Cell Wall Modification during Ripening of 'Keitt' and 'Tommy Atkins' Mango Fruit

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Abstract. 'Keitt' and 'Tommy Atkins' mango (*Mangifera indica* L.) fruit were evaluated for selected ripening criteria at six ripening stages, from mature green to overripe. 'Tommy Atkins' mangos developed more red and yellow pigmentation (CIE a* and b*) in peel and mesocarp tissues than 'Keitt'. The outer mesocarp of 'Keitt' remained firm longer than 'Tommy Atkins', and the inner mesocarp was softer than the outer at each stage in both cultivars. Cell wall neutral sugars, particularly arabinosyl, rhamnosyl, and galactosyl residues, decreased with ripening in both cultivars. 'Keitt' had more loosely associated, chelator-soluble pectin, accumulated more soluble polyuronides, and retained more total pectin at the ripe stage than 'Tommy Atkins'. Both cultivars had similar polygalacturonase (EC 3.2.1.15) activity which increased with ripening. The amount and molecular weight of cell wall hemicellulose decreased with ripening in both cultivars. These data indicate that enzymatic and/or nonenzymatic processes, in addition to polygalacturonase activity, are involved in the extensive softening of mango fruit.

The mango is one of the most popular tropical fruits worldwide, second only to banana. More than 14 million tons are produced worldwide, with 65% produced in India (Food Agriculture Organization, Annual Statistics, 1986). Southern Florida is the only location in the continental United States where mangos are commercially produced. With expanding production in southern Florida, mango consumption in the United States has increased due to increased availability of more desirable cultivars, such as 'Keitt' and 'Tommy Atkins'. There is tremendous potential for export, particularly to countries such as the United Kingdom, whose consumers prefer the brightly colored Florida cultivars (Jabati, 1989).

Despite the potential, there are several problems associated with the marketing of mango fruit. Mangos soften very quickly and extensively. Loss of fruit firmness increases susceptibility to bruising and decay during shipping and storage. Also, mangos are very susceptible to anthracnose (*Colletotrichum gloeosporioides* Penz.) and stem-end rot (*Diplodia natalensis* P.; *Phomopsis citri*). No fungicides are approved for postharvest use on mango fruit, and prospects for future approval are poor. High-temperature water dips help, although up to 80% of the fruit can be lost to fungal attack before fully ripe. It is important to reduce the rate of fruit softening to maintain the fruit's inherent resistance to bruising and decay.

Softening in fleshy fruits is primarily due to cell wall modification. Limited information is available on mango cell walls and the softening process during ripening (Brinson et al., 1988; Lazan et al., 1986; Roe and Bruemmer, 1981; Seymour et al., 1989). There are considerable differences between cultivars (Selvaraj and Kumar, 1989). We have conducted an analysis of the biochemistry of mango fruit softening, including cell wall

composition and molecular weight analysis using two commercially important Florida-grown cultivars, 'Keitt' and 'Tommy Atkins'.

Materials and Methods

Mango fruit were obtained from a commercial packinghouse in Homestead, Fla. ('Tommy Atkins' in June 1990 and 'Keitt' in July 1990). Fruit were transported to Orlando, Fla., dipped 3 min in 1000 ppm Imazilil at 35C to reduce decay, and stored at 20C, 85% $\pm$ 5% RH. Some fruit were analyzed immediately, while other fruit were allowed to ripen at 20C. Four fruit at each of six ripeness stages, determined subjectively by firmness, were selected for analysis: immature green (IG), fruit hard, mostly flat with undeveloped shoulders; mature green (MG), fruit hard, shoulders well rounded; firm (F), fruit yields slightly under pressure; fairly firm (FF), fruit yields significantly under pressure; soft ripe (SR), fruit soft; overripe (OR), fruit extremely soft, mushy.

