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Research Article

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Contrasting effects of polysaccharide components on the cooking properties of roots, tubers and bananas

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Abstract

BACKGROUND: Consumer preferences for boiled or fried pieces of roots, tubers and bananas (RTBs) are mainly related to their texture. Different raw and cooked RTBs were physiochemically characterized to determine the effect of biochemical components on their cooking properties.

RESULTS: Firmness in boiled sweetpotato increases with sugar and amylose contents but no significant correlation was observed between other physicochemical characteristics and cooking behaviour. Hardness of boiled yam can be predicted by dry matter (DM) and galacturonic acid (GalA) levels. For cassava, no significant correlation was found between textural

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properties of boiled roots and DM, but amylose and Ca^{2+} content were correlated with firmness, negatively and positively, respectively. Water absorption of cassava root pieces boiled in calcium chloride solutions was much lower, providing indirect evidence that pectins are involved in determining cooking quality. A highly positive correlation between textural attributes and DM was observed for fried plantain, but no significant correlation was found with GalA, although frying slightly reduced GalA.

CONCLUSION: The effect of main components on texture after cooking differs for the various RTBs. The effect of global DM and major components (i.e. starch, amylose) is prominent for yam, plantain and sweetpotato. Pectins also play an important role on the texture of boiled yam and play a prominent role for cassava through interaction with Ca^{2+}.

Supporting information may be found in the online version of this article.

Keywords: cooking behaviour; texture; dry matter; multivariate statistics; galacturonic acid; amylose; pectins

INTRODUCTION

Roots, tubers and bananas (RTB) play an essential role as staple foods in the tropics and subtropics, particularly in Africa. As a result of their adaptability in different ecosystems and high yields compared to local cereals, they are a primary and reliable source of calories.[1] Breeding programmes for RTB crops initially gave priority to yield and disease/pest resistance, but now end-product quality traits and processor and consumer preferences must be considered for improving varietal adoption.[2]

The main characteristics preferred by RTB consumers have been described recently.[1] Generally, important RTB quality traits for consumers are texture attributes such as rapid softening and/or the development of friability or mealiness and/or short cooking time for boiled products[3,4]; smooth and stretchy dough for pounded products (matooke, pounded yam, eba)[5]; softness and texture in the mouth for cassava-derived products[6]; and softness of cooked plantain.[7,8] However, reliable means of phenotyping textural properties and an understanding of the biochemical and genetic basis of textural variation are not available for most RTB.

Progress has been made in understanding the molecular basis of cooking time in some RTB crops. In potato (*Solanum tuberosum*) Ducreux *et al.*[9] showed that tubers from the Phureja Group have much shorter cooking time than those from the Tuberosum Group.[10] Expression profiles in tubers from Tuberosum and Phureja types were significantly different for genes involved in cell wall modification, which could contribute to textural differences.[9] In particular, the differentially expressed genes included a pectin methyl esterase gene (PME; EC 3.1.1.11) involved in the modification of pectin structure. PME activity was significantly lower in Phureja genotypes and transgenic experiments demonstrated a linkage between PME gene expression and tuber texture and cooking time.[11,12] PME may extend cooking time in Tuberosum group tubers by strengthening of cell walls through the removal of methyl esters from pectin in a blockwise fashion.[13] These demethylated pectin chains can then chelate calcium ions to form egg box structures that strengthen the cell wall.[14]

The textural properties of sweetpotato are complex but not directly linked to total starch and amylose contents.[3] The joint effects of starch and pectin breakdown during cooking appear to be the major factors in cooking time and may explain the soggy texture of cooked roots[15] of some genotypes. Sweetpotato β-amylase catalyzes the hydrolysis of starch to oligomers during cooking and contributes to the mealy texture of cooked roots.[16] A negative correlation between β-amylase activity and firmness for boiled roots has been reported.[3] In addition, an increase in cell wall thickness has been observed in cooked roots, particularly in precooked roots at 70 °C.[15] This may be linked to PME activity, which can modify the cell wall during cooking at 100 °C and at 70 °C.[17] Precooking sweetpotato root has been recommended to reduce enzymatic pectin hydrolysis.[15]

