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The roles of cell wall polymers and intracellular components in the thermal softening of cassava roots

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Abstract

Cassava varieties Iapar 19 – *Pioneira* (short cooking time, domestic vegetable), *Taquari* (medium-to-long cooking time, domestic vegetable), and *Branca de Santa Catarina* (long cooking time, industrial vegetable), were selected in order to investigate the cell wall and compositional basis for these textural differences. *Pioneira* had lower levels of Ca^{2+} and Mg^{2+}, and higher levels of phytic acid and monovalent cations than the longer cooking time varieties. Detailed cell wall analysis indicated that the longer cooking *Branca* cultivar had higher levels of chelator-insoluble pectic polysaccharides. The potential causative roles of these different features were evaluated using vortex-induced cell separation (VICS) studies. Time to achieve the complete VICS of *Branca* cultivar was reduced to that of *Pioneira* with externally-supplied chelating agents (CDTA) and Na_2CO_3. *Taquari* roots did not respond in this way indicating a different biochemical basis for the maintenance of cell adhesion. The results are discussed in relation to the thermal stability of texture in these cassava varieties.

Keywords: *Manihot esculenta* Crantz; Monosaccharides; Phytic acid; Minerals; Cell adhesion

1. Introduction

Cassava (*Manihot esculenta* Crantz) is one of the most important food crops in tropical regions of the world, being a staple source of energy carbohydrates for human consumption. Isolated cassava starch is a functional ingredient used in food, paper, textile and pharmaceutical industries and has economic value for the starch exporting countries. Cassava roots may be consumed in different ways, for example: as locally fermented products, as industrialized flour or after boiling the fresh roots (similar to potatoes). The main problem for the consumers of boiled fresh cassava roots concerns the final texture. In certain cases, root tissues fail to soften, or soften poorly even after a prolonged period of cooking (Padonou, Mestres, & Nago, 2005 and Ngeve, 2003). Cooking time varies with varieties and time elapsed from planting date; older roots generally take longer to cook (Beleia, Prudencio-Ferreira, Yamashita, Sakamoto, & Ito, 2004 and Ngeve, 2003). In Brazil a variety is considered of good cooking quality when it cooks to a final, friable texture in less than 20 min (Pereira, Lorenzi, & Valle, 1985). Many investigations have focused on the role that starch plays in determining cooking time and final texture, but no clear conclusions have been reached (Padonou et al., 2005; Safo-Kantanka & Owusu-Nipah, 1992). Whilst it is accepted that the softening of starchy vegetables, brought about by hydrothermal treatment, is accompanied by the hydration, swelling and gelatinization of intracellular starch (Shomer,

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1995), softening is also influenced by the cell wall and the intercellular material (Waldron, Parker, & Smith, 2003). The final texture is likely to be dependent on the properties of cell wall components, their compositions, proportions and interactions in relation to the different levels of structure (Waldron et al., 2003), including the molecular mechanism by which cells adhere to each other. Thermal treatments can reduce intercellular adhesive strength resulting in cell separation and tissue softening (Parker, Parker, Smith, & Waldron, 2001).

Cassava cell wall composition has been described by Salvador, Suganuma, Kitahara, Tanoue, & Ichiki, 2000 and Kajiwara & Maeda, 1983, but these studies did not investigate the cooking of fresh roots. The objective of this study was to characterize and evaluate the compositions of a range of cassava roots and identify any possible relationships with the time taken for thermally-induced softening.

2. Materials and methods

2.1. Plant material

Cassava varieties used in the experiment were IAPAR-19 *Pioneira*, *Taquari* and *Branca de Santa Catarina*. Materials were harvested seven and 12 months after planting date. The seven month old samples were prepared as AIR (alcohol insoluble residue) for cell wall fractionation and chemical composition.

2.2. Cooking time

Cooking time was determined by cutting roots into 1.5 cm cubes and thermally treated in boiling, distilled water (300 g L^{-1}) in covered stainless steel processing equipment, until soft enough for a fork to penetrate the friable tissue. Softening time was evaluated in four replicates. Subsequently, thermally-processed tissue and accompanying liquor were recovered separately. Root tissues were analyzed for mass gain (hydration) and the cooking water for soluble and insoluble solids.