Respiration. Individual fruit, four at each stage, were sealed in 3.8-liter jars at 20C. After 15 min, 1-ml gas samples from jar headspaces were analyzed for CO₂ using a Hewlett Packard 5880 gas chromatograph (Hewlett Packard, Palo Alto, Calif.) equipped with a Porapak Q column and a thermal conductivity detector. Nitrogen, at a flow rate of 30 ml·min⁻¹, was the carrier gas.

Color. Color measurements (CIE L*a*b*) were taken on four fruit at each ripeness stage. A Minolta CR200 Colorimeter (Minolta, Ramsey, N.J.) was used to measure external and internal color. For external (peel) color, the mean of six measurements per fruit (stem and blossom end and four equator readings) was determined. For internal color, a 3-cm diameter section of peel was removed from each of the two fruit lobes. The mean of six measurements per fruit (three per lobe) was determined.

Firmness. Mesocarp firmness was measured using an Instron 4301 (Instron, Canton, Mass.). Two lobes were cut from a fruit by slicing parallel to the seed. Resistance to compression (3 mm) with a 7-mm diameter probe was measured on the inner

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Abbreviations: ASP, alkaline-soluble pectin; CSP, Chelator-soluble pectin; F, firm; FF, fairly firm; HF, hemicellulosic fraction; IG, immature green; MG, mature green; OR overripe; SR, soft ripe.

(near seed) and outer (under peel, peel removed from 3 cm area) mesocarp of each lobe. The means of four measurements per fruit (two per lobe) were determined for inner and outer tissues.

Soluble polyuronides. Soluble polyuronides were » extracted from previously frozen mesocarp tissue (10 g). Tissue was homogenized in two volumes 200 mM K_2O_3 and filtered. The filtrate was mixed with 1.50 μ l 40% $MgCl_2$ and centrifuged ($27,000 \times g$, 5 min). The pellet was suspended in 95% ethanol and recentrifuged. The resulting pellet was suspended in 80C dH_2O , cooled, and recentrifuged. The supernatant was assayed for uronic acid using the carbazole method (Dische, 1947).

Cell wall extraction. Cell walls were extracted from mesocarp tissue as described for tomato (*Lycopersicon esculentum* Mill.) (Mitcham et al., 1989) with slight modification. Outer pericarp was homogenized in 80% ethanol and further disrupted in a cell disruption bomb. The residue was rinsed with 20 mM Hepes-NaOH (pH 6.9), stirred in 2 phenol : 1 acetic acid : 1 dH_2O (by volume) (Selvandran, 1975) for 20 min, and rinsed in 20 mM Hepes-NaOH (pH 6.9). The residue was suspended in 90% DMSO (1 ml·g⁻¹ fresh weight mesocarp tissue) and stirred for 18 h at room temperature to remove starch. Isolated cell walls were tested with KI/I_2 to verify the absence of starch. Cell walls were successively rinsed in 1 chloroform : 1 methanol (v/v) and acetone, then dried in a vacuum oven at 40C over P_2O_5 .

Cell wall uronide. Cell walls (10 mg) were incubated on ice in 2-ml concentrated H_2SO_4 on a gyratory shaker. Two 500- μ l aliquots of dH_2O (4C) were slowly added, and the solution was incubated on a shaker until dissolved (6 h). Uronic acid concentration was determined by the carbazole method (Dische, 1947).

Cell wall neutral sugars. Neutral sugars were analyzed by gas chromatography as described by Mitcham and McDonald (1992). Cell walls (5 mg) were treated with 2 N trifluoroacetic acid to hydrolyze noncellulosic neutral sugars, and alditol acetate derivatives were prepared, separated, and quantified by gas chromatography. Allose was the internal standard.

Cell wall fractionation. Cell walls (300 mg) were fractionated as described by Mitcham et al. (1989) with modifications. Cell walls were incubated under N_2 6 h at 25C in 50 mM Na-acetate (pH 6.5) containing 50 mM CDTA. The suspension was filtered through a fritted glass filter, and the filtrate dialyzed (1000 mol weight cut off) for 72 h at 4C against dH_2O [chelator-soluble

Fig. 1. Carbon dioxide production of mango fruit at various ripeness stages: immature green (IG), mature green (MG), firm (F), fairly firm (FF), soft ripe (SR), and overripe (OR). Each value represents the mean of four fruit. Vertical lines represent SE.