Preparation of each type of yam product requires specific quality attributes, but texture attributes are always important. For boiled yam, friability is the most important,[4] whereas pounded yam must be stretchable, mouldable, smooth, fairly firm, soft and sticky,[4,5,18] and 'amala' should be elastic, soft and non-sticky.[19] Several studies have shown a link between starch content, starch structure or composition and the texture of the desired products. 'Amala' stickiness was associated with soluble amylose, starch gelatinization temperature and enthalpy changes,[20] whereas pounded yam firmness was associated with DM, soluble starch and amylose content.[21] Several studies found correlation between yam cooking properties with intrinsic starch properties.[22-25] In addition, the structure of cell walls must play a role in texture. The extent of cell disintegration appears to be linked to firmness,[25] as well as the thickness of cell walls.[21] Also, studies with chelating agents (phytates) indicate the possible importance of pectins and the level of lignins have also been implicated.[26]

The texture and cooking quality of boiled cassava is highly variable depending on cultivar,[27-29] age at harvest and environmental conditions.[30] Although sensory-based phenotyping is available, limitations exist.[31] No clear link between starch and texture of cooked cassava roots has been found,[28] but several studies have indicated possible effects of intercellular adhesion, cell wall components and pectins.[32] Moreover, a recent genome-wide association study provided the first insights into understanding the underlying genetic basis of boiled cassava roots texture and pointed to the putative role of α-amylase and PME inhibitors, which impact the structure and properties of starch and pectins, respectively.[31]

The texture and cooking behaviour of cooking and dessert bananas depend on variety, ripening stage and cooking method.[7,33-35] For boiled banana and plantain, Gibert *et al.*[34] established a correlation between the initial DM content of raw crops (positively correlated to starch content) and firmness, as well as a strong contribution of starch gelatinization to thermal softening. Thermal softening in the early stages of boiling has also been related to middle lamella dissolution causing cell wall separation.[33] However, to our knowledge, no data has been published on relationships between polysaccharides and fried plantain textural characteristics.

Robust standard operating procedures for assessing biochemical components and their relationship with textural characteristics of boiled or fried pieces for whole RTBs are described in the present study. Investigations across a broad spectrum of RTB products would provide novel insights possibly suggesting that a diversity of biochemical traits is important for textural traits in RTB crops. Robust phenotyping methods and the development of genetic markers will accelerate breeding efforts to develop varieties with improved traits that are important to the consumer.

MATERIALS AND METHODS

Sweetpotato

Seventeen sweetpotato genotypes were grown in replicated field trials in Uganda in 2019 using standard agronomic practices. Roots were harvested and firmness were measured after cooking cubes of 2.5 cm^3 at 85 °C for 15 min,[3] with 300 g of sample cooked in 2 L of water. Fresh samples were freeze-dried for 48–72 h for further analyses: DM was assessed by weight difference after freeze-drying[3]; free sugars were measured by HPLC[36]; starch was predicted by near infrared spectroscopy; amylose content, starch gelatinization temperature and enthalpy were determined by DSC,[20,37] PME[38] and β-amylase (BETAMYL-3® METHOD) activities; and temperature, peak and final viscosities for 7% flour dry basis (db) suspension were evaluated with a Rapid Visco Analyser (RVA) (PerkinElmer, Waltham, MA, USA) in 25 mL of water with or without inhibitor.[39] In addition, cell walls were prepared after starch hydrolysis and protein solubilization[40] and monosaccharide analysis of cell walls was carried out according to McDougall et al., (2021).[41] Fourier transform infrared (FT-IR) spectroscopy was used to investigate the degree of esterification of pectin, a major cell wall component, McDougall *et al*.[42]

Yam

Yam tubers were harvested in 2021 and 2022 at INRAE and CIRAD stations (five and six genotypes, respectively) in Guadeloupe (France) and others collected from different markets in 2022 in Benin (three cultivars). Each cultivar (three tubers) was washed and peeled; proximal, central and distal parts were analyzed separately.[43] Hardness and DM were determined on fresh and stored yams,[43,44] whereas starch and galacturonic acid (GalA) contents were determined on freeze dried samples.[45,46]

