ELSEVIER

Food Chemistry **52** (1995) 405–410

0308-8146/95/$9.50

Microscopic and chemical changes occurring during the ripening of two forms of jackfruit (*Artocarpus heterophyllus* L.)

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(Received 16 March 1994; revised version received and accepted 6 June 1994)

Trees known to produce two distinct textural forms of jackfruit, in which the fruit either remained firm when ripe or became soft and pulpy, were sampled when fruit was immature (10–11 weeks after anthesis) and when judged ripe (15–16 weeks after anthesis). The dry matter content of the edible perianth increased with maturity from 125 to 215 and 140 to 240 g kg^{-1} wet weight perianth in the firm and soft fruits respectively. Perianth from immature fruits had a high water-insoluble content (840–890 g kg^{-1} dry matter) consisting largely of cell wall material (450–530 g kg^{-1} dry matter) and starch (approximately 330 g kg^{-1} dry matter). Microscopic examination of fruit at this stage showed the perianth to contain thin-walled cells packed with starch granules, some organised into distinct clusters. In ripe fruits the starch (20–110 g kg^{-1} dry matter) and cell wall (170–200 g kg^{-1} dry matter) contents were substantially reduced, the extent of hydrolysis being greatest in the soft form. Cell maceration and starch dissolution were evident in both forms of the fruit when examined by light microscopy, but were more pronounced in the soft form. Concomitant with the decrease in water-insoluble dry matter was a substantial increase of water-soluble material (660–790 g kg^{-1} dry matter) which included fructose (76–113 g kg^{-1} dry matter) and sucrose (approximately 95 g kg^{-1} dry matter). Mannitol (22–68 g kg^{-1} dry matter) was also found in ripe but not immature fruits. Concentration of low molecular weight carbohydrate was greatest in the soft form. Polygalacturonase and pectin esterase activities were 12-fold and 40-fold higher in ripe fruits of the soft form compared to those of the firm form. This was reflected in the greater extent of tissue maceration and loss of homogalacturonan in the soft form. Since both forms of fruit demonstrated a common pattern of ripening, textural differences evidently related to the extent of change which was greatest in the soft form. The firm form of jackfruit may represent fruit in which cell wall degradation is arrested or delayed during ripening and possibly this was related to a reduced capacity to produce pectic and other cell wall degrading enzymes.

INTRODUCTION

Jackfruit, a dicotyledonous compound fruit of the jack-tree (*Artocarpus heterophyllus* L.), grows in many of the countries of south-east Asia, but is particularly abundant in India and Bangladesh. Fruits, which usually reach 10–25 kg in weight, grow in summer when staple food-grains are often in short supply. During this lean period, the fruit can contribute substantially to the nutrition of the local population and their livestock. The energy available to humans in jackfruit has been calculated to provide approximately 2 MJ kg^{-1} wet weight ripe perianth (Ahmed *et al.*, 1986). For this reason it is commonly referred to as 'the poorman's food'.

Although the gross composition of jackfruit, its vitamin content and some of the volatile compounds contributing to its flavour have been documented (see Narasimham, 1990), little is specifically known about the chemical changes which accompany fruit ripening. The water-soluble sugar content of the ripe perianth

has been determined (Wills *et al.*, 1986; Selvaraj & Pal, 1989) and the presence of pectic substances and a mixed-linked (1,3),(1,4)-glucan briefly described (Sen-Gupta & Rao, 1963; Sen-Gupta & Das, 1964). Bobbio *et al.* (1978) also have reported the isolation of starch (25–40% of the total solid) from immature perianth. Considerable interest has also been shown in the properties of Jacalin, an α-D-galactose-binding lectin from jackfruit seed (see Kumar *et al.*, 1982).

Textural change in ripening fruit is associated with changes in cell wall composition and, particularly, in the loss of pectic substances. Increased production of pectic enzymes on ripening has been observed in a wide variety of temperate (King, 1990) and tropical fruits (Roe & Bruemmer, 1981; Joseph & Aworh, 1991; Aina & Oladunjoye, 1993). It has also been shown that fruit from transgenic tomato plants, in which polygalacturonase has been down-regulated, ripen naturally but retain a firm texture for longer periods than fruit from unmodified plants (Smith *et al.*, 1988). The jack-tree occurs naturally in two distinct locally recognised forms: in one the fruit becomes soft and pulpy when ripe while, in the other, the flesh remains firm. The present study was undertaken to examine the changes that occur during the ripening of jackfruit and to determine whether the two textural forms of the fruit could be related to differences in enzymatic activity and cell wall composition during maturation and the post-harvest ripening period.