2.3. Hydration analysis

Hydration was defined as the mass gain of the tissue after thermal processing and was quantified by the difference between the fresh weight and the weight after processing using the following formula:

$$\%\ \text{Hydration} = \frac{(\text{mass after cooking} - \text{mass of fresh tissue}) \times 100}{\text{mass of fresh tissue}}$$

2.4. Total solids

Total solids were determined in fresh tissues by drying at 60 °C for 16 h in a forced air circulation oven (Fanen 320 SE, Brazil). Cooking water was centrifuged at 4000 rpm (Sanyo Harrier 15/80 Japan) for 20 min, and fractionated in soluble and insoluble material. Soluble fraction was concentrated at 78 °C in the forced circulation oven in dried, pre-weighted aluminum dishes, then for 16 h at 45 °C and then transferred quantitatively to a Petri dish. Soluble and insoluble residues were lyophilized and then quantified gravimetrically.

2.5. Proximate composition

Measurements of protein, lipids, starch and ashes were made following AOAC methods (AOAC, 1984).

2.6. Minerals

Ashes were dissolved in hydrochloric acid 3 M and divalent ions, Ca^{++} and Mg^{++} were determined by atomic absorption (Perkin Elmer 503) while monovalent ions K^{+} and Na^{+} were analyzed by a flame photometer (Micronal – B262, Brazil).

2.7. Phytic acid

Phytic acid was extracted with a solution of 2.4% hydrochloric acid, separated in glass column with resin Dowex-1 AG X-4 (Sigma) eluted with 0.7 M NaCl and quantified by Wade reagent (Latta & Eskin, 1980).

2.8. Isolation of cell wall material

Cell wall material (CWM) was isolated as follows: Initially, a cold alcohol-insoluble residue (AIR) was prepared from fresh cut cassava tissue by homogenizing in a blender with 95% (w/w) ethanol, vacuum filtered and washed successively with ethanol in a ratio of 1 kg cassava: 4 L 95% ethanol. Extracted solids were air-dried at 45 °C for 48 h in a forced circulation oven (Tecnal, Brazil). Light microscopy showed that the AIR contained intact cells rich in starch. AIR (13 g) was further disrupted by suspending in 35 mL deionised water and 50 mL 1.5% SDS containing 3 mM Na_2S_2O, and homogenizing for 5 min with an Ystral homogenizer after which the volume was brought to 200 mL and centrifuged at 8000 rpm for 30 min at 20 °C. The precipitate was suspended in 100 mL 0.5% SDS in 3 mM $Na_2S_2O_5$ (100 mL) and ball milled for 3 h at 4 °C, centrifuged and again extracted successively with 250 mL 90% dimethylsulfoxide (DMSO) four times: first for 16 h, 3 h, 3 h, and again for 16 h until all visible starch (as visualized by microscopy and staining in I/KI) was eliminated. The final residue was suspended in water (final volume 200 mL). An aliquot of 10% of the final volume was taken, centrifuged, suspended in acetone and filtered through GF/C, air-dried and the weight recorded to calculate the CWM yield. Determination of monosaccharide and uronic acids was from the dry CWM material while the remaining volume was frozen at −20 °C in hydrated form until required.

2.9. Carbohydrate composition

To quantify carbohydrate sugars were released from dry CWM by dispersing in 720 g kg^1 H_2SO_4 for 3 h at room temperature, followed by dilution to 1 M and hydrolyzing for 2.5 h at 100 °C (Saeman, Moore, Mitchell, & Millett, 1954). Neutral sugars were reduced with $NaBH_4$ and acetylated by the method of Blakeney, Harris, Henry, and Stone (1983) using 2-deoxyglucose as an internal standard. Alditol acetates were quantified by gas chromatography on a Carlo Erba Vega gas chromatograph with automatic injection. Alditol acetates were separated with base line resolution on a Restek RT_x 225 WCOT column (15 m × 0.32 mm i.d.; 0.25 u film) using an oven temperature program of 90 °C for 1 min, 45 °C increase per min to 150 °C, 150 °C for 1 min, 2 °C per min to 210 °C, and 210 °C for 1.5 min. Carrier gas was helium with a column head pressure of 60 Kpa. Detection was by flame ionisation. Total uronic acid content was determined by colorimetric method using *m*-hydroxydiphenyl (Ahmed & Labavitch, 1977) after dispersal in 720 g kg^{-1} H_2SO_4 dilution to 1 M, and hydrolysis for 1 h at 100 °C (Selvendran, Verne, & Faulks, 1989).

