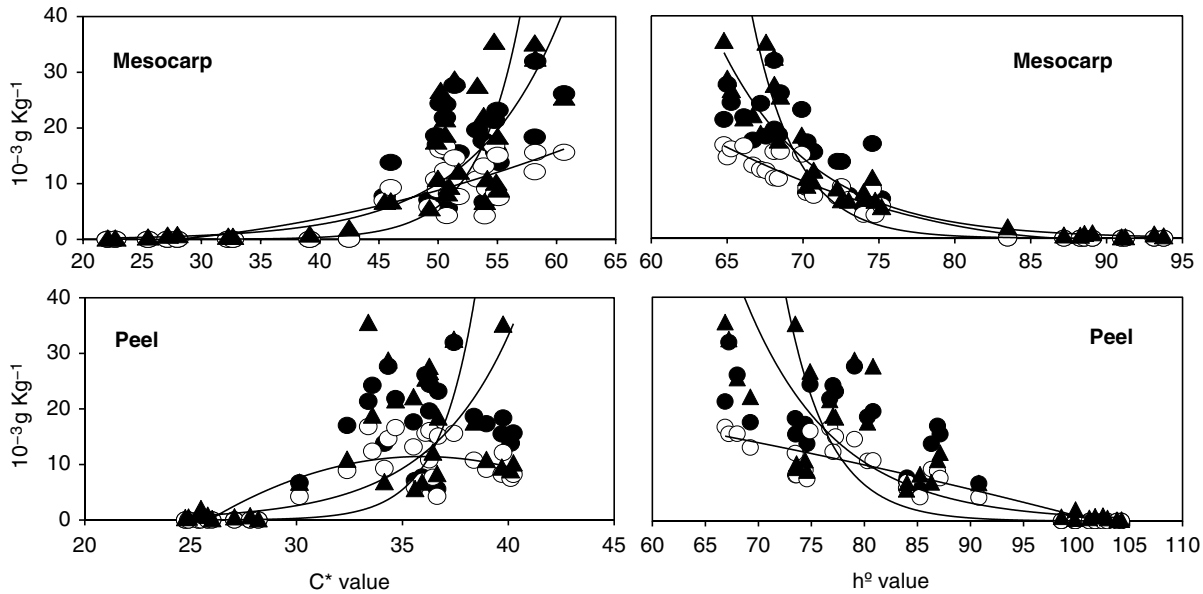

Fig. 21.7. Relationships between the content of all-*trans*-β-carotene (▲), all-*trans*-violaxanthin (as dibutyrate, ●), 9-*cis*-violaxanthin (as dibutyrate, ○) in mesocarp and the C* and h° values, measured in mesocarp or peel of `Manila` mango fruit during ripening. Each point represents the mean of two independent measurements ± the standard error (vertical bars). The continuous line represents an exponential or second order polynomial regression (Ornelas-Paz *et al.*, 2008).

'Tongdum' mangoes, which ripen without changing the green peel colour, have threefold more chlorophyll and slightly more β-carotene in the peel and have higher rates of ethylene production compared with 'Nam Dok Mai' mangoes, in which the peel colour changes from green to yellow upon ripening (Ketsa *et al.*, 1999). Activities of chlorophyllase (EC 3.1.1.14) and peroxidase in the peel of ripe 'Tongdum' fruit are about half of that in 'Nam Dok Mai' fruit. Changes in the peel of ripe

green mangoes are due to either or both a lower activity of chlorophyllase or peroxidase activity and are not a result of low ethylene production.

21.4.5 Phenolic compounds

Phenolic concentrations in mango peak in early fruit development, then decrease to ripening where they remain fairly steady during ripening (Lakshminarayana *et al.*, 1970; Maldonado-Celis *et al.*, 2019; Yahia *et al.*, 2023). This is associated with loss of astringency (Selvaraj and Kumar, 1989). The peel of mango fruit has a higher phenolic content than the flesh at all stages of fruit development (Jain, 1961; Lakshminarayana *et al.*, 1970).

Polyphenol oxidase (EC 1.14.18.1; PPO) catalyses the oxidation of mono- and di-phenols to *o*-quinones, which polymerize to produce brown pigments. After harvest the PPO activity was found to increase slightly up to the half-ripe stage and then decline in 'Banganapalli', 'Dasheri', 'Fazli' and 'Langra', while PPO activity was found to decrease in 'Alphonso', 'Suvarnarekha', and 'Totapuri' mangoes (Selvaraj and Kumar, 1989). The PPO isolated from 'Haden' mango was demonstrated to be active towards the o-diphenolic compounds, showing higher activity in the presence of catechol, followed by chlorogenic acid, but not with monophenols (Park *et al.*, 1980).

21.4.6 Flavour (taste, aroma)

Sugar changes are very important for organoleptic attributes in the mango fruit (Maldonado-Celis *et al.*, 2019). Fruit flavour is mostly a balance between the content of sugars and organic acids (Medlicott and Thompson, 1985) as well as aromatic volatiles. Kapse *et al.* (1989) determined that increasing TSS and decreasing TA increases flavour ratings of mango fruit. Sucrose is the predominant sugar in ripe mango fruit (Tandon and Kalra, 1983; Medlicott and Thomson, 1985; Vazquez-Salinas and Lakshminarayana, 1985). The predominant acid in mango fruit is citric (Medlicott and Thompson, 1985; Lizada, 1993). Several factors affect sugar and acid contents in mango, including cultivar (Kapse *et al.*, 1989; Kundu and Gosh, 1992; Gowda *et al.*, 1994), stage of maturity at harvest (Shashirekha and Patwardhan, 1976; Morga *et al.*, 1979; Tandon and Kalra, 1983), postharvest treatments (Kumar *et al.*, 1993) and storage conditions (Vazquez-Salinas and Lakshminarayana, 1985).

Ripe mangoes contain >300 volatiles (Pino *et al.*, 2005), but not all of them are odour-active and thus do not contribute significantly to aroma. Several studies have identified the volatiles of mango, but not their aromatic activity. The predominant volatiles in some cultivars are monoterpenes and sesquiterpenes (MacLeod and De Troconis, 1982; Engel and Tressl, 1983; Pino *et al.*, 2005), as well as lactones and some fatty acids (MacLeod and Pieris, 1984; MacLeod and Snyder, 1985; Wilson *et al.*, 1990). However, there is no indication of the presence of a single flavour impact component (Engel and Tressl, 1983). Some mango cultivars have a peach-like flavour that may be related to the presence of lactones, which contribute to the flavour of peaches (*Prunus persica*) (Lakshminarayana, 1980; MacLeod *et al.*, 1988, Wilson *et al.*, 1990). MacLeod *et al.* (1988) detected four lactones in 'Kensington Pride' that are also the major volatiles of peach. Monoterpene hydrocarbons represent about 49% (w/w) of the total volatiles in 'Kensington Pride', with α-terpinolene being the most abundant (26%) and 16 esters representing 33% (MacLeod *et al.*, 1988). The esters, together with some of the lactones, contribute to the flavour of 'Kensington' mangoes.