MATERIALS AND METHODS

Fruit samples

Fruits were harvested immature (10–11 weeks after anthesis) and when mature (15–16 weeks after anthesis) from two trees growing in Dhaka, Bangladesh. One tree was of the kind that produced hard fruits, the perianth of which remained firm even at full ripeness. The second tree produced fruit whose perianth become soft and pulpy on ripening. Samples harvested from these two trees are referred to as FI (firm, immature), FM (firm, mature), SI (soft, immature) and SM (soft, mature). A fifth sample (SM2) was collected at maturity from a third tree that produced fruit of the soft variety. Mature fruits were stored after collection for a short period (1–2 days) at ambient temperature until judged fit for consumption. Immature fruits were processed immediately after harvest. In each case the edible perianth was manually separated from the remaining parts of the fruit and prepared for analysis or microscopic examination or freeze-dried for subsequent extraction and analysis.

Preparation of samples for chemical analysis

Extraction of water-soluble carbohydrate

Perianth (approximately 150 g dry matter) was homogenised with cold distilled water (500 ml) to produce a fine slurry. The slurry was filtered through cotton cloth and the residue retained by the cloth washed with water (2 × 250 ml). The initial filtrate and washings were combined and centrifuged (3500 rpm). The supernatant from the centrifugation was concentrated by rotary evaporation under reduced pressure at 40°C and clarified by re-centrifugation. All insoluble materials from centrifugations were added to the residue retained by the cloth (Fraction E). Ethanol (4 vols) was added to the clarified supernatant and left overnight, and the precipitate formed was collected by centrifugation. The supernatant from ethanol precipitation was freed from alcohol by the repeated addition of water followed by rotary evaporation and then freeze-dried (Fraction A). Material precipitated by addition of ethanol was dissolved in water and dialysed for 16 h against 4-hourly changes of distilled water. Material passing through the dialysis bag (< 10 000 mol. wt) was separately collected, concentrated and freeze-dried (Fraction B). A small amount of material precipitated out of solution on dialysis. This was collected by centrifugation and freeze-dried (Fraction D). The clear supernatant containing material retained by the dialysis bag was also concentrated by rotary evaporation and freeze-dried (Fraction C).

Removal and measurement of starch

Starch removal and measurement essentially followed the method described by Aman and Hesselman (1984) based on the use of a thermostable α-amylase (Termamyl, NOVO a/s, Copenhagen, Denmark, EC 3.2.1.1). For starch determinations, samples (400 mg) were incubated with Termamyl for 30 min at 100°C in 0·1 M, pH 5·6, sodium acetate buffer followed by treatment with amyloglucosidase (AMG, EC 3.2.1.3) at pH 4·5 for 16 h at 60°C. The starch content was calculated from the released glucose estimated by the glucose hexokinase (Stein, 1963) or phenol-sulphuric acid (Dubois *et al.*, 1956) methods. Volumes of Termamyl and buffer were increased proportionally for the bulk removal of starch from water-extracted residues (Fraction E) and the subsequent treatment with AMG excluded. Starch-free residues were recovered, after washing, by centrifugation and then freeze-dried (Fraction F).

Extraction of pectic polysaccharide

Trans-1,2-diamino cyclohexane-N-N-N'-N'-tetraacetic acid (CDTA, 0·05 M, 500 ml) was added to 10 g of the destarched perianth (Fraction F) and stirred overnight (Jarvis, 1982: Redgwell *et al.*, 1988). The resulting suspension was centrifuged for 30 min and the supernatant from centrifugation dialysed exhaustively (60 h) against distilled water. High molecular weight material retained in the dialysis bag was concentrated by rotary evaporation and freeze-dried (Fraction G) and the residue thoroughly washed and freeze-dried (Fraction H).