2.10. Fractionation of CWM

Cell wall polysaccharides were sequentially extracted by the method based on that developed for extracting polymers from the cell walls of onion bulbs (Redgwell & Selvendran, 1986). CWM (1.5 g) was sequentially extracted with (i) 2 M imidazole (150 mL) pH 7.0 at 20 °C overnight; (ii) 50 mM cyclohexane-trans-1,2-diamine-*N*,*N*,*N*′,*N*′-tetra-acetate (CDTA, Na salt, 150 mL) pH 6,5 at 20 °C for 6 h (CDTA 1); (iii) CDTA (150 mL) pH 6,5 at 20 °C for 2 h (CDTA-2); (iv) 50 mM Na_2CO_3 + 20 mM $NaBH_4$ (150 mL) at 1 °C for 16 h (Na_2CO_3-1); (v) 50 mM Na_2CO_3 + 20 mM $NaBH_4$ (150 mL) at 20 °C for 2 h (Na_2CO_3-2); (vi) 0.5 M KOH + 20 mM $NaBH_4$ (150 mL) at 20 °C for 2 (kOH-1); (vii) 1.0 M KOH + 20 mM $NaBH_4$ (150 mL) at 20 °C for 2 (kOH-2); (vii) 4.0 M KOH + 20 mM $NaBH_4$ (150 mL) at 20 °C for 2 (kOH-3). Alkaline extraction solvents were prepared using degassed water. All residues were suspended initially in 75 mL of degassed water and then the solvents were added to make up the final concentration. After each extraction, the soluble polymers were separated from the insoluble residue by centrifugation at 4 °C. The extracts were filtered through glass fiber filter GFC (Whatman). The alkali extracts after filtration and the cellulose-rich residue remaining after the final extraction (KOH 1 M) were neutralized to pH 7.0 with acetic acid. The extracts and residue were dialysed exhaustively at 1 °C and lyophilised.

2.11. Vortex-induced cell separation (VICS)

Frozen tissue was tested for VICS as described by Parker & Waldron (1995). The tendency for cell separation was determined by placing two cassava sections (2 mm × 2 mm × 2 mm) from frozen tissue into each of eight screw-capped tubes with 2 mL of one of the following solutions: water, 2 M imidazole, 50 mM CDTA pH 6.5 and 50 mM Na_2CO_3. The tubes were heated for 5 min intervals in boiling water, shaken vigorously 10 times, and vortexed for 1 min. Scores were assigned according to the degree of disruption: (0) each tissue section intact; (1) 80% of intact amylaceous parenchyma tissue; (2) 60% of intact tissue; (3) 40% of intact tissue; (4) 20% of intact tissue; (5) tissue completely disrupted, only intact vessels present. Intermediate values were apportioned if necessary. The VICS assays were generally carried out up to 60 min and the score recorded.

3. Results and discussion

3.1. General composition

Proximate compositions of peeled fresh cassava varieties of 7 and 12 months in age are shown in Table 1. Although some analyses show significant differences between the varieties and ages, there are no clear trends to indicate any relationships between the levels of the measured components and cooking times.

CWM was prepared from 7-month old cassava roots and their yields were similar at between 3.3 and 3.5 g 100 g^{-1}. This is consistent with values of cell wall-rich fiber which varied between 2.63 and 4.92 g 100 g^{-1} in the cultivars analyzed by Padonou et al. (2005). However, Salvador et al. (2000) found 7.3% of CWM in cassava, but starch was separated by washing in running water (23.3% residue) followed by alpha-amylase hydrolysis of the residual starch. Considering the greater care taken in this study to remove the starch component, it is possible that their sample still had some starch included in intact cells and calculated as CWM after using the alpha-amylase hydrolysis method for starch elimination.

3.2. Cooking times, hydration and dissolution

Cooking times were evaluated by thermally processing uniform cubes of root tissue at 100 °C until they reached similar, acceptable levels of softness. The results are shown in Table 1. As expected, *Pioneira* exhibited the fastest cooking times which were 13 and 16 min for 7 and 12-month-old root tissues respectively. In contrast, the *Taquari* and *Branca* root tissues exhibited the slowest cooking times, mostly around 30 min except for 12-month-old *Branca* which cooked in 23 min. Softening was accompanied by hydration and the release of soluble and insoluble solids.