Indian mangoes have a unique flavour, which has been attributed to (Z)-ocimine (Engel and Tressl, 1983; Lizada, 1993). Pino *et al.* (1989) detected 83 volatiles in 'Corazon', 'Bizcochuelo' and 'Super Haden' mangoes, and total volatiles ranged between 39 mg/kg in 'Bizcochuelo' to 70 mg/kg in 'Corazon'. The identified volatiles include α-cubebene, β-maaliene, ethyl(Z)-9-hexadecanoate, ethyl(Z)-9,12-octadecanoate, ethyl(Z)(Z)(Z)-6,9,12-octadecanoate, cucarvone, 2-methylpropane-2-ol, 3-methylepentan-ol, thymol and carvacrol (Pino *et al.*, 1989). MacLeod and Snyder (1985) listed the volatile components of several mango cultivars including 'Willard' and 'Parrot' from Sri Lanka, and reported that levels of α-terpinolene were similar to those in 'Kensington Pride'.

Kostermans and Bompard (1993) considered lack of fibre in mango mesocarp tissue to be linked to an absence of aroma and flat taste and smell, but some cultivars such as 'Kensington Pride' that are low in fibre have a distinctive flavour and aroma profile, including a high level of the aroma volatile α-terpinolene (Bartley and Schwede, 1987; MacLeod *et al.*, 1988). Lipid content of the flesh is correlated with the flavour characteristics of some mango cultivars (Bandyopadhyay and Gholap, 1973a; Gholap and Bandyopadhyay, 1975b, 1976). The ripening of 'Alphonso' mangoes at ambient temperature is accompanied by a sharp increase in triglyceride content, together with the development of a strong aroma and flavour (Gholap and Bandyopadhyay, 1976), but ripening at 10°C results in a bland aroma and flavour (Bandyopadhyay and Gholap, 1973b). 'Totapuri' mangoes, a bland cultivar, showed no change in the development of aroma or in the flesh lipid content (Gholap and Bandyopadhyay, 1975b). During ripening at ambient temperature, palmitoleic acid content is higher than that of palmitic acid in 'Alphonso', whereas ripening at low temperature does not affect the proportions of these two fatty acids (Bandyopadhyay and Gholap, 1973b). The relative proportions of palmitoleic and palmitic acids in 'Totapuri' mango flesh are constant, irrespective of the ripening conditions (Gholap and Bandyopadhyay, 1975b). Gholap and Bandyopadhyay (1976, 1980) suggested that the relative contents of palmitic and palmitoleic acids determine the flavour quality of mango fruit.

The absence of lactones having coconut-like odour notes in 'Totapuri' mangoes may be significant for differentiating its aroma characteristics from 'Alphonso', together with the presence of certain similar and dissimilar components (Bandyopadhyay, 1983). The aroma of green mangoes has been attributed to *cis*-ocimine in 'Alphonso' and β-myrcene in 'Batali' mangoes (Gholap and Bandyopadhyay, 1976; Bandyopadhyay, 1983). Table 21.4 lists characteristic aromas of 'Alphonso' and 'Totapuri' mangoes and their possible chemical identities.

Table 21.4. Characteristic aromas in 'Alphonso' and 'Totapuri' mangoes and their possible chemical causes (Bandyopadhyay, 1983).

Aroma	'Alphonso'	'Totapuri'
Fruity, estery	Acetaldehyde Methyl acetate, Ethyle acetate, n-Butyl acetate	Propionaldehyde Methyl acetate
Green-mango-like	*cis*-Ocimine	β-Myrcene
Camphoraceous	Not detected	Detected, but not identified
Earthy	Caryophyllene-pinene	Not detected
Almond-like	Benzaldehyde	Not detected
Burnt-sugar-like	Benzonitrile	Not detected
Spicy	Not detected	α-terpinene
Sweet, sugar-like	Detected, but not identified	Not detected
Coconut oil-like	α-Caprolactone, α-Octalactone, α-Undecalactone	

In almost all fruits, aromatic volatiles are produced at later stages of ripening (Yahia, 1994). Tree-ripe 'Tommy Atkins' mangoes produce much higher levels of all aroma volatiles except hexanal than do mature-green fruit (Bender *et al.*, 2000a). Both mature-green and tree-ripe mangoes stored in 25 kPa CO_2 tended to have lower terpene (especially p-cymene) and hexanal concentrations than those stored in 10 kPa CO_2 and in regular air. Acetaldehyde and ethanol levels tended to be higher in tree-ripe mangoes held in 25 kPa CO_2 than in those held in 10 kPa CO_2 or air, especially at 8°C. Inhibition of volatile production by 25 kPa CO_2 was greater in mature-green than in tree-ripe mangoes, and at 8°C compared with 12°C for tree-ripe fruit. However, aroma volatile levels in tree-ripe mangoes held in 25 kPa CO_2 were equal or greater than those in mature-green fruit treatments. Bender *et al.* (2000a) concluded that atmospheres that prolong mango postharvest life by slowing ripening processes can allow tree-ripe mangoes to be stored or shipped without sacrificing their aroma quality.

Quality enhancement has been used to determine properties critical to flavour acceptability of mangoes, and focus group interviews have been conducted to determine sensory attributes important to mango purchase and consumption (Malundo, 1996). Sugars and acids enhance perception of specific flavour notes in mango, including the aroma (Malundo *et al.*, 2001). Sung *et al.* (2019) identified the fruity esters, 1-octanol, (E,Z)-2,6-nonadienal, and γ-octalactone, along with high sugar content as contributing to hedonic liking for 'Glenn', 'Mamme' and 'Saigon' mango fruit, while high contents of amino acids and terpenes were associated with low liking.

21.5 Transpiration and Water Loss

Water loss lowers fruit weight, resulting in shrivelling, and may further reduce quality by causing poor colour development and uneven ripening (Brecht and Yahia, 2017). Water is lost from mango fruit through stomata, lenticels and other openings. Relative humidity (RH) inside the fruit is 100% and water is lost when RH surrounding the fruit is <100%. Water loss is also greatly influenced by temperature. With constant RH and air movement, water loss increases significantly with increase in temperature. Transpiration rate is influenced by cultivar and ripeness stage. It is correlated with peel thickness, morphological structure, epidermal cells and surface wax coating. For example, waxes usually develop on the epidermis of fruit in the later stages of development and thus it is common for fruit harvested early to shrivel faster compared with those harvested at a more advanced stage of development (Yahia *et al.*, 2006a).