Chemical analysis

Total carbohydrates were measured by the phenol-sul-

phuric acid method (Dubois *et al.*, 1956) and total uronic acids by the method described by Blumenkrantz and Asboe-Hansen (1973). The monosaccharide composition of the polysaccharides was determined as their alditol acetates (Blakeney *et al.*, 1983) after hydrolysis with 2 M trifluroacetic acid at 121°C. Soluble sugars were separated and measured by HPLC on a 25 cm × 4·6 mm i.d. Apex 5 μm silica column modified with amine modifier 1 (AM1, Institute für Naturwissenschaftliche Technische, Dienste GmbH, Hamburg, Germany). Samples were eluted with acetonitrile:water: AM1 (78:22:0·01) at a rate of 1·5 ml min^{-1} and detected by change in refractive index of the eluent stream.

Extraction and measurement of pectic enzymes

Fresh perianth (approximately 50 g) was homogenised with 200 ml of 0·1% CHAPS (3-[(3- cholamidopropyl)-dimethylammonio]-l-propanesulphonate) in 0·1 M, pH 6·5 acetate buffer. The resulting suspension was centrifuged for 30 min at 4°C, and the recovered supernatant dialysed against running tap water for 12 h and then against distilled water for a further 6 h. Material retained in the dialysis bag was centrifuged at 20000 rpm for 30 min at 4°C and the clear solution recovered was divided into portions and stored at –25°C until required.

Polygalacturonase (PG, EC 3.2.1.15) and endo-β-glucanase (EC 3.2.1.4) activities were detected by the release of reducing groups from polygalacturonic acid and carboxymethyl cellulose respectively. Assays were made at pH 4·5 (0·1 M acetate buffer and pH 7·0 (0·1 M phosphate buffer) and reducing group release after 1 h at 40°C measured following the Nelson-Somogyi method (Somogyi, 1952). Pectin esterase (PE, EC 3.1.1.11) activity was detected by the release of methanol from a high-methoxy citrus pectin at 40°C and pH 4·5 and 7·0 measured by the colorimetric method of Wood and Siddiqui (1971). A unit of enzyme activity was defined as that amount of enzyme required to release 1 μmol reducing group equivalent (PG and β-glucanase) or methanol (PE) min^{-1} under the conditions described.

Preparation of samples for microscopy

Fresh perianth samples were fixed in 2·5% glutaraldehyde in 0·1 M, pH 7·3, phosphate buffer, and dehydrated with increasing concentrations of ethanol. Samples for examination by light microscopy were embedded in LKB historesin (Cambridge Instruments, Cambridge, UK). Transverse 3μm sections were cut from the embedded perianth using a Riechert-Jung microtome and stained with toluidine blue or with iodine in potassium iodide for the detection of starch. Stained slides were viewed and photographed using Leitz Orthoplan and Orthomat microscopes. For scanning electron microscopy, the fixed and dehydrated perianth samples were placed on stubs and coated in an emscope SC500 splutter coater with 22 nm of platinum. These were viewed and photographed in a Cambridge Stereoscan-600 scanning electron microscope.

RESULTS AND DISCUSSION

The dry matter content of the fruit increased with maturity. Values rose from 125 to 215 and 140 to 240 g kg^{-1} wet weight perianth in the case of the firm and soft fruits respectively. Fruit of the soft type from the second tree (SM2) had a similar dry matter content (237 g kg^{-1} wet weight perianth) at maturity. These values are in good agreement with previously published dry matter contents of jackfruit (Selvaraj & Pal, 1989). With the exception of banana (248–312 g kg^{-1}) and the semi-wild lukluki (502 g kg^{-1}), the dry matter content of jackfruit perianth is considerably higher than those of other edible fruits found in Bangladesh (Nahar *et al.*, 1990; Rahman *et al.*, 1991).