The degree of hydration was inversely associated with the rate of thermal softening (Fig. 1). Water absorption during cooking is often considered to be a desirable quality for cassava tissue because it is considered to be associated with a short cooking time and final texture, and the hydration results of this study are in keeping with the findings of

Table 1
Composition (dry basis) of peeled fresh and cooking times roots of cassava varieties harvested at seven and twelve months after planting

Variety age (months)	*Pioneira*		*Taquari*		*Branca*	
	7	12	7	12	7	12
Cooking time (min)	13 ± 0.82	16 ± 0.3	29 ± 3.6	33 ± 3.4	30 ± 6.3	23 ± 1.4
Composition (g 100 g^{-1})						
Solids	$37.1^{b} \pm 1.5$	$37.1^{b} \pm 0.4$	$40.1^{a} \pm 1.1$	$39.6^{a} \pm 0.2$	$39.5^{a} \pm 1.2$	$34.3^{c} \pm 0.2$
Ashes	$1.9^{a} \pm 0.1$	$2.3^{a} \pm 0.1$	$1.7^{b} \pm 0.2$	1.7b ± 0.5	1.4c ± 0.1	1.8b ± 0.1
Protein	$2.7^{a} \pm 0.1$	$2.0^{c} \pm 0.1$	$2.2^{b} \pm 0.1$	$2.0^{b} \pm 0.1$	$2.6^{a} \pm 0.2$	$2.8^{a} \pm 0.1$
Lipids	$0.4^{a} \pm 0.1$	ND	$0.5^{a} \pm 0.1$	ND	$0.4^{a} \pm 0.1$	ND
Phytic acid(mg 100^{-1} g)	$365.3^{a} \pm 35$	$320^{b} \pm 21$	$315.3^{b} \pm 14$	$258.8^{c} \pm 27$	$266^{c} \pm 22$	$181^{d} \pm 5.6$
Minerals (mg 100^{-1} g)						
Calcium	$72.5^{b} \pm 1.7$	$81.5^{b} \pm 1.8$	$81^{a} \pm 3.6$	$87.5^{b} \pm 7.1$	$78.3^{a} \pm 1.7$	$141.7^{a} \pm 3.5$
Magnesium	$68.8^{c} \pm 2.5$	$56.0^{c} \pm 0.6$	$118.5^{a} \pm 2.4$	$135.0^{a} \pm 1.3$	$100.0^{b} \pm 0.8$	$103.0^{b} \pm 9.4$
Potassium	$981.3^{a} \pm 26$	$1010^{a} \pm 18$	$748.0^{b} \pm 21$	$572.0^{b} \pm 14$	$665.0^{c} \pm 12$	$500.0^{c} \pm 21$
Sodium	$14.0^{b} \pm 1.8$	$16.0^{b} \pm 1.4$	$18.5^{ab} \pm 2.4$	$22.0^{a} \pm 3.3$	$20.5^{a} \pm 2.6$	$21.0^{a} \pm 2.2$
Cell wall material (g 100 g^{-1})						
CWM	3.5	ND	3.3	ND	3.4	ND
Hydration after cooking, soluble solids and insoluble solids in the cooking water						
Hydration	$12^{a} \pm 1.6$	$19.4^{a} \pm 0.9$	$15.4^{a} \pm 2.1$	$3.7^{c} \pm 1.9$	$3^{c} \pm 2.1$	$7.4^{b} \pm 1.1$
Soluble solids	$1a^{b} \pm 0.1$	$2.6^{a} \pm 0.1$	$0.7^{b} \pm 0.1$	$1.8^{b} \pm 0.3$	$1.3^{a} \pm 0.2$	$1.8^{b} \pm 0.1$
Insolublesolids	$11.8^{a} \pm 1.3$	2.75	$4.3^{bc} \pm 1$	0.05	$6.1^{b} \pm 1.9$	0.15

Mean values with different letters in the same row are statistically different (Tukey $p < 0.05$). ND: not determined.
Data are mean ($n = 4$) ± standard deviation ($n = 3$).