Fig. 2. Mango peel color at various stages of ripeness. (A) green to red; the greater the value, the more red pigment. (B) blue to yellow; the greater the value, the more yellow pigment. See legend to Fig. 1 for stage abbreviations. Each value represents the mean of four fruit (six measurements per fruit) at each ripeness stage. Vertical bars represent SE.

pectin (CSP)]. The residue was suspended in 50 mM Na_2CO_3 containing 2 mM CDTA and incubated under N_2 20 h at 4C, then 1 h at 25C. The suspension was filtered and the filtrate was adjusted to pH 6.5 and dialyzed as described for CSP above [alkaline-soluble pectin (ASP)]. The residue was suspended in 8 M KOH containing 100 mM $NaBH_4$ and incubated under N_2 3 h at 25C. The suspension was filtered and filtrate adjusted to pH 6.5 and dialyzed [hemicellulosic fraction (HF)]. The residue was rinsed with dH_2O and lyophilized [cellulosic fraction (CF)]. Carbohydrate content of HF was estimated by the phenol-sulfuric acid method (Dubois et al., 1956), uronic acid content of CSP, and ASP was estimated by the carbazole method (Dische, 1947). Cellulose content of crude cell walls was estimated according to the procedure of Updegraff (1969) using the anthrone method (Spiro, 1966).

Polygalacturonase activity. Mesocarp tissue (40 g fresh weight, stored at -80C) was homogenized 3 min in dH_2O (pH of dH_2O adjusted to 3.0 with HCl, 1 ml·g⁻¹ fresh weight mesocarp). After centrifugation at $5000 \times g$ for 10 min, the pellet was retained and rinsed with dH_2O as above. The pellet was suspended in 1 M NaCl (1 ml·g⁻¹ fresh weight mesocarp), homogenized 1 min, adjusted to pH 6.0 with dilute HCl, and incubated and stirred 3 h at 4C. The suspension was centrifuged, as above,

Fig. 3. Mango mesocarp color (CIE a*/b*) at several stages of ripeness. CIE a* represents green to red; the greater the value, the more red pigment. CIE b* represents blue to yellow; the greater the value, the more yellow pigment. A 3-cm diameter portion of peel was removed from each of two fruit lobes and color of the exposed mesocarp determined. Each value represents the mean of four fruit (three measurements per lobe; six per fruit) at each ripeness stage. See legend to Fig. 1 for stage abbreviations. Vertical bars represent SE.

and the supernatant dialyzed (6000-8000 mol weight cut off) against 500 mM NaCl, yielding a crude enzyme extract. The pH optimum for 'Tommy Atkins' and 'Keitt' polygalacturonase enzymes was determined to be 4.7. The crude enzyme extract (50 μ l) was incubated 0.5, 1, 3, or 5 h at 37C in a 200 μ l solution containing 0.25% polygalacturonic acid (Sigma P-1879), 50 mM Na-acetate (pH 4.7), and 125 mM NaCl. The reaction was stopped by addition of 1 ml 100 ml borate buffer (pH 9.0). Release of galacturonic acid residues was estimated by the 2-cyanoacetamide method (Gross, 1982). The enzyme activity was determined by regression analysis of product formation over time.

Hemicellulose fractionation. Hemicellulose fractions were stored at 4C with 0.02% Na-azide until concentrated for gel filtration. Four milligrams HF in 2 ml 20 mM Hepes-NaOH (pH 6.0) containing 150 mM NaCl were loaded onto a bed (1.5 $\times$ 60 cm) of Spectra/Gel ACA 34 (Medical Industries, Los Angeles) and eluted with the same buffer at a flow rate of 16 ml·h⁻¹. Fractions of 1.5 ml were collected and carbohydrates detected using the phenol-sulfuric acid method (Dubois et al., 1956). Blue dextran (2 $\times$ 10⁶ molecular weight), dextran (4 $\times$ 10⁴ molecular weight), and glucose were used for molecular weight calibration.