Cassava

Two populations of cassava roots were evaluated. Firstly, a panel of 200 cassava genotypes from a NaCRRI population was evaluated at Namulonge and Serere (Central and Eastern Uganda, respectively). Second, a panel of 29 cassava landraces with good to poor cooking behaviour were grown and harvested from the same field at CIAT (Palmira, Colombia) at three different ages: 9, 10 and 12 months after planting (MAP). DM of fresh roots was determined by NIRS (at both NaCRRI and CIAT[47]) and confirmed by oven drying (105 °C overnight). Texture of boiled roots (18 min) was determined using the same standard operating procedure (SOP) at NaCCRI and CIAT[48]; and maximum force (g), area (g × mm) and initial gradient (g/mm, after 1 mm of extrusion) were calculated. For the NaCRRI population, amylose content also was determined using a colorimetric assay,[49] and, for the CIAT population, water absorption (WA) after 30 min boiling[29,50] and total pectin content (as GalA equivalent[46]) were determined in triplicate. Calcium content of freeze-dried cassava roots from CIAT was determined by X-ray fluorescence spectrometry[51,52] on duplicates (harvests at 9 and 12 MAP). To test the effect of calcium on cooking behaviour, fresh cassava root pieces were marinated in solutions of calcium chloride ($CaCl_2$, concentrations from 0 to 8 g Ca^{2+} L^{-1}) at room temperature for 24 h, then boiled in the marinating $CaCl_2$ solutions for 30 min and WA measured.

Fried plantain

Seven plantain varieties (Corne 1, Saci, Bita 3, Pita 3, Zakoi, FHIA 21) were grown under conventional growing conditions. Fruits were harvested at commercial maturity corresponding to the appearance of the first yellow finger on the bunch and kept to ripen at room temperature. They were sampled at four ripening stages: green (G), yellow tip green (GT), yellow (Y), and yellow tiger (YT). *Aloco* was prepared as described before[53] and the sensory analysis performed by a trained panel. Three texture attributes were evaluated directly on a scale of 1 (very weak) to 10 (very strong) for firmness and stickiness. For chewiness, the chew count varies greatly from one panellist to another. Therefore, the number of chews was previously computed in a non-dimensionalized form for each panellist and then converted to a scale value between 1 and 10 (1 being the lowest dimensionless value of all products and all panellists and 10 being the highest). DM and starch were determined in the raw samples as described[45] and on alcohol insoluble solids using the total starch enzymatic assay kit (K-TSTA Megazyme, Wicklow, Ireland), respectively. Pectin content in Gal A equivalents was determined in both raw and fried form as described by Mestres et al.[46] Measurements were performed in triplicate.

Statistical analysis

Analysis of variance, mean comparison tests (Tukey), and one way or two ways correlations tests (using Pearson's test) were performed.

RESULTS

Boiled sweetpotato

Roots exhibited a wide range of firmness (from 1.1 to 3.5 kg) (see Supporting information, Table S1) with a significant effect of cultivar. Several physico-chemical properties of sweetpotato did not vary much between cultivars (e.g. starch characteristics and pasting properties with inhibitor), whereas others displayed very wide variation such as β-amylase (from 0.09 to 2.87 μmol s^{-1} g^{-1}) or PME (0.51–2.92 pmol s^{-1} g^{-1} db) activities (see Supporting information, Table S2). The cell walls (CW) from the different genotypes (approximately 10% db) all yielded similar main monosaccharide products, with arabinose and galactose as major constituents (more than 50% of CW). The amount of GalA is indicative of pectin content; and it varied considerably from 0.9 to 10.1% of CW (i.e. 0.03–0.47% of root db). The ratio of FT-IR signals at 1730/1625 cm^{-1} and 1415/1235 cm^{-1} of CW preparations can be used to assess the relative level of pectin methylation and the intensity of these signals varied considerably between the different genotypes (see Supporting information, Fig. S1).