Mangoes are susceptible to physical damage at every step of the postharvest handling chain (see Chapter 22, this volume) and reduction/elimination of mechanical injury is essential to reduce qualitative and quantitative losses. Mango fruit are susceptible to various physiological disorders that influence fruit quality (Brecht, 2018). These disorders are either induced or inherent, and several of them become apparent during fruit ripening. Disorders, such as CI and heat injury (HI), may be induced after harvest. Inherent physiological disorders include 'spongy stem-end' in 'Kensington Pride' (Brown *et al.*, 1981), 'soft nose' in Florida cultivars (Young, 1957) and 'internal breakdown', 'spongy tissue' or 'soft nose' in the Indian 'Alphonso' cultivar (Subramanyam *et al.*, 1971).

21.6 Temperature Injury

21.6.1 Chilling injury (CI)

Low storage/shipping temperatures can injure mango fruit, especially at the mature-green stage, if exposure duration exceeds a day or so at or near 0°C to a few weeks at just below 12°C. This problem limits the use of low storage/shipping temperature to manage postharvest ripening and seriously affects the ability of handlers to store mangoes or transport them over long distances, because temperatures that are low enough to delay ripening, decay and senescence can damage the fruit. The symptoms of CI include red to brown lenticel discoloration, greyish scald-like discoloration on the peel, followed by peel pitting, uneven ripening and poor flavour, aroma and colour development (Hatton *et al.*, 1965; Medlicott *et al.*, 1990; Pesis *et al.*, 1997). The symptoms are often not apparent

during exposure to low temperature, but develop later, when the fruit are brought to warmer temperatures for ripening or are displayed for sale. Symptoms in mango fruit held at room temperature for 1–2 days after low temperature storage were described as discoloured and pitted areas on the surface (Srivastava, 1967; Kane, 1977) followed by increased susceptibility to microbial spoilage (Sadasivam *et al.*, 1971; Subramanyam *et al.*, 1975). Inhibition of aroma development is the most sensitive CI symptom, such that mild chilling exposure may result in fruit without visible CI symptoms, but which lack flavour (aroma) (Nair and Singh, 2004; Dea *et al.*, 2010).

Chilling susceptibility varies with cultivar (Farooqui *et al.*, 1985); 'Ataulfo' ('Honey'), 'Haden' and 'Keitt' are particularly susceptible. 'Sensation' developed more peel symptoms than 'Sammar Bahisht' mangoes (Farooqui *et al.*, 1985). While CI has generally been reported to occur in mature-green mango fruit at temperatures below about 10–13°C (Mukherjee, 1958; Akamine, 1963; Hatton *et al.*, 1965; Musa, 1974; Couey, 1986), some cultivars, i.e., 'Dasheri' and 'Langra', were reported to be safely stored at 7–8°C for up to 25 days (Mann and Singh, 1976). While most cultivars show injury at <10°C if fruit have just reached maturity, tolerance of CI increases as fruit ripen (Medlicott *et al.*, 1990; Mohammed and Brecht, 2002). Tolerance of 'Keitt' and 'Tommy Atkins' fruit to CI was induced by pre-storage heat treatments (McCollum *et al.*, 1993; Pesis *et al.*, 1997).

21.6.2 Heat injury (HI)

Mango is highly tolerant of heat (Yahia *et al.*, 2000; Jacobi *et al.*, 2001b), therefore heat (hot water or hot air) is commonly used to control decay and insects after harvest (Yahia, 2011; Brecht and Yahia, 2017). However, exposure to temperatures higher than tolerated by the fruit (>30°C for >10 days for air; >48°C for >1 h for water) can lead to injury. The heat disinfestation treatments of mangoes that are used for decay control or insect quarantine security can injure fruit that are not fully mature, if the treatment is not applied correctly, or if the fruit are not cooled adequately immediately after the treatment (Jacobi and Giles, 1997; Jacobi *et al.*, 2001a; Yahia, 2011; Brecht and Yahia, 2017; Brecht, 2018).

External symptoms of HI include lenticel spotting and peel browning ('scald') with secondary disease development, while internal symptoms include mesocarp browning, tissue cavitation and 'starch spots'. Ripening of heat-injured mangoes can also be inhibited (Jacobi and Wong, 1992; Jacobi and Giles, 1997; Mitcham and McDonald, 1997; Jacobi *et al.*, 2001a, b; Brecht and Yahia, 2017; Brecht, 2018).

21.7 Modified and Controlled Atmospheres (MA and CA)

Long-term marine shipping of mangoes in MA and CA has been used for transit from several countries (Yahia, 1993, 2009; Brecht, 2020). Research results are contradictory due to the different cultivars and maturity stages of the mangoes used, different atmospheres implemented and lack of experimental controls. The most commonly recommended optimum atmosphere conditions for prolonged shipping or storage of mangoes are reported to be 3–5 kPa O_2 and 5–10 kPa CO_2, which can delay ripening (Brecht, 2020). The benefits may not be significant during storage but may be beneficial during marine transport for 2 weeks or more, depending on MA/CA system used, cultivar, fruit maturity/ripening stage, treatment duration, temperature and RH, among other factors.

Bender *et al.* (2000c) determined the tolerance of preclimacteric 'Haden' and 'Tommy Atkins' fruit to reduced O_2 levels for storage times in typical marine shipments. They reported that mangoes can tolerate 3 kPa O_2 for 2–3 weeks at 12-15°C and tolerance of low O_2 decreases as mangoes ripen. All low O_2 treatments reduced mature-green mango respiration; however, elevated ethanol production occurred in 2 and 3 kPa O_2 storage, with the levels two- to threefold higher in 'Tommy Atkins' than in 'Haden'. 'Haden' fruit at the onset of the climacteric accumulated ethanol in 4 kPa O_2 and produced 10–20× more ethanol in 2 and 3 kPa O_2 than preclimacteric fruit. There were no visible injury symptoms, but off-flavour developed in mature-green fruit at 2 kPa O_2 and in ripening-initiated fruit at 2 and 3 kPa O_2. Ethanol production was not affected by storage in 25 kPa CO_2. Ethylene production was reduced slightly by low O_2; however, 'Haden' fruit also showed a residual inhibitory effect on ethylene production at 2 or 3 kPa O_2 storage, while 'Tommy Atkins' fruit stored in 2 kPa O_2 produced a burst of ethylene after transfer to air at 20°C. Fruit firmness, total sugars and starch levels did not differ among treatments, but 2, 3 or 4 kPa O_2 and 25 kPa CO_2 maintained significantly higher acidity than 5 kPa O_2 or air. The epidermal ground colour responded differently to low O_2 and high CO_2 in both cultivars. Only 2 kPa O_2 maintained 'Haden' colour better than air, while all low O_2 levels maintained 'Tommy Atkins' colour better than air. High CO_2 was more effective than low O_2 in maintaining 'Haden' colour, but had about the same effect as low O_2 on 'Tommy Atkins'.