Results and Discussion

The pattern of respiration for 'Tommy Atkins' and 'Keitt' mango fruit was typical of climacteric fruit (Fig. 1) and was similar to that reported for mango fruit by Krishnamurthy and Subramanyam (1973). The climacteric peak occurred at the F stage in both cultivars; however, the respiration rate remained higher in 'Tommy Atkins' than in 'Keitt' after the peak. A higher respiration rate may indicate a decreased shelf life for 'Tommy Atkins'.

'Tommy Atkins' and 'Keitt' develop more colorful peels than some of the green or yellow-skinned mango cultivars. 'Tommy Atkins' developed more red (CIE a*) and yellow (CIE b*) peel pigmentation than 'Keitt' (Fig. 2), which could make the former more visually appealing to consumers. In addition, the mesocarp

Fig. 4. Firmness (newtons) of inner and outer mango mesocarp at various stages of ripeness. Two lobes were cut from the fruit by slicing parallel to the seed. Resistance to compression (3 mm) with a 7-mm diameter probe was measured on inner (near seed) and outer (under peel) mesocarp of each lobe. Each value represents the mean of four measurements (two measurements per lobe) for four fruit (16) at each stage of ripeness. See legend to Fig. 1 for stage abbreviations. Vertical bars represent SE.

of 'Tommy Atkins' developed a deeper orange (CIE a*/b*) (Fig. 3).

Both mango cultivars ripened from the inside outward (Fig. 4), as in 'Harumanis' mangos (Lazan et al., 1986). Internal softening had already begun at the MG stage, when the fruit's shoulders were well-rounded and the fruit was externally judged to be hard (Fig. 4). This was particularly true for 'Keitt' where the outer mesocarp was very hard (> 100 N), while the internal mesocarp had softened to < 40 N (Fig. 4). Undetectable internal ripening is largely responsible for nonuniformity in ripening within a harvested lot of fruit, leading to postharvest problems. The outer mesocarp of 'Keitt' mangos remained firm longer than that of 'Tommy Atkins' (Fig. 4), a condition which may afford 'Keitt' mangos greater resistance to postharvest bruising and decay.

Cell wall material (dry weight per gram fresh weight of mesocarp) was consistently higher in 'Tommy Atkins' than in 'Keitt' (Table 1), although the amount of cell wall material decreased during ripening in both cultivars. As with tomato (Huber, 1983), muskmelon (*Cucumis melo* L.) (McCollum et al., 1989) and blueberry (*Vaccinium corymbosum* L.) (Proctor and Peng, 1989), there was a significant increase in soluble uronides between MG and F stages of ripening of mango fruit (Table 1). Both cultivars

Table 1. Changes in cell wall dry weight, cell wall uronide, and soluble uronide content with ripening.

Ripeness stage	Cell wall dry wt (mg·g ⁻¹ fresh wt)		Cell wall uronide (mg·g ⁻¹ fresh wt)		Soluble uronide (μg·g ⁻¹ fresh wt)	
	TA ^z	Keitt	TA	Keitt	TA	Keitt
MG ^y	21.5 ± 0.9 ^x	16.4 ± 1.0	6.2 ± 0.5	4.3 ± 0.5	53 ± 2	51 ± 3
F	16.6 ± 1.4	12.3 ± 1.0	4.7 ± 0.5	3.2 ± 0.3	113 ± 16	225 ± 6
FF	13.1 ± 0.1	12.3 ± 0.8	3.6 ± 0.1	3.7 ± 0.3	142 ± 22	168 ± 14
SR	10.7 ± 1.4	8.2 ± 0.5	2.4 ± 0.4	2.1 ± 0.3	110 ± 10	220 ± 9
OR	10.9 ± 2.2	7.3 ± 0.3	2.6 ± 0.5	1.7 ± 0.1	123 ± 8	210 ± 7

^zTA = 'Tommy Atkins'.^yMG = mature green, F = firm, FF = fairly firm, SR = soft ripe, OR = over ripe.^xMean ±SE of 4 fruit at each stage of ripeness.