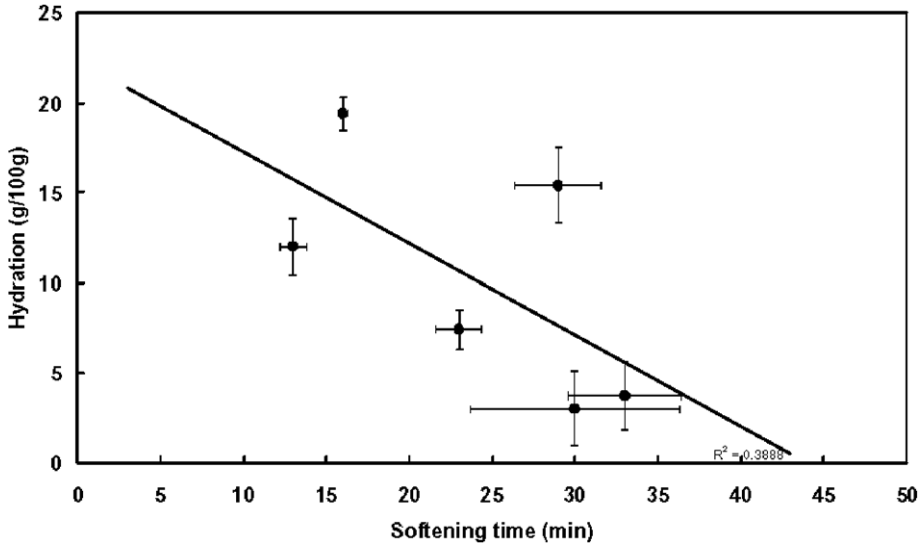

Fig. 1. Association between cooking time and hydration of cassava tissues.

Beleia et al. (2004) and Pereira et al. (1985). The release of insoluble solids was greatest in 7-month old Pionera, and much reduced in all the other samples.

This property relates to the ease by which cells are sloughed from the surface of the tissues during cooking as a result of the breakdown of cell adhesion and associated cell separation. The reduced cell sloughing in the tissues with longer cooking times is consistent with more robust cell adhesion, indicative of a more thermally stable middle lamella. Soluble solids showed no relationship with cooking time, but were significantly higher in 12-month old root tissues compared with those of 7 months age (Table 1).

3.3. Role of phytate and cations in thermal softening

Phytic acid is known to influence the rate of softening of plant tissues during thermal processing by acting as a chelator of divalent cations, thereby preventing them from combining with pectic polysaccharides to form cross-linked, insoluble pectates. The latter is important in maintaining the structural integrity of the tissue hampering softening during the cooking process. This relationship has been discussed mostly for legume grains, and demonstrated in beans where high phytic acid content favored a rapid rate of softening (Moscoso, Bourne, & Hood, 1984). In the current

study the levels of phytate exhibited a general inverse correlation with the increased time of thermal softening (Fig. 2).

Phytic acid varied from 365.3 mg/100 g for *Pioneira* seven months to 188 mg/100 g for *Branca* 12 months. All varieties exhibited lower levels of phytic acid as the roots aged; *Branca* had a decrease of 32.1% from 7 to 12 months. Marfo, Simpson, Idowu, & Oke, 1990 determined phytic acid in cassava as 624 mg/100 g of dry matter and Adeyeye, Arogundade, Akintayo, Aisida, & Alao, 2000 as 530 mg/100 g (Table 1).

Cations also exhibited differences in relation to the rate of softening. *Pioneira* had the lowest concentration of divalent ions (calcium plus magnesium), and the highest of the monovalent, (sodium plus potassium). Indeed, the ratio of divalent/monovalent cations increased with cooking time (Fig. 3).

3.4. Cultivar differerences in cell wall chemistry

Since there is little definitive information on the composition of Cassava cell walls in relation to texture, CWM was prepared from the 7-month old cultivars (Table 1). Hydrolysis with 72% sulfuric acid resulted mostly in glucose, galactose and uronic acid. The bulk of the glucose was derived from cellulose, as inferred from the observation that only a small proportion was released by hydrolysis solely in 1 M H_2SO_4. The sugar composition was similar to that reported by Kajiwara and Maeda (1983) and Salvador et al. (2000) in CWM isolated using amylase to hydrolyze starch components. Little difference was observed in the CWM sugar compositions of the different cultivars (Table 2).