Among the 17 cultivars, the roots exhibited a wide range of pasting properties measured by RVA, with or without inhibitor (see Supporting information, Table S1). As expected, we observed a negative correlation between starch content and free sugars ($r = -0.83$); and positive correlations between starch content and pasting viscosities (particularly with inhibitor; see Supporting

Source	Value	Standard error	Pr > |t|
Constant	−3.19	1.93	0.12
Free sugars (%, db)	0.10	0.04	0.028
Amylose (%, db)	0.28	0.13	0.050

db: dry basis

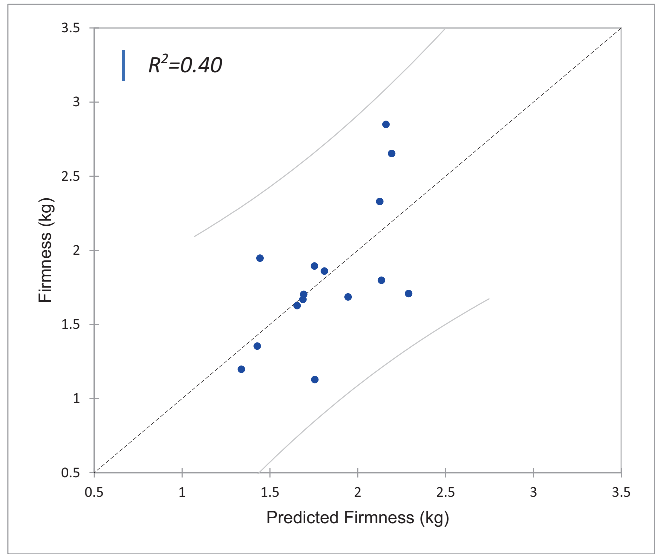

Figure 1. Model parameters for predicting firmness of sweetpotato and plot of predicted *versus* observed firmness.

information, Table S3); and also between DSC gelatinization temperature and pasting peak temperature. There was a dramatic decrease of pasting viscosities when inhibitor was omitted, which was surely linked to amylase activity. CW yield was negatively correlated with pasting viscosities with inhibitor (see Supporting information, Table S3), although there was no significant correlation between PME activity, or FTIR ratio with peak viscosities or flour pasting behaviour.

No evidence of a direct correlation between biophysical characteristics and firmness was observed (see Supporting information, Table S3). However, a multiple regression performed on 15 samples (because some data were lacking for two samples) identified two characteristics that can be used to predict firmness (Fig. 1), with firmness increased with sugars and amylose contents. On the other hand, no significant correlation between firmness and beta-amylase activity was found (see Supporting information, Table S3), as already noted for sweetpotato,[3] and/or with PME activity and pectin methylation as already observed for potato.[11,12]

Boiled yam

DM content varied between 25.7% and 40.5% and starch content, between 55.9 and 82.5 g per 100 g db (see Supporting information, Table S4). Both ranges similar to those previously published.[21,25,54] GalA content varied widely from 0.62 up to 3.18 g per 100 g db (see Supporting information, Table S4), which was higher than reported earlier[55] (i.e. 0.11–0.29 g GalA per 100 g for cell walls from *Dioscorea rotundata* and *Dioscorea dumetorum*). Hardness after boiling varied between 1.5 and 14.5 N.

DM and starch contents were not significantly different between the different tuber sections (see Supporting information, Table S4). However, GalA levels were significantly higher in the proximal sections for most cultivars. In parallel, a significant section effect was observed for the hardness for two cultivars (61F and 74F) with the proximal section always the hardest.

Considering the results obtained from all tubers, hardness of boiled yam was found to be related to DM and GalA (Table 1). However, it is important to note that correlations were not significant when hardness was low (between 1.5 and 5.9 N, 80% of total dataset). This led to the conclusion that 20% of the dataset, with hardness > 6 N, made the correlation significant. Hence, further work is required with samples of more contrasting hardness to confirm or rule out this tendency.

Nevertheless, considering DM and GalA contents as predictive variables, a model for hardness was developed by linear regression (Fig. 2). This model satisfactorily predicts hardness (r^2 = 0.76 and root mean square error = 0.37) for this particular set. Again, such a model must be tested and adjusted using a larger set of samples exhibiting larger differences in terms of hardness after cooking.