Table 2. Noncellulosic neutral sugar content of cell walls from mango fruit at five stages of development.

Ripeness stage	Total noncellulosic neutral sugars (percentage of cell wall)		μg·mg ⁻¹ cell wall											
			RHA ^z		ARA		GAL		XYL		MAN		GLC	
	TA ^y	Keitt	TA	Keitt	TA	Keitt	TA	Keitt	TA	Keitt	TA	Keitt	TA	Keitt
MG ^x	28 ± 0 ^w	36 ± 2	17 ± 0	22 ± 1	163 ± 4	164 ± 5	65 ± 4	76 ± 9	63 ± 1	80 ± 2	7 ± 0	10 ± 1	32 ± 2	34 ± 2
F	19 ± 1	26 ± 2	9 ± 1	11 ± 1	64 ± 6	73 ± 11	38 ± 1	56 ± 5	72 ± 2	71 ± 2	10 ± 0	12 ± 0	33 ± 2	38 ± 6
FF	17 ± 1	19 ± 1	7 ± 0	8 ± 1	41 ± 4	38 ± 9	36 ± 1	37 ± 4	78 ± 4	76 ± 5	10 ± 0	10 ± 1	35 ± 2	33 ± 3
SR	14 ± 0	21 ± 2	4 ± 0	6 ± 1	17 ± 1	33 ± 7	30 ± 1	38 ± 4	80 ± 2	79 ± 2	8 ± 0	12 ± 1	27 ± 1	46 ± 8
OR	14 ± 0	20 ± 2	4 ± 0	5 ± 1	17 ± 2	29 ± 6	31 ± 1	38 ± 4	83 ± 2	79 ± 5	10 ± 1	12 ± 1	29 ± 1	32 ± 2

^wRHA = rhamnose, ARA = arabinose, GAL = galactose, XYL = xylose, MAN = mannose, GLC = glucose.^zTA = 'Tommy Atkins'.^yMG = mature green, F = firm, FF = fairly firm, SR = soft ripe, OR = overripe.^xMean of four fruit at each stage ± SE.

Table 3. Amount of CSP, ASP, HF, and cellulose (CF) in cell walls of mango fruit at various stages of ripeness.

Ripeness stage	Cell wall fractions (mg per 100 mg cell wall)							
	CSP		ASP		HF		CF	
	TA ^z	KEITT	TA	KEITT	TA	KEITT	TA	KEITT
MG ^y	3.0 ± 0.5 ^x	5.2 ± 0.5	15.0 ± 2.3	9.1 ± 0.9	13.6 ± 0.2	17.8 ± 2.3	28.6 ± 1.2	34.2 ± 0.6
F	5.7 ± 1.5	6.0 ± 0.8	15.2 ± 1.2	8.8 ± 1.6	14.4 ± 0.5	17.1 ± 1.5	31.9 ± 1.5	30.2 ± 2.8
FF	7.0 ± 0.5	7.9 ± 0.7	13.0 ± 0.8	8.1 ± 2.0	15.1 ± 0.6	15.4 ± 2.5	36.8 ± 2.5	33.7 ± 1.6
SR	4.8 ± 1.1	8.3 ± 0.1	9.9 ± 1.2	9.0 ± 0.1	12.2 ± 0.6	11.8 ± 2.2	38.1 ± 1.5	36.4 ± 1.6

^zTA = 'Tommy Atkins'.^yMG = mature green, F = firm, FF = fairly firm, SR = soft ripe.^xMean from 4 fruit at each stage of ripeness ± SE.

had similar amounts at the MG stage; however, 'Keitt' accumulated almost two times more soluble uronide than 'Tommy Atkins' beginning at the F stage. The amount of cell wall uronide per gram fresh weight was higher in 'Tommy Atkins' than in 'Keitt' at MG, F, and OR stages and decreased with ripening in both cultivars (Table 1).