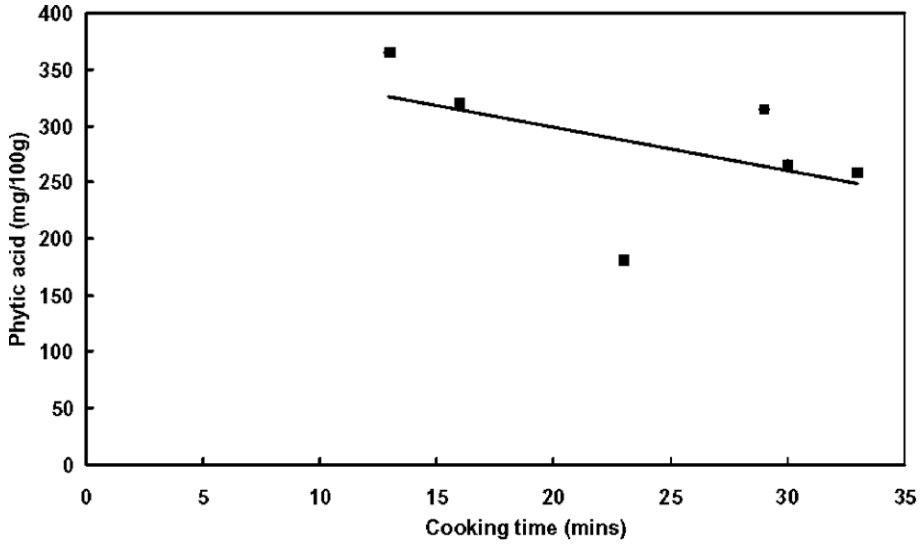

Fig. 2. Relationship between phytic acid and cooking time.

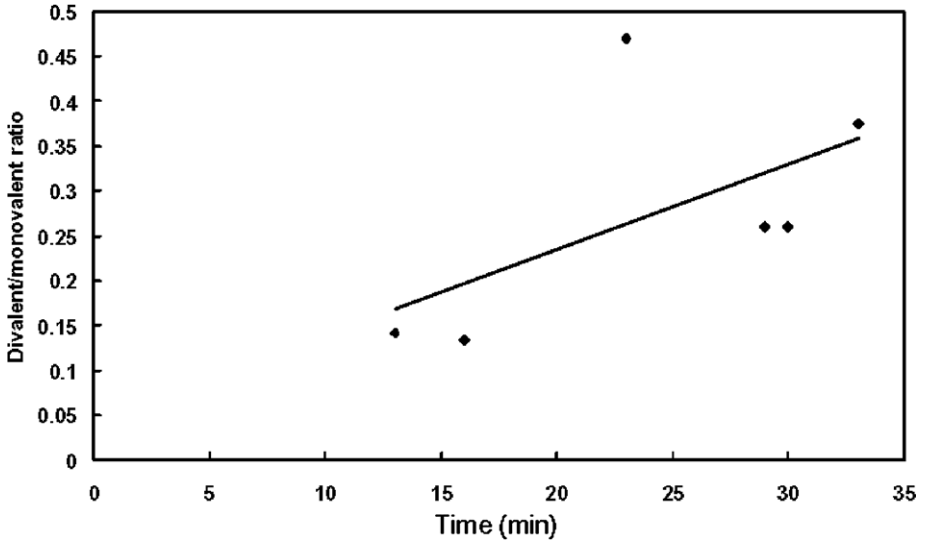

Fig. 3. Relationship between the ratio of divalent/monovalent cations, and cooking time of cassava tissues.