Correctly selected atmospheres, which prolong mango postharvest life by slowing ripening processes, can allow tree-ripe fruit to be stored or shipped without sacrificing their superior aroma. Mature-green and tree-ripe 'Tommy Atkins' mangoes were stored for 21 days in air or in a CA (5 kPa O_2 + 10 kPa or 25 kPa CO_2) at 12°C (mature-green) or at either 8 or 12°C (tree-ripe) (Bender *et al.*, 2000a). Tree-ripe mangoes produced much higher levels of all aroma volatiles than mature-green fruit after ripening for 2 days except for hexanal. Both mature-green and tree-ripe mangoes stored in 25 kPa CO_2 had lower terpene (especially p-cymene) and hexanal levels than those stored in 10 kPa CO_2 and air-stored fruit. Acetaldehyde and ethanol levels were higher in tree-ripe mangoes from 25 kPa CO_2 than in those from 10 kPa CO_2 or air storage, especially at 8°C. Inhibition of volatile production by 25 kPa CO_2 was greater in mature-green than in tree-ripe mangoes, and at 8°C compared with 12°C for tree-ripe fruit. Aroma volatile concentrations in tree-ripe fruit from the 25 kPa CO_2 treatment equalled or exceeded those in mature-green fruit treatments.

Mangoes have high tolerance of short-term elevated CO_2 atmospheres (Yahia, 1998). Mangoes can tolerate CO_2 atmospheres of up to 25 kPa for 2 weeks at 12°C (Bender *et al*., 2000c). High (25 kPa) CO_2 inhibited ethylene production, but increased ethanol production. Aroma volatiles were reduced following 25 kPa CO_2 treatment, while 10 kPa CO_2, low O_2 atmospheres and storage temperature did not significantly influence production of terpene hydrocarbons, which are characteristic of Florida-type mangoes. Mature-green 'Tommy Atkins' mangoes could be stored for 21 days in CA (5 kPa O_2 + 10 kPa or 25 kPa CO_2) at 12°C, while tree-ripe fruit could be stored for 21 days in the same atmospheres at either 8 or 12°C (Bender *et al*., 2000a).

Teixeira *et al*. (2018) stored 'Palmer' mangoes in CA with low O_2 (5 kPa) and different CO_2 levels (0, 1, 5, 10, 15 and 20 kPa) at 12°C for 30 days followed by shelf life at 25°C for 5 days. They found no differences in respiration rates among the CA treatments. The CA treatments (5 kPa O_2 + 15 kPa CO_2 and 5 kPa O_2 + 20 kPa CO_2) exhibited higher respiration rates during shelf life, while no differences were observed in colour, firmness, carbohydrates and physicochemical attributes. Mangoes ripened normally without showing any signs of CO_2 injury, but higher CO_2 did not improve fruit quality nor did it present a synergistic effect with low O_2 (5 kPa).

Rao and Rao (2008) evaluated the effects of pre-storage hot water treatment (52°C for 5 min) prior to CA storage (at 5 kPa O_2 + 5 kPa CO_2; 3 kPa O_2 + 5 kPa CO_2; 5 kPa O_2 + 3 kPa CO_2; or 3 kPa O_2 + 3 kPa CO_2) for 'Banganapalli' and 'Alphonso' fruit stored at 13°C and 85–80% RH for 30 days followed by shelf life in air at 25°C for 6 days. They reported O_2 at 5 kPa reduced respiration and ethylene production rates whereas 3 kPa O_2 + 5 kPa CO_2 for 'Alphonso' and 3 kPa O_2 + 3 kPa CO_2 for 'Banganapalli' induced abnormal respiration and ethylene production rates indicative of fermentative metabolism. Following CA storage, the mangoes ripened normally, exhibiting better peel colour, with higher firmness, TSS, sugar contents and total carotenoids, plus acceptable organoleptic quality. Overall, 5 kPa O_2 + 5 kPa CO_2 for 'Alphonso' and 5 kPa O_2 + 3 kPa CO_2 for 'Banganapalli' increased storage life by 4 and 5 weeks, respectively. Hot water treatment before CA resulted in higher amounts of ascorbic acid and carotenoids in both mango cultivars at the end of the storage and shelf life periods.

Low O_2 tolerance limits (1, 5, 10 kPa O_2) for 'Shelly' mangoes were evaluated by Ntsoane *et al*. (2019) in terms of quality attributes, including pigments and volatile organic compounds (VOCs). They found that O_2 restricted production of many VOCs with storage at 13°C for 21 days followed by shelf life in air at 18°C for 7 days. They reported that low O_2 did not affect pigment contents, while TSS and individual sugars increased during storage. The 1 kPa O_2 treatment resulted in accumulation of anaerobic metabolites (ethanol, ethyl acetate, 3-hydroxy-2-butanone, ethyl butanoate, 1-butanol, 2, 3-butanediol, ethyl propanoate, 2, 3-butanediol, undecane) and sensory panellists rejected those fruit due to undesirable odour and taste. They determined that 5 kPa is the low O_2 limit for 'Shelly' mangoes, below which anaerobic metabolites accumulated and compromised the fruit marketability, whereas storage at 10 kPa O_2 reduced respiration rates and fruit mass loss, and maintained firmness, TSS and individual sugars.

Mangoes harvested tree-ripe develop prime quality compared with mature-green harvested mangoes. Bender *et al*. (2021) determined the effect of fruit ripeness (tree-ripe *versus* mature-green mangoes), storage temperature (5, 8, 12, or 15°C) and CA conditions (with 2, 5, or 21 kPa O_2 plus 0, 10, or 25 kPa CO_2) on the volatiles comprising the aroma profile of 'Haden', 'Keitt' and 'Tommy Atkins'. They reported that terpene concentrations were lower in mangoes stored under CA compared with air control. The sesquiterpene α-copaene and the monoterpenes did not present recognizable peaks (in 'Haden' and 'Keitt') in almost all elution sequences, whereas 'Tommy Atkins' had β-pinene concentrations <1.06 µl/l. CA storage at 2 kPa O_2 resulted in higher ethanol and acetaldehyde content compared with air control or other CA treatments.

The quality of 'Keitt' mangoes was evaluated during storage for 6 days at 20°C in an extremely low O_2 (LO) CA (ca. 0.3 kPa) before storage in modified atmosphere packaging (MAP) made from three low-density polyethylene (LDPE) films with different gas permeability characteristics (Gonzalez-Aguilar *et al*., 1997). Both LO and MA treatments delayed the losses of colour, weight and firmness. Fruit maintained good appearance with a significant delay of ripening. 'Keitt' was very tolerant of LO treatment; however, some MAP fruit developed a fermented taste after 10 and 20 days at 20°C. Short-duration (6-day) storage of mangoes in LO did not otherwise have any deleterious effect on fruit quality during subsequent storage under MA or normal atmosphere. Properly selected atmospheres, which prolong mango postharvest life by slowing ripening, can permit fruit to be shipped without sacrificing superior aroma.