Aqueous extraction of perianth samples gave five fractions, Fraction A representing low molecular weight material not precipitated by ethanol, Fraction B material precipitated by ethanol but not retained on dialysis, Fractions C + D high molecular weight polymers retained on dialysis and Fraction E, the insoluble residue. It is evident from Table 1 that most dry matter was found in Fractions A and E and that, during ripening, there was major solubilisation of the water-insoluble material contributing to Fraction E of the immature fruit. The extent of this solubilisation was greater in the soft than in the firm fruit. This was supported by the analysis of the pooled Fractions A + B which showed that the soluble sugars, glucose, fructose and sucrose, largely absent from the immature fruits, accounted for 20% (FM) and 30% (SM) of perianth dry matter in ripe fruits (Table 2). Unusually, mannitol, a hexitol not normally associated with plant tissues, was found in ripe fruits in amounts representing 2% of the firm fruit and 7% of the soft form. Its identity was confirmed by reference to the chromatographic properties of the authentic compound and by ^{13}C NMR (data not shown). Ribitol (1–2 g kg^{-1} perianth dry matter) was also detected in ripe but not immature fruits while *myo*-inositol, a frequently occurring component of

Table 1. Recovery of dry matter in Fractions A–E obtained by the aqueous extraction of perianth from firm (F) and soft (S) forms of jackfruit harvested at two stages of maturity

Sample	Dry matter content of fractions (g kg^{-1} perianth dry matter)					
	A	B	C	D	E	Total
FI	56·6	13·3	8·7	10·0	885·0	973·6
FM	424·7	149·3	56·0	2·6	336·0	968·6
SI	95·1	11·1	7·9	3·7	840·0	957·8
SM	527·2	172·0	38·4	2·3	210·0	949·9
SM2	554·0	nd	41·0	nd	nd	

nd = Not determined.

Table 2. Total low molecular weight carbohydrate (TC), uronic acid (TUA), monosaccharides, alditols and disaccharide in Fractions (A + B) extracted with water from the perianth of firm (F) and soft (S) forms of jackfruit harvested at two stages of maturity

Sample	g kg^{-1} Perianth dry matter						
	Glucose	Fructose	Sucrose	Mannitol	Total	TC	TUA
FI	1·3	15·0	nd	nd	13·6	9·0	1·8
FM	1·8	75·6	97·0	22·3	197	274	7·1
SI	nd	20·0	nd	nd	20·0	13·6	2·2
SM	7·2	113	92·7	67·5	280	365	7·0

nd = Not detected.

Table 4. Starch content of the perianths of firm (F) and soft (S) forms of jackfruit harvested at two stages of maturity (g kg^{-1} perianth dry matter)

Sample	Dry matter loss on extraction (g)	Starch content calculated from released glucose determined by		Starch-free cell wall (g)
		Phenol-sulphuric	Glucose-hexokinase	
FI	352·5	298	299	532·5
FM	140·0	99·4	109	196·0
SI	386·4	316	326	453·6
SM	41·4	22·1	20·0	168·5

plant tissues, was found in trace amounts in the immature perianths but not in the ripe fruit. The difference between the measured total carbohydrate (Table 2) and the dry matter content of Fractions A + B (Table 1) indicated the presence of other low molecular weight material, probably the organic acids, salts and nitrogenous compounds detected by Selvaraj and Pal (1989), although these were not identified.

Very little high molecular weight material (Fractions C and D) was extracted from immature fruits (10–20 g kg^{-1} perianth dry matter) although this value increased with maturity (40–60 g kg^{-1} perianth dry matter). Glucose was the found in all hydrolysates of Fraction C and was probably a product of the hydrolysis of a small amount of soluble starch present (Table 3). Certainly the material precipitated during dialysis (Fraction D) provided largely glucose on hydrolysis, stained positive with iodine/KI and could be digested with α-amylase. After glucose, arabinose and galactose were the predominate monosaccharides obtained after hydrolysis of Fraction C from immature fruit and probably derived from a small amount of soluble arabinogalactan extracted from perianth cell walls. Uronic acid, in the form of water-soluble (rhamno)galacturonan, was present in high amounts in Fraction C from the SM samples but not in the corresponding sample from the firm fruit; this could indicate a greater mobilisation of cell wall material in the soft form of jackfruit on ripening.