Table 2
Cell wall sugars in CWM of cassava varieties

Sample	Yield (% CWM)	Cell wall sugars (mol %)							Uronic acids
		Rha	Fuc	Ara	Xyl	Man	Gal	Glc (1 M)[a]	
CWM									
Pioneira		2.9	0.9	6.4	9.4	2	19.2	45.3 (6.1)	14
Taquari		2.2	0.7	4.8	4.6	1.5	22.3	50.4 (7.2)	13.5
Branca		2.5	0.7	5.7	7.5	1.8	18.5	42.1 (6.4)	21.2
Imidazole 2 M									
Pioneira	1	4.4	0.5	27.9	0	2.3	24.8	14.1	26
Branca	0.8	3.6	0.3	30.8	0.6	1.4	28.2	21.1	14
CDTA 6 h									
Pioneira	12.8	4.7	0.4	4.9	5.3	1.8	8.2	3.7	71
Branca	9.1	3.4	0.4	3.8	1	0.3	6.5	2.1	82.5
CDTA 2 h									
Pioneira	18.6	7.5	1.2	17.3	10.8	3.1	12.2	11.6	36.4
Branca	11.4	4.3	1.5	21.2	8	4.3	11.2	15.9	34
Na_2CO_3 1 °C									
Pioneira	7.6	4.9	0.5	10.7	0.8	0.5	28.6	3.3	50.6
Branca	7.7	5.5	0.4	12.5	0.7	0.3	27.8	3.0	49.7
Na_2CO_3 20 °C									
Pioneira	1.2	6.6	0.5	15.3	1.7	0.7	44.5	4.5	26.2
Branca	1.2	4.5	0.3	12.6	1.1	0.7	49.9	2.9	28
KOH 0.5 M									
Pioneira	1.6	2.4	0.8	5.3	63.6	0.5	10.5	6.7	12.4
Branca	2.1	2.4	0.9	5.7	53.8	0.6	13.8	9.2	13.4
KOH 1 M									
Pioneira	2.4	1.2	3.4	2.4	48.6	1.5	10.9	24.6	7.4
Branca	3.5	1.3	3.5	2.6	47.6	0.5	11.5	24.6	8.3
KOH 4 M									
Pioneira	4.3	1	4.3	2	28.7	10.6	11.5	34.8	7.2
Branca	5.1	1	4.3	3	32.6	9.9	11.4	34.5	3.4
Final residue									
Pioneira	42.6	3	0.3	5.7	2.3	0.8	19.4	55.5	12.9
Branca	51.5	3.2	0.3	5.9	2.2	1.1	24	51.9	11.3

[a] Hydrolysis in 1 M H_2SO_4.

In order to see if the cell wall polymer chemistry might provide insight into the different cooking characteristics, CWM from the *Pioneira* and *Branca* cultivars were extracted sequentially using approaches that minimize their degradation (Redgwell & Selvendran, 1986). The initial extractions involved the solubilization of calcium-cross-linked pectic polysaccharides using the chelating agents Imidazole and CDTA. The extracted polymers comprised mainly pectic polysaccharides as inferred from the levels of uronic acid, rhamnose, arabinose and galactose. The imidazole extracted relatively small quantities of pectic polysaccharides (Table 2) compared with both CDTA extractions. However, the Imidazole-extracted pectic polymers were more highly-branched as indicated by their higher levels of galactose and arabinose, and concomitantly lower levels of uronic acid. CDTA (2)-extracted polymers also contained significant quantities of xyloglucan polymers as inferred from the levels of glucose and xylose. Sodium carbonate releases additional cell wall polymers probably through de-esterification. Both sodium carbonate treatments released more highly-branched pectic polysaccharides compared with the chelator-soluble pectic polymers, and this was particularly evident in the second sodium carbonate extracts. Extraction of the sodium carbonate residues with increasing strengths of alkali was carried out to release hemicellulosic polymers. 0.5 M KOH solubilized a mixture of polymers. The high levels of xylose indicated the presence of xylan hemicelluloses, probably along with xylogclucans since glucose was also present. The remainder included pectic polymers, as indicated by the uronic acid, arabinose and galactose. Higher concentrations of alkali extracted further xylose-containing hemicellulosic polymers, increasingly rich in xyloglucans; 4 M KOH also contained significant quantities of mannose and galactose, indicating the presence of galactomannans. The final cellulosic residue was comprised mainly of cellulose (approximately 50%) and highly-branched galactan-rich pectic polymers. There were no obvious compositional differences between the cell wall fractions from *Pioneira* and *Branca*. However, according to the yields, *Pioneira*