Beaulieu and Lea (2003) studied 'Keitt' and 'Palmer' mangoes to assess volatile and quality changes in stored fresh-cut mangoes prepared from firm-ripe (FR) and soft-ripe (SR) fruit, and to assess what effect MAP may have on cut fruit physiology, overall quality and volatile retention or loss. Subjective appraisals of fresh-cut mangoes based on aroma and cut edge or tissue damage indicated that most SR cubes are unmarketable by day 7 at 4°C. Both cultivars stored in MAP at 4°C had almost identical O_2 consumption, which was independent of ripeness. The CO_2 and O_2 concentrations measured for cubes stored in passive MAP indicated that the system was inadequate to prevent potential anaerobic respiration after 7 days of storage.

21.7.1 Injuries associated with MA and CA

A 10 kPa CO_2 atmosphere alleviated CI symptoms in 'Kensington Pride' fruit, but higher concentrations were injurious; low O_2 (5 kPa) had no significant effect (O'Hare and Prasad, 1993). Higher concentrations of CO_2 (>10 kPa) were ineffective for alleviating CI at 7°C, and tended to cause tissue injury and high levels of ethanol in the flesh. Injury caused by higher levels of CO_2 appeared to be more severe at lower temperatures (O'Hare and Prasad, 1993; Bender *et al*., 1994,

1995), which could be due to either compounding injury (CI + CO_2) or reduced sensitivity of ripe mango to CO_2.

'Rad' mangoes developed internal browning and off-flavour in atmospheres containing 6 or 8 kPa CO_2 (Noomhorm and Tiasuwan, 1995). The presence of starchy mesocarp in 'Carabao' mangoes, which is characteristic of internal breakdown, increased during storage in MA (Gautam and Lizada, 1984). Fruit stored for 4–5 days had severe symptoms, including air pockets in the mesocarp resulting in spongy tissue (Nuevo *et al.*, 1984a, b). Parenchyma cells of affected tissues had around 18 starch granules per cell, compared with only ca. two starch granules in healthy adjacent cells. However, no difference in starch granule shape was detected between the spongy and healthy tissues. The spongy tissue, which usually occurs in the inner mesocarp near the seed and becomes evident during ripening, had almost 10× the starch content of healthy tissue in the same fruit. External symptoms of internal browning due to MA included failure of the peel to develop colour beyond the half-yellow stage.

'Carabao' mangoes stored in polyethylene bags (0.04 mm thickness) had a faint fermented odour that disappeared during ripening when the fruit were held for 1 day (Gautam and Lizada, 1984). The fermented odour increased with time and persisted throughout ripening when the fruit were stored for 2-5 days. The respiratory quotient of this cultivar ranged from 0.59 at 21 kPa O_2 and 6.03 at 2.4 kPa O_2, which indicates a progressively anaerobic metabolism (Sy and Mendoza, 1984). CO_2 production decreased as O_2 was decreased from 21 to 3 kPa, but increased at <3 kPa O_2. Fermentative decarboxylation could explain the odour (Lakshminarayana and Subramanyam, 1970).

Pronounced decay appeared after storage of 'Rad' mangoes for 20 days in atmospheres containing 4–6 kPa O_2 with 4–8 kPa CO_2 at 13°C and 94% RH, and severe incidence appeared after 25 days (Noomhorm and Tiasuwan, 1995). Greater incidence of decay (stem-end rot and anthracnose) occurred in 'Carabao' mango stored in MA for 2–5 days at 25–31°C (Gautam and Lizada, 1984).

21.7.2 Modified atmosphere packaging (MAP)

Modified atmosphere packaging (MAP) is used to create a beneficial MA around a packaged product using semipermeable film to restrict the movement of respiratory gases into and out of the package; at equilibrium, the respiration rate of fruit in MAP is equal to the diffusion of the respiratory gases through the film (Yahia, 2009). Fruit wrapped in polyethylene bags 0.08 mm thick, with and without perlite-$KMnO_4$ and stored for 3 weeks at 10°C before treatment with ethylene developed normal colour, texture and flavour (Esguerra *et al.*, 1978). Individually sealed 'Keitt' in low density (LDPE) and high density (HDPE) polyethylene films for 4 weeks at 20°C exhibited delayed ripening, reduced weight loss and did not develop any off-flavours (Gonzalez *et al.*, 1990). The LDPE had a thickness of 0.010 mm and permeabilities of 700 cc O_2 /m^2/h/atm and 0.257 g H_2O /m^2/h/atm. The HDPE film had a thickness of 0.020 mm and permeabilities of 800 cc O_2 /m^2/h/atm, and 0.166 g H_2O /m^2/h/atm.

In a study to model MAP for mango, 'Keitt' fruit were individually vacuum packaged in LDPE film (24.5 mm thick, 25.0 g/m^2) and stored at 7°C/80–90% RH, 12°C/75–85% RH, 17°C/70–80% RH, 22°C/65–75% RH or 2°C/65–75% RH (Yamashita *et al.*, 1997). After mass transfer had reached steady state, respiration rates, moisture loss, permeability of peel and film to water vapour and composition of atmosphere around the fruit were determined for 33 days. Daily rates of weight loss increased from 4.1 g/kg of fruit at 7°C to 10.9 g/kg at 25°C. Respiration rates also increased with storage temperature for both packaged and unpackaged mangoes, although they were 21%, 38% and 43% less in packaged fruit at 12°C, 17°C and 22°C, respectively. Permeability of peel was 600-fold greater than that of the plastic film. The in-package CO_2 levels increased and O_2 decreased with time; concentration changes were greatest during the first 10–15 days of storage and were more marked at the higher temperatures. Experimental and calculated values for CO_2 levels differed by 29%, depending on temperature.

'Tommy Atkins' mangoes individually sealed in heat-shrinkable films and stored for 2 weeks at 12.8°C and then ripened at 21°C had less weight loss. They did not show differences in firmness, peel colour development, decay development or time to fruit ripening, but had more off-flavours than unwrapped fruit (Miller *et al.*, 1983). Polyethylene films used were Clysar EH-60 film of 0.01 nominal thickness, Clysar EHC-50 copolymer film of 0.013 mm nominal thickness and Clysar EHC-100 copolymer film of 0.025 mm nominal thickness. Individual mature fruit of the same cultivar were later sealed in Clysar EHC-50 copolymer film with 0.013 mm thickness, and Cryovac D955 with 0.015 thickness, and stored at 21°C and 85–90% RH (Miller *et al.*, 1986). The O_2 permeabilities of the films were 620 cm^3 /24 h/m^2/atm and 9833 cm^3 /24 h/m^2/atm, respectively. Water permeability was 1.5 g /24 h/m^2 and 2.0 g/h/m^2 at 23°C, respectively. Fruit in MAP had less weight loss, but higher incidence of decay and off-flavour at soft-ripeness than unsealed fruit. The authors concluded that there were no practical benefits from wrapping the fruit in these films and storage at 21°C or even at lower temperatures. They concluded that film wrapping at various stages of ripeness after harvest will not improve the maintenance of mango quality during storage for ripening.