The starch content of the immature perianth accounted for approximately one-third of dry matter, while in the ripe perianth concentrations fell to 100 g kg^{-1} dry matter in the case of firm fruit and 20 g kg^{-1} dry matter in the soft fruit (Table 4). Microscopic observations (LM and SEM) showed that the perianth of immature fruits consisted predominantly of thin-walled cells densely packed with starch granules, some granules occurring in well-defined clusters. Numbers of starch granules were much reduced both in number and in size in the ripe fruit and many cells were free of iodine-staining material. Garcia and Lajolo (1988) similarly noted a reduction in the dimensions of starch granules in ripening banana fruit. There was good agreement between the two methods used to measure glucose released by α-amylase and AMG, and the estimated starch content accounted in large measure for the loss of dry matter following starch extraction. Hydrolysis of starch and generation of free sugars and other soluble carbohydrates during the ripening process has been commonly observed in fruits including kiwifruit (MacRae *et al.*, 1989), Indian mangoes (Selvaraj *et al.*, 1989), banana (Chacon *et al.*, 1987; Garcia & Lajolo, 1988) and breadfruit (Biale & Young, 1981).

Coincidental with the breakdown of starch and increase in soluble sugar content in the ripening fruit was the loss of cell wall material (Table 5). The starch-free cell wall content fell from approximately 450–530 g kg^{-1} perianth dry matter in the immature fruit to less than 200 g kg^{-1} perianth dry matter in the ripe fruit. Cell wall content was lowest in the SM sample. Extensive cell separation (maceration) and breakdown was evident in light micrographs of ripe jackfruit perianth, particularly in the soft form.

Table 3. The monosaccharide composition of the high-molecular weight material extracted with water from the perianth of firm (F) and soft (S) forms of jackfruit (Fraction C) harvested at two stages of maturity

Sample	Monosaccharides (mole%)						
	Rhamnose	Arabinose	Xylose	Mannose	Galactose	Glucose	Uronide
FI	1·9	10·3	5·1	2·6	17·0	54·4	8·7
FM	0·7	2·7	0·4	6·9	3·5	79·7	6·1
SI	3·4	19·3	8·0	7·2	37·3	13·5	11·3
SM	2·5	7·0	0·6	0·9	7·0	41·7	40·3
SM2	2·2	18·8	0·4	1·2	7·6	32·1	37·8

Table 5. CDTA extraction of starch-free cell walls from the perianth of firm (F) and soft (S) forms of jackfruit harvested at two stages of maturity. Results are expressed as g kg^{-1} perianth dry matter

Sample	Dry matter solubilised by CDTA	CDTA-soluble carbohydrate recovered after dialysis	Amount of residue remaining after CDTA extraction
FI	106·2	119	426·3
FM	78·7	52·7	117·0
SI	117·6	135	336·0
SM	88·2	38·4	80·0

Table 6. Monosaccharide and uronic acid content of CDTA extracts (Fraction G) of perianth from firm (F) and soft (S) forms of jackfruit harvested at two stages of maturity

Sample	Monosaccharides (mole%)							
	Rhamnose	Fructose	Arabinose	Xylose	Galactose	Mannose	Glucose	UA
FI	0·13	1·44	4·35	nd	13·1	0·57	1·54	78·9
FM	0·06	0·83	1·00	1·38	1·05	0·39	7·97	87·3
SI	nd	1·42	5·38	0·32	15·3	0·52	7·78	69·2
SM	nd	2·38	2·88	0·40	2·79	0·70	2·09	88·8

nd = Not detected.

Table 7. Polygalacturonase (PG), pectin esterase (PE) and β-glucanase (BG) activity in the perianths of mature firm (F) and soft (S) jackfruit

Sample	pH of assay	Enzyme activity (units g^{-1} wet weight perianth)		
		PG	PE	BG
FM	4·5	55	11	166
	7·0	33	55	61
SM	4·5	676	47	181
	7·0	262	2215	105

Extraction of starch-free cell walls with CDTA, known to selectively remove homogalacturonan from the wall (Jarvis, 1982), solubilised greater amounts of carbohydrate from immature cell walls than from walls of the ripe fruit (Table 5). However, this was a product of the greater amount of cell wall material present in the immature fruits. When expressed on a proportional basis, approximately one-quarter of the wall was solubilised regardless of the form of the fruit or its stage of maturity. This implied that the loss of cell wall material during ripening was not selective and that pectic and non-pectic components were removed from the wall at a similar rate.