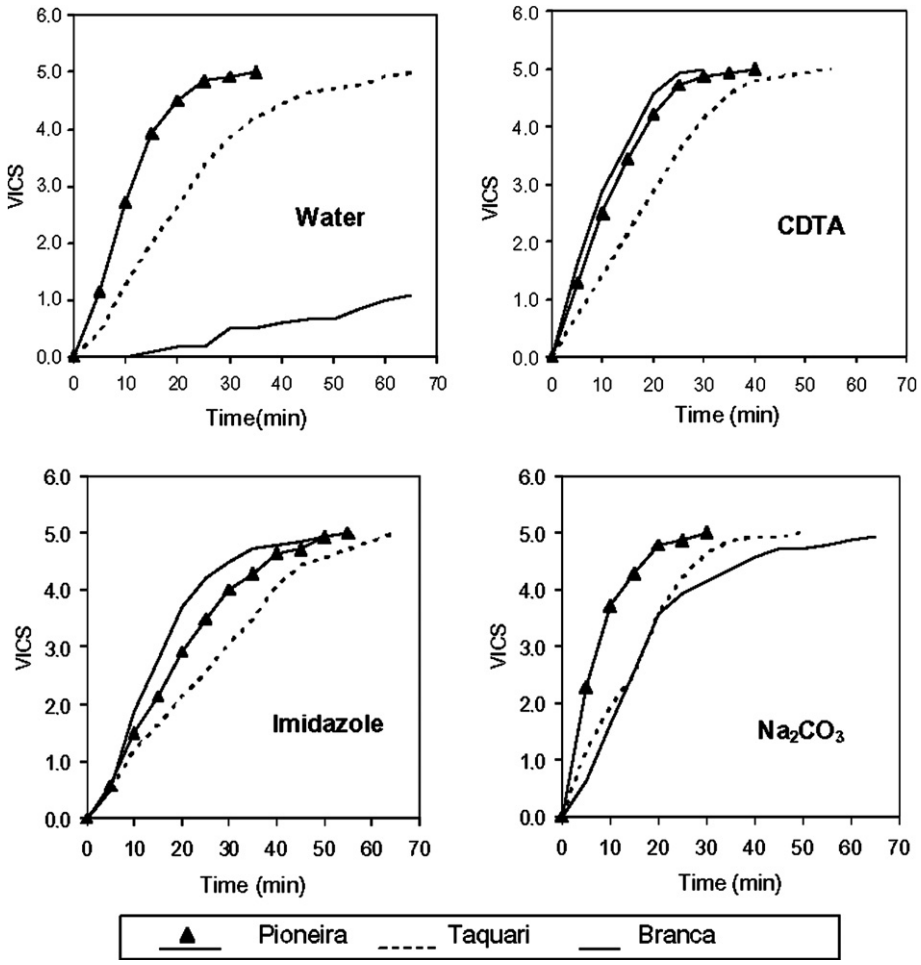

Fig. 4. Vortex-induced cell separation (VICS) profile of cassava root tissues in different solvents at 100 °C.

contained larger quantities of CDTA-soluble pectic polymers and correspondingly less in the cellulose-rich residue, indicating a lower level of covalent cross-linking within the pectic community.

As discussed above, the longer cooking times of *Branca* and *Taquari* were associated with larger ratios of divalent to monovalent cations, and lower quantities of intracellular phytate. In order to evaluate whether or not these criteria might be causally related to the cooking properties, sections of the cassava roots were subjected to vortex-induced cell separation (VICS) in the presence of a range of chelating and other cell wall modifying solvents. VICS is a technique which enables information on the chemistry of cell adhesion to be gained. By extracting intact tissues in solvents that modify cell wall chemistry and then observing the degree of cell separation on vortexing, aspects of adhesion chemistry can be inferred (Ng & Waldron, 1997; Waldron, 1997). Initially, VICS was evaluated in water at 100 °C. *Pioneira* tissue was completely disrupted within 30 min. However, in keeping with their longer cooking times, *Taquari* took about 60 min to become completely disrupted, and *Branca* was only partially disrupted after an hour (Fig. 4).

VICS in 2 M Imidazole or 0.1 M CDTA had no significant impact on *Pioneira*, but completely reversed the thermal stability of texture demonstrated by *Branca* as did VICS in hot Na_2CO_3 (Fig. 4) which would have depolymerised pectic polysaccharides involved in cell adhesion. Interestingly, these chelating agents had little impact on the tissues of the *Taquari* cultivar. This indicates that the *Taquari* cultivar rate of softening is not limited by the levels of chelating agents. It is possible that the rate of beta-elimination of those pectic polysaccharides involved in cell adhesion is an important rate-limiting characteristic in this cultivar and requires further investigation.

4. Conclusions

The results of this study support the hypothesis that the rapid thermal softening of *Pioneira* root tissues is dependent, in part, on the phytate-chelation of divalent cations that cross-link pectic polysaccharides involved in cell adhesion. The longer cooking times of *Branca* root tissues can be reversed with external-supplied chelating agents, and is probably related to the lower levels of intracellular phytate and higher levels of cross-linking divalent cations. In

contrast, chelators had no effect on thermal softening of *Taquari* cultivar, indicating that some other mechanism is involved in the thermal stability of texture. In this respect, further studies to investigate the levels of pectic methyl esterification are being considered.

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