'Keitt' mangoes were individually sealed in LDPE films and in a heat-shrinkable copolymer (Cryovac D-955) film with non-sealed mangoes as the control and stored for up to 5 weeks at 12°C, 17°C or 22°C (Yamashita *et al.*, 1999). MAP reduced the rate constant of vitamin C degradation at all temperatures and vitamin C content of individually packaged mangoes was less affected by storage temperature than the control. Values for Q10 were 1.3 and 1.0 for mangoes wrapped with the heat-shrinkable copolymer and the LDPE films, respectively, and 2.8 for the non-sealed control.

The combined effect of hot benomyl (1000 ppm) at 55°C for 5 min and seal packaging in 0.01 mm PVC was extended storage life of mature-green 'Nam Dok Mai' mangoes at 13°C (Sornsrivichai *et al.*, 1992). Fruit quality was not affected by film packaging after 4 weeks, but fruit had inferior quality after 6 weeks. The inhibition of carotene pigmentation in the peel of this cultivar may be related to O_2 concentration inside the package and not to CO_2 concentration (Yantarasri *et al.*, 1994).

At least 16 kPa O_2 was essential for development of peel colour to the marketable stage (greenish).

'Kensington' mangoes treated with heated benomyl (0.5 g/l at 51.5°C for 5 min) and sealed in polyethylene bags (0.04 mm thickness) for various durations at 20°C, had off-flavour and lacked normal peel colour when ripened, but ripened satisfactorily in perforated bags (Chaplin *et al.*, 1982). The postharvest life of these fruit was not consistently longer than the control. The CO_2 concentration in the bags was >20 kPa while the O_2 concentration was <5 kPa. The incidence of off-flavours was reduced by including C_2H_4 absorbent blocks in the bags. The authors concluded that 'mangoes cannot be stored satisfactorily at ambient temperature by such technique'; however, Stead and Chithambo (1980) reported that fruit ripening at 20-30°C was delayed 5 days by sealing in polyethylene bags (0.02 mm thickness) with C_2H_4 absorbent without any abnormal flavour.

'Tommy Atkins' and 'Keitt' mangoes were individually sealed in shrinkable Cryovac polyolefin films (15 mm or 19 mm thickness), either non-perforated or perforated with eight holes of 1.7 mm diameter per square inch or eight holes of 0.4 mm diameter per square inch (Rodov *et al.*, 1994). After 2–3 weeks at 14°C and an additional week at 17°C, mangoes packaged in perforated polyolefin films ripened normally, with optimum results achieved when film with 0.4 mm perforations was combined with increased free volume inside the package by sealing the fruit within polystyrene trays. After 3 weeks of storage and 1 week of shelf life, sealed 'Keitt' mangoes were inferior to the control; they were less ripe, but beyond 4 weeks (up to 6 weeks) sealed fruit had better quality scores because they were less overripe. Sealing did not reduce decay of fruit stored for long periods.

Non-perforated PVC film packaging of 'Nam Doc Mai' mangoes was not sufficiently permeable for O_2 exchange to allow proper ripening (Yantarasri *et al.*, 1995). Therefore, a 'perforated MA' was used in which fruit in polystyrene trays (three fruit per pack) at 20°C were wrapped in PVC with perforation area of >0.004 cm^2. Fruit ripened normally with no off-flavours. Colour development in the peel required a higher concentration of O_2 than the flesh. A film of perforation area >0.008 cm^2 allowed fruit colour to develop after 3 weeks, while an area of >0.39 cm^2 allowed the fruit to colour within 2 weeks.

Pliakoni *et al.* (2015) investigated whether MAP can allow transport of mixed marine container loads of ethylene-sensitive and ethylene-producing crops. They found that two commercial MAP systems (Breatheway® (Hazel Technologies) and Xtend® (StePac)) were essentially impermeable to ethylene gas. This suggests that ethylene may therefore accumulate inside MAP when the package contains an ethylene-producing crop. Since ripening mango fruit produce ethylene, scrubbing the ethylene in MAP so that it does not accumulate and counteract the MA effects in inhibiting ethylene production and action may be an essential system component for maximum effectiveness of MAP for mangoes. Excessive ethylene production rates by producing tissues or high ethylene levels in the surrounding environment can undermine both quality and postharvest storage life, resulting in waste and economic losses. Brecht *et al.* (2023) recently investigated this possibility with tree-ripe 'Keitt' and 'Tommy Atkins' mangoes using It's Fresh!™ ethylene filters inside Breatheway® MAP that established an atmosphere of about 6 kPa O_2 plus 9 kPa CO_2 at 7°C and found that the MAP with ethylene removal resulted in better retention of desired quality attributes such as reduced CI, lenticel discoloration and decay, along with higher fruit firmness and acidity, resulting in better organoleptic quality.

21.7.3 Semipermeable coatings

In addition to reducing water loss, some fruit coatings can create an internal MA within the fruit due to semipermeable restriction of O_2 and CO_2 movement in and out of the fruit. Baldwin *et al.* (1999) tested two types of fruit coatings (polysaccharide-based and carnauba wax-based) for their effect on external and internal mango fruit atmospheres and quality factors during simulated commercial storage at 10 or 15°C with 90–99% RH followed by simulated marketing conditions at 20°C and 56% RH. The coatings exhibited markedly different O_2 permeability characteristics under laboratory conditions. Polysaccharide coatings were less permeable to respiratory gases and more permeable to water vapour compared with carnauba wax. When applied to fruit under simulated commercial conditions, however, the differences between the coatings in permeance to respiratory gases were much reduced, most likely due to high RH during cold storage. Both coatings created a MA within the fruit, reduced decay and improved appearance by imparting a subtle shine; but only the polysaccharide coating delayed ripening and increased concentrations of flavour volatiles. The carnauba wax coating significantly reduced water loss compared with uncoated and polysaccharide-coating treatments.

'Julie' mangoes treated with 0.75% w/v aqueous solution of Pro-long semipermeable fruit coating (a mixture of sucrose esters of fatty acids and sodium salt of carboxy methyl cellulose) and stored at 25°C and 85–95% RH exhibited reduced weight loss, retarded ripening and increased storage life (6 days longer) without evidence of adverse effects on quality (Dhalla and Hanson, 1988). Treatment with 1.0% Pro-long could increase ethanol concentration in the flesh. Treatment with Pro-long (0.8–2.4%) also delayed ripening of 'Haden' (Carrillo-López *et al.*, 1996).

The effects of chitosan monolayer and chitosan/nano TiO_2 coatings on the postharvest physiology of mangoes were evaluated during storage at 13°C for 20 days by Xing *et al.* (2020). They reported that mangoes coated with chitosan and chitosan/nano TiO_2 exhibited lower decay index, TSS and malonaldehyde contents, whereas higher firmness, enzyme activities (peroxidase and PPO), total flavonoids and phenol contents were found in this treatment.

Fucoidan (1, 3, or 5%) coating effect on mango quality was determined during storage at 20°C with 80% RH for 5 weeks by Xu and Wu (2021). They reported that 5% fucoidan coating exhibited a preservation effect by delaying respiration increase and reducing weight loss and fruit decay incidence, while better retaining ascorbic acid content, firmness, TA, TSS and overall acceptability.