Determination of the neutral sugar and uronic acid content of the carbohydrate solubilised with CDTA (Table 6) confirmed the presence of homogalacturonan as previously reported (Sen-Gupta & Rao, 1963; Sen-Gupta & Das, 1964). Very little rhamnogalacturonan was co-extracted with the homogalacturonan, as shown by the low levels of rhamnose detected. However, further small amounts of arabinogalactan, in addition to that detected in aqueous extracts (Fraction C), were extracted by CDTA from the immature perianth of both firm and soft forms of the fruit. Although arabinogalactans are commonly associated with pectic polysaccharides, often linked through the O-4 of in-chain rhamnose (Lau *et al.*, 1985), the water- and CDTA-soluble arabinogalactan extracted probably represented a discrete polymer little associated with galacturonan. This fraction of the cell wall appeared largely absent in the ripe fruit.

The concentration of polygalacturonase and pectin esterase was 12-fold and 40-fold higher respectively in mature fruit of the soft form compared to mature firm fruit (Table 7). Both of these enzymes have been implicated in the ripening process and, PG in particular, with loss of fruit texture (Ahmed & Labavitch, 1980; Soda *et al.*, 1987; Aina & Oladunjoye, 1993). The high levels of these enzymes observed were compatible with microscopic observations which showed considerable evidence of maceration in the soft fruit consistent with a loss of pectic polysaccharide. Activity against carboxymethyl cellulose was also monitored to provide a marker for other wall-degrading activities. The general loss of cell wall material measured in fruits of both forms required the presence of β-glucanase and other enzymes active against wall polysaccharides other than the pectic polysaccharides. There was, however, no evidence to suggest that β-glucanase activity was greater in the soft form of jackfruit.

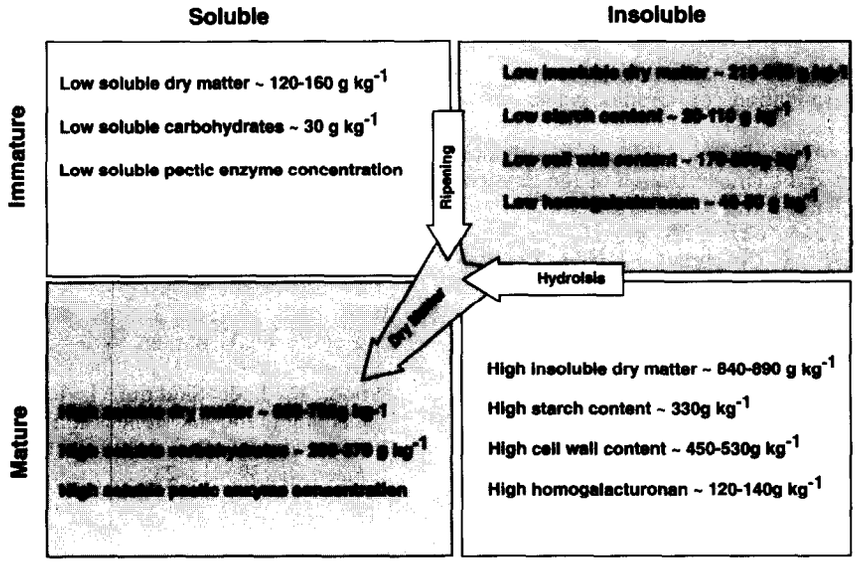

Fig. 1. A summary of the principal changes occurring during the ripening of the firm and soft forms of jackfruit.

Although both the firm and soft forms of jackfruit followed the ripening process summarised in Fig. 1 and common to most other fruits, there were clear differences between the two forms which related to the extent of change rather than its nature. Thus the soft form, when ripe, showed a greater loss of starch, perianth cell wall and pectic polysaccharide than the firm form and, conversely, a greater accumulation of soluble, low molecular weight carbohydrate and more extensive tissue maceration. It is possible that the textural differences between the two forms of fruit which appear on ripening reflect their various capacities to produce pectic enzymes related during the ripening process and that the firm form represents fruit in which cell wall degradation is arrested or delayed.

ACKNOWLEDGEMENTS

The authors would like to thank the British Council for the provision of a fellowship for A.K.M.M.R to work at the Rowett Research Institute and the Scottish Office Agriculture and Fisheries Department (SOAFD) for making available the necessary facilities.

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