'Keitt' mangos contained significantly more neutral sugar at each stage of ripening than did 'Tommy Atkins' (Table 2). Total noncellulosic neutral sugars decreased with ripening in both cultivars, and the decrease was particularly rapid from the MG to the F stage, when most of the fruit softening occurred (Fig. 4). Arabinosyl, galactosyl, and xylosyl residues were the most abundant neutral sugars, representing 45%, 20%, and 19%, respectively, of the total neutral sugars detected. The amount of arabinosyl, galactosyl, and rhamnosyl residues in mango cell walls decreased steadily throughout ripening; however, 'Keitt' had a consistently higher rhamnosyl content than 'Tommy Atkins' (Table 2). Rhamnosyl residues serve as branch points be-

tween the rhamnogalacturonan backbone of pectin and arabinogalactan sidechains. A higher rhamnosyl content in 'Keitt' may indicate a more highly branched pectin that may be less tightly bound because of reduced bonding between rhamnogalacturonan chains. Arabinosyl and galactosyl concentrations were similar for the two cultivars, except at the F stage, where 'Keitt' had more galactosyl residues, and the SR and OR stages where 'Keitt' retained more arabinosyl and galactosyl residues. Xylosyl residues increased steadily during ripening in 'Tommy Atkins', while in 'Keitt', xylose levels decreased from MG to F, then steadily increased to original levels at the SR stage (Table 2).

In contrast to our results, cell wall neutral sugar analysis of 'Ngowe' mango indicated that galactosyl, arabinosyl, and glucosyl were the most abundant cell wall neutral sugar residues, with galactosyl residues being most abundant (Brinson et al., 1988). The high level of glucose reported by these researchers was likely due to starch contamination, as no effort was made

Fig. 5. Polygalacturonase activity at various stages of ripeness. Each value represents the rate of release of galacturonic acid equivalents per gram fresh weight of mesocarp tissue at each ripeness stage. See legend to Fig. 1 for stage abbreviations. Each value represents mean from four fruits at each stage and vertical bars represent SE.

to remove starch. Galactose was the only cell wall neutral sugar to show a significant decrease during ripening of 'Sensation' mango (Seymour et al., 1989). We found considerable decreases in arabinosyl, galactosyl, and rhamnosyl residues in both, 'Keitt' and 'Tommy Atkins' mango fruit (Table 2). These findings suggest considerable variability among mango cultivars in cell wall composition and its modification with ripening. Some of the differences may also be due to use of dissimilar analytical procedures.

'Keitt' mangos retained more total pectin when ripe (SR) than 'Tommy Atkins', but the total amount of pectin was higher in 'Tommy Atkins' at all other stages (Table 3). 'Tommy Atkins' mangos have been described as fibrous in comparison to 'Keitt' (Sauce and Galvan, 1990). These textural differences may be the result of differences in cell wall composition and a greater amount of cell wall material per gram fresh weight in 'Tommy Atkins'.

There was more of the loosely bound CSP and less of the more tightly associated ASP at all stages in cell walls of 'Keitt' than in 'Tommy Atkins' (Table 3). The amount of CSP increased during ripening in both cultivars, and 'Tommy Atkins' exhibited a decrease at the SR stage.

The major portion of pectic substances in both cultivars was ASP and was released by 50 mM Na_2CO_3 (Table 3). ASP was also the major type of pectin in kiwifruit (*Actinidia deliciosa* (A. Chev.) C.F. Liang et A.R. Ferguson) (Redgwell et al., 1988). The amount of ASP decreased from the F to SR stage in 'Tommy Atkins', while there was little change in 'Keitt' cell wall ASP (Table 3).