Chitosan (1%) plus thyme oil (400 µl/l) was evaluated for control of anthracnose (*Colletotricum gloeosporioides*) decay and improvement of mango 'White Chaunsa' shelf life (Shah *et al.*, 2021). Thyme oil inhibited the *in vitro* mycelial growth of the fungus, while the combined chitosan plus thyme oil treatment was more effective than thyme oil alone in controlling the disease in inoculated mangoes. Fruit resistance to anthracnose was attributed to elevated phenylalanine ammonia-lyase (EC 4.3.1.24) and peroxidase activities compared with air control or the synthetic imidazole fungicide prochloraz. The combined chitosan plus thyme oil treatment retained physicochemical attributes including weight loss, colour, firmness, TSS, TA and higher scoring for sensory perception.

Hydroxypropyl methylcellulose and beeswax (in concentrations of 10, 20, or 40%) was tested on 'Palmer' mangoes held at 21°C for 15 days (Sousa *et al.*, 2021). They reported that the coating improved peel and flesh colour, firmness, TSS, TA, TSS:TA ratio, sugars, ascorbic acid, phenolic compounds, flavonoids, β-carotene and antioxidants activities. Moreover, the coatings delayed ripening and reduced weight loss, oxidative stress and disease incidence without inducing alcohol dehydrogenase (EC 1.1.1.1) activity, indicating that fermentative metabolism was not induced. Overall, hydroxypropyl methylcellulose plus beeswax at 20% was the best treatment, increasing shelf life at 21°C by 6 days, and seemed suitable for commercial application.

A shellac-based coating containing tannic acid was tested for its effect on physiological variation of mangoes stored at 25°C with 85–90% RH for 18 days (Ma *et al.*, 2021). The tannic acid-shellac coating exhibited a synergistic effect by maintaining weight loss and fruit firmness, retarding respiration rate, browning and lipid peroxidation, preserving aromatic volatiles and regulating relevant enzymes. They reported that the combined tannic acid–shellac coating improved shelf life and overall mango quality, with ca. 10 days' extension of shelf life.

Khalil *et al.* (2022) determined the effect of hot water treatment (55°C for 5 min) and chitosan (1%) coating on mangoes stored at 13°C and 85–90% RH for 28 days. They found that the hot water plus chitosan coating treatment reduced weight loss, fruit ripening and decay incidence, while lessening the increase in TSS and decrease in TA and retaining superoxide dismutase (EC 1.15.1.1) and peroxidase activities. The same treatment exhibited higher flesh hue angle, vitamin C content and membrane stability index when compared with control or either component alone.

Ali *et al.* (2022) investigated the effect of tragacanth gum (0, 0.5, 1, or 1.5%) on postharvest softening and ripening of mangoes. They reported that tragacanth (1.5%) reduced respiration and ethylene production rates, thereby lowering decay incidence and weight loss as well as superoxide anion and hydrogen peroxide content in comparison with the control. Moreover, fruit coated with tragacanth (1.5%) had higher total chlorophyll content and lower L*, a* and b* along with substantially lower total carotenoids in the peel. Tragacanth (1.5%) exhibited markedly lower water-soluble pectin and higher chelate-soluble pectin, Na_2CO_3-soluble pectin, protopectin, cellulose and hemicellulose in flesh tissues in comparison with the control. Enzyme activities of polygalacturonase, cellulase, pectin methylesterase (EC 3.1.1.11), β-galactosidase and β-glucosidase (EC 3.2.1.21) were lower in the flesh of fruit treated with tragacanth (1.5%) along with substantially higher texture compared with control. Also, the same treatment resulted in higher antioxidant activities and delayed increase in TSS and ripening index along with retaining higher TA compared with the control, altogether exhibiting retardation of ripening and softening in mangoes.

21.7.4 Insecticidal CA

Mangoes are very tolerant of insecticidal atmospheres (<1 kPa, >50 kPa CO_2) (Yahia, 1998, 2009) and thus a potential commercial application is feasible, especially in combination with other treatments, i.e., hot air. 'Keitt' mangoes tolerated as low as 0.2 kPa O_2 and as high as 80 kPa CO_2 for up to 5 days at 20°C without any injury upon ripening, although fermentative odours could be noted while the fruit were under atmosphere stress (Yahia, 1993, 1994, 1995, 1997; Ortega and Yahia, 2000). Other mango cultivars were also evaluated and were very tolerant of extreme atmospheres (Yahia, 1998).

Storage of 'Keitt' mangoes in an insecticidal MA (0.03–0.26 kPa O_2, 72–79 kPa CO_2, balance N_2) and CA (0.2 kPa O_2, balance N_2, or 2 kPa O_2 + 50 kPa CO_2, balance N_2) for up to 5 days at 20°C delayed fruit ripening as indicated by respiration, flesh firmness and colour development (Yahia *et al.*, 1989; Yahia, 1993; Yahia and Tiznado, 1993; Yahia and Vazquez, 1993). The activity of phosphofructokinase, alcohol dehydrogenase and pyruvate decarboxylase was enhanced but activity of pyruvate kinase, succinate dehydrogenase and α-keto-glutarate dehydrogenase was unaffected. Although these atmospheres caused changes in glycolysis and tricarboxylic acid cycle, there was no indication of injury and the fruit ripened normally in air after the treatment. Sensory evaluation conducted after fruit ripening showed no off-flavours, and there were no differences between fruit maintained in the MA or CA and those maintained continuously in air. 'Keitt' mangoes are therefore very tolerant of insecticidal atmospheres and 5 days of exposure in these insecticidal atmospheres is sufficient to control many insects (Rojas-Villegas *et al.*, 1996).

Storage of 'Keitt' and 'Tommy Atkins' mangoes for 21 days at 12°C in atmospheres containing 25, 45, 50, or 70 kPa CO_2 plus either 3 kPa O_2 or air induced ethanol production of 0.18–3.84 ml/kg/h after transfer to air at 20°C for 5 days (Bender *et al.*, 1994). Atmospheres containing 50 or 70 kPa CO_2 caused fruit injury and resulted in the highest ethanol production rates. Enclosure of 'Haden' and 'Tommy Atkins' mangoes in sealed 20-litre jars with an initial atmosphere of 90 kPa CO_2 in air or 97 kPa N_2 + 3 kPa O_2 for 24 h prior to storage delayed their ripening and no injury was reported (Pesis *et al.*, 1994).

21.8 Manipulation of Postharvest Physiology by Molecular Biology

Mango fruit show extreme variability in quality traits in >1,000 cultivars, a result of mostly random evaluation of chance seedlings (Bally *et al.*, 2021). Potential mango postharvest biotechnology

advances fall into three areas: (1) control of fruit ripening, which is the main determinant of mango potential postharvest life; (2) control of abiotic stress responses, since the two major postharvest disorders, CI and HI, are temperature-related; and (3) improvement in mango composition in terms of sensory and nutritional quality.