Despite the differences in pectin composition and soluble polyuronide accumulation, PG activity was similar in the two cultivars (Fig. 5) except for a loss of activity at the OR stage in 'Tommy Atkins'. Polygalacturonase activities were similar to those reported previously for 'Keitt' (Roe and Bruemmer, 1981); however, 200-fold higher activity was reported in 'Harumanis' mangos (Lazan et al., 1986). The higher polygalacturonase activity in 'Harumanis' mangos may in part be due to the use of β -mercaptoethanol in the extraction medium. There appears to be considerable variability in biochemistry between some mango cultivars; however, 'Keitt' and 'Tommy Atkins' appear to be similar to each other.

Fig. 6. Elution pattern of 'Tommy Atkins' and 'Keitt' mango cell wall hemicellulose fractions (4 mg) from Spectra/Gel ACA 34 (20 mM Hepes-NaOH, pH 6.9, 150 mM NaCl). Glucose equivalents in 1.5-ml fractions were determined by the phenol-sulfuric acid method. Hemicellulosic fractions from four fruit at each stage per cultivar were analyzed. Representative profile presented. MG = mature green, F = firm, and SR = soft ripe stage of ripeness. Elution of calibration standards: a = blue dextran, b = 40,000 molecular weight dextran, c = glucose.

The amount of hemicellulosic polymers in 'Keitt' cell walls exceeded that in 'Tommy Atkins' at the MG and F stages. The amount of hemicellulose decreased steadily during ripening in 'Keitt' cell walls, but increased from MG to FF in 'Tommy Atkins' before decreasing at the SR stage (Table 3). The amount of cell wall cellulose was similar and increased with ripening in both cultivars (Table 3).

The decrease in cell wall hemicellulose with ripening (Table 3) was accompanied by a considerable decrease in mean molecular weight expressed as glucose equivalents (Fig. 6), which may contribute to fruit softening. The molecular weight profiles for the two cultivars differed slightly, with more low molecular weight hemicellulose observed in 'Keitt' than in 'Tommy Atkins' at the SR stage (Fig. 6). A decrease in molecular size of hemicellulosic polymers has been reported in ripening strawberries (*Fragaria × ananassa* Duch.) (Huber, 1984), muskmelons (McCollum, et al., 1989), and tomatoes (Huber, 1983). Modification of cell wall hemicellulose may, in part, be due to cellulase (EC 3.2.1.4) activity that we have detected in 'Tommy Atkins' mangos (unpublished results). Cellulase activity has been reported in several Indian mango cultivars (Selvaraj and Kumar, 1989). Gel filtration of CSP and ASP indicated little change in pectin molecular weight with ripening (unpublished results), in agreement with Seymour et al. (1989). However, pectin aggregation potentially makes gel filtration a poor technique for molecular weight determination of pectins, particularly at ionic strength <100 mM (Fishman et al., 1990; Mort et al., 1991).

Despite apparent differences in biochemistry between 'Keitt' and 'Tommy Atkins', the two cultivars were similar when compared with other mango cultivars such as 'Ngowe', 'Harumanis', and 'Sensation'. Cell walls of both 'Keitt' and 'Tommy Atkins' had decreasing amounts of arabinosyl, galactosyl, and rhamnosyl residues with ripening, an increase in the amount of soluble uronides and CSP, and a considerable decrease in the molecular weight of the hemicellulosic fraction.