Mango fruit quality is compromised when harvest occurs before the fruit are fully mature, since they are unable to achieve the full complement of flavour and aroma during the postharvest handling period compared with fruit harvested at a fully mature or ripening initiated stage of development. As a climacteric fruit, maturity in mango corresponds to attainment of ripening competence. Focus on genes regulating ethylene biosynthesis and signalling would appear to be the most efficient way to control (slow) ripening. The presence of ethylene is required for the progression and completion of mango ripening. Thus, strategies for prolonging the postharvest life and maintaining postharvest quality of mango other than disease control are focused on reducing the effects of ethylene. This situation provides an excellent opportunity to utilize genetic transformation to improve mango postharvest quality by manipulating the role of ethylene (see Chapter 9, this volume). Cruz-Hernandez *et al.* (1997) transformed 'Hindi be Sennara' mango with mango ACC oxidase and ACC synthase (EC 4.4.1.14) RNA in the antisense orientation. A cDNA that codes for mango ACC oxidase was also isolated and characterized by Zainal *et al.* (1999). Dautt-Castro *et al.* (2015) identified upregulation of several members of the multigene ACC synthase and ACC oxidase families during ripening. Suppression of mango ethylene biosynthesis should allow harvesting of advanced maturity fruit that contain high levels of sugars and possess enhanced capacity to produce ripe aroma volatiles after exposure to exogenous ethylene. Progression of ripening in such fruit can be easily halted at the most desirable and convenient time by simply removing exogenous ethylene.

A cDNA homologue of the ethylene receptor gene *ETR-1*, referred to as *METR1*, which codes for a polypeptide of 802 amino acids with a predicted 89 kDa MW has been isolated (Gutierrez-Martinez *et al.*, 2001). Two or more ETR homologues exist in mango. The level of *METR1* mRNA in the mesocarp increases transiently during wounding. Dautt-Castro *et al.* (2015) identified both upregulation and downregulation of components of the ethylene signalling pathway during ripening. Repression of genes involved in ethylene action in mango fruit should result in ethylene-insensitive fruit that are minimally affected by exposure to ethylene in the postharvest environment, resulting in better control of ripening and senescence to maintain mango postharvest quality.

Omics approaches to achieve insights into the molecular basis of abiotic stress responses in mango have been recently reviewed by Muthuramalingam *et al.* (2023). Although much of the existing research has been focused on whole plant stress responses, it seems likely that abiotic stress-responsive genes and their associated abiotic stress-signalling pathways are conserved across mango plant organs, including the fruit. Responses to abiotic stress appear to be centred on the fruit antioxidant system, with increased levels of antioxidant compounds like phenolics being associated with stress resistance (Datir and Regan, 2022). Transcriptomics analysis revealed that chilling stress is associated with upregulation of stress response genes, including those encoding transmembrane receptors, calcium-mediated signal transduction, NADPH oxidase, MAP kinases and WRKYs, which can lead to cell death (Sivankalyani *et al.*, 2016).

Datir and Regan (2022) reviewed how omics can be used to achieve insights into the molecular basis of mango fruit quality. Since soft texture seems to be associated with low fibre in mango fruit (Bally and deFaveri, 2021), it may be useful to attenuate genes associated with cell wall degradation, of which polygalacturonase (PG), pectin lyase (EC 4.2.2.10; PL) and rhamnogalacturonase (EC 4.2.2.23; RGL) seem to play central roles. Bally and deFaveri (2021) investigated the heritability and stability of 13 mango fruit quality traits, with the one of most significant interest to the mango trade being fruit texture (firmness and fibrousness). They found that mesocarp texture has very low average heritability (0.35) and suggested that separating mesocarp texture into its components of firmness, fibre abundance, and fibre strength may be a more fruitful approach in breeding efforts. Sane *et al.* (2005) isolated and characterized an ethylene-dependent a-expansin gene, *MiExpA1*, which is correlated with softening in mango. Expression of *MiExpA1* increases with the progression of ripening and treatment with 1-methylcyclopropene (1-MCP) inhibits both ripening/softening as well as MiExpA1 transcript and protein accumulation. A pectate lyase (EC 4.2.2.2) gene homologue from ripening mango (*MiPel1*) has been cloned (Chourasia *et al.*, 2006). A progressive increase in transcript accumulation was observed during ripening but expression was delayed significantly in fruit in air without exogenous ethylene. The expression was specific to fruit and was triggered only during ripening. Increased transcript accumulation during ripening was associated with pectin solubilization. Pectate lyase may be closely associated with pectin degradation and have an important role in mango softening.

Mango fruit flavour is determined by the interaction between the taste components, sugars and acids, and the aroma components, of which there are several hundred, with the wide variations that exist in the flavour of mango varieties being mainly attributable to the latter. Wang and colleagues (Sung *et al.*, 2019; Suh *et al.*, 2022) have recently been working to identify the characteristic aroma compounds that are responsible for the unique flavours of different mango cultivars, associating flavours with consumer appreciation as well. This work promises to be of great help in identifying markers for consumer-favoured flavours in mango breeding efforts.

The potential certainly exists for integrating knowledge of molecular regulation of fruit ripening, abiotic stress responses and composition with genome-based breeding approaches and gene editing to improve mango postharvest performance and fruit quality.

21.9 Conclusions

Mango fruit are rich sources of nutritional and bioactive components of great benefits for human nutrition and health and have the potential to develop extremely desirable texture, taste and aroma that make this fruit highly appreciated and desirable.

Strategies used to extend mango postharvest life are based on control of ripening, particularly ethylene action and ethylene production. Therefore, for fruit destined for distant markets, mangoes are often harvested at the mature-green stage, prior to ripening initiation, and stored and transported at low temperatures at or below the threshold for induction of CI. These practices result in poor-quality mangoes on the market. Successful handling of ripening-initiated mangoes would improve this situation, but is problematic due to the fruit's short postharvest life, making international transport of tree-ripe mangoes challenging. However, recent research into the use of MAP with ethylene scrubbing has yielded promising results for successful international marketing of tree-ripe mangoes (Brecht *et al.*, 2023).

Future expansion of mango consumption will require further understanding of mango postharvest physiology in order to overcome the problems of CI, internal breakdown and premature and uneven ripening. This may involve increased transport of tree-ripe mangoes in CA-equipped marine containers, although equipment availability is currently limiting and significant work is needed for CA to be applied properly, making MAP and semipermeable fruit coatings more practical choices in the short term. Increasing mango marketing and consumption will require development of improved procedures for storage and ripening to offer preconditioned, ripening initiated, ready-to-eat mangoes to consumers. It may also involve genetic transformation of mango to manipulate the progression and uniformity of ripening and softening, as well as providing cultivars with attenuated ripening, better resistance to abiotic stresses, improved flavour and higher levels of nutritional and bioactive components.

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