Literature Cited

- Brinson, K., P.M. Dey, M.A. John, and J.B. Pridham. 1988. Post-harvest changes in *Mangifera indica* mesocarp cell walls and cytoplasmic polysaccharides. *Phytochemistry* 27:719-723.
- Dische, Z. 1947. A new specific color reaction of hexuronic acids. *J. Biol. Chem.* 167:189-198.
- Dubois, M., K.A. Gilles, J.K. Hamilton, P.A. Rebers, and F. Smith. 1956. Calorimetric method for determination of sugars and related substances. *Anal. Chem.* 28:350-356.
- Food and Agriculture Organization, Annual Statistics. 1986.
- Fishman, M.L., K.C. Gross, D.T. Gillespie, and S.T. Sondney. 1990. Macromolecular components of tomato fruit pectin. *Arch. Biochem. Biophysics*. 274:179-192.
- Gross, K.C. 1982. A rapid and sensitive spectrophotometric method for assaying polygalacturonase using 2-cyanoacetamide. *Hort-Science* 17:933-934.
- Huber, D.J. 1983. Polyuronide degradation and hemicellulose modifications in ripening tomato fruit. *J. Amer. Soc. Hort. Sci.* 108:405-409.
- Huber, D.J. 1984. Strawberry fruit softening: The potential roles of polyuronides and hemicelluloses. *J. Food Sci.* 49:1310-1315.
- Jabati, M. 1989. Mangoes: An exotic choice. *Brit. Food J.* 91(3):31-33.
- Krishnamurthy, S. and H. Subramanyam. 1973. Pre- and post-harvest physiology of the mango fruit: A review. *Trop. Sci.* 15:167-193.
- Lazan, H., Z.M. Ali, L.K. Wah, J. Voon, and G.R. Chaplin. 1986. The potential role of polygalacturonase in pectin degradation and softening of mango fruit. *ASEAN Food J.* 2(3-4):93-98.
- McCollum, T.G., D.J. Huber, and D.J. Cantliffe. 1989. Modification of polyuronides and hemicelluloses during muskmelon fruit softening. *Physiol. Plant.* 76:303-308.
- Mitcham, E.J., K.C. Gross, and T.J. Ng. 1989. Tomato fruit cell wall synthesis during development and senescence. In *viva radiolabeling of wall fractions using [14C] sucrose*. *Plant Physiol.* 89:477-481.
- Mitcham, E.J. and R.E. McDonald. 1992. Effect of high temperature on cell wall metabolism associated with tomato (*Lycopersicon esculentum* Mill.) fruit ripening. *Postharvest Biol. Technol.* 1:257-264.
- Mort, A.J., B.M. Moerschbacher, M.L. Pierce, and N.O. Maness. 1991. Problems encountered during the extraction, purification, and chromatography of pectin fragments, and some solutions to them. *Carbohydrates Res.* 215:219-227.
- Proctor, A. and L.C. Peng. 1989. Pectin transitions during blueberry fruit development and ripening. *J. Food Sci.* 54:385-387.
- Redgwell, R.J., L.D. Melton, and D.J. Brasch. 1988. Cell-wall polysaccharides of kiwifruit (*Actinidia deliciosa*): Chemical features in different tissue zones of the fruit at harvest. *Carbohydrates Res.* 182:241-258.
- Roe, B. and J.H. Bruemmer. 1981. Changes in pectic substances and enzymes during ripening and storage of 'Keitt' mangos. *J. Food Sci.* 46: 186-189.
- Sauco, V.G. and D.F. Galvan. 1990. Differences between mango cultivars regarding their facility to be halved and spoon-eaten, and association with fiber. *Fruits* 45:381-385.
- Selvandran, R.R. 1975. Analysis of cell wall material from plant tissues: Extraction and purification. *Phytochemistry* 14:1011-1017.
- Selvaraj, Y. and R. Kumar. 1989. Studies on fruit softening enzymes and polyphenol oxidase activity in ripening mango (*Mungifera indica* L.) fruit. *J. Food Sci. Technol.* 26:218-222.
- Seymour, G.B., H. Wainwright, and G.A. Tucker. 1989. Cell wall changes in ripening mangoes. *Aspects Applied Biol.* 20:93-94.
- Spiro, R.G. 1966. Analysis of sugars found in glycoproteins. *Methods Enzymology.* 8:4-6.
- Updegraff, D.M. 1969. Semi-micro determination of cellulose in biological materials. *Anal. Biochem.* 32:420-424.