Boiled cassava

Significant differences were observed among cassava genotypes for DM, amylose, and total pectins), and cooking quality traits (force, area, and gradient; WA). Among the NaCRRI breeding population, the average DM (28% wb) (Fig. 3) was lower than the CIAT population (average 36.4%) (Fig. 4). The amylose content of NaCRRI genotypes ranged from 20% to 30% (db), which is slightly higher than typical literature values,[56] possibly because the perchloric acid extraction procedure could overestimate amylose content as already observed with potato starch.[49]

DM was not directly correlated with cooking quality of boiled cassava, as determined by WA and texture measurements of both NaCRRI and CIAT populations (Figs 3 and 4, respectively), which confirmed previous observations.[28,29] A significant negative relationship was observed between amylose content and textural

Table 1. Pearson correlation between hardness, dry matter, starch and GalA contents measured for 24 yam samples

Variables	DM	Starch	GalA
Starch	0.223 (0.30)	1	
GalA	−0.082 (0.70)	**−0.524 (0.01)**	1
Hardness	**0.694 (0.00)**	−0.265 (0.21)	**0.464 (0.02)**

Note: Probability levels are shown within parenthesis. Bold value represent the correlation is significant.
Abbreviations: DM, dry matter; GalA, galacturonic acid.

Source	Value	Standard error	Pr > |t|
Constant	–14.3	2.5	< 0,0001
Dry matter (g/g wb)	0.51	0.07	< 0,0001
Galacturonic Acid (g/100 g db)	3.41	0.70	< 0,0001

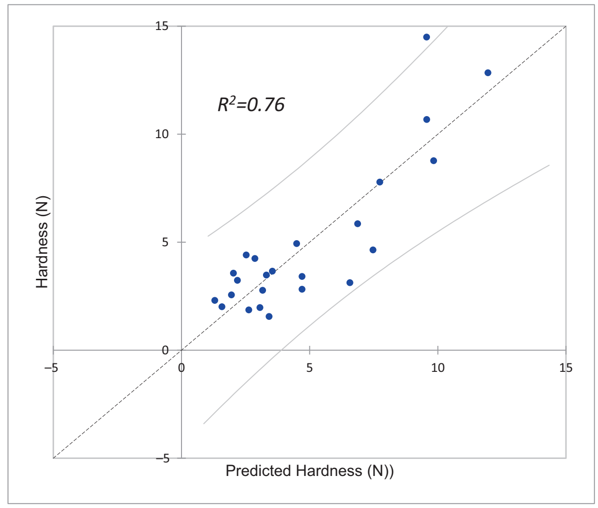

Figure 2. Model parameters for predicting hardness of boiled yam and plot of predicted *versus* observed hardness.

properties of boiled roots (Fig. 3). A higher total pectin content was related to harder texture after boiling and lower WA (Fig. 4). However, the coefficients of determination between gradient, for example, were low with amylose and pectins ($r^2 = 0.20$ and 0.38, respectively), indicating that other factors may be at play in determining cooking quality.

Ca^{2+} content appeared highly correlated with texture ($r^2 = 0.53$, gradient $= 0.81 \times Ca^{2+} + 0.81$), possibly because of pectin and Ca^{2+} complexation resulting in a stiffer pectin network.[14] The increased WA of root pieces marinated and then boiled in $CaCl_2$ solutions provided additional indirect evidence that pectins are involved in determining cooking quality (see Supporting information, Fig. S2). As the Ca^{2+} concentration increased and strengthened the pectin network through complexation,[14] WA30 decreased towards the same lower limit (2–3%) across several genotypes of contrasting cooking quality. That lower limit may correspond to the point when the pectin network became saturated with Ca^{2+} ions. Additionally, higher pectin content appeared related to lower DM and higher calcium content in fresh cassava roots ($r^2 = 0.25$ and 0.47, respectively), which may reflect both the water retention properties of pectins and their chelation of calcium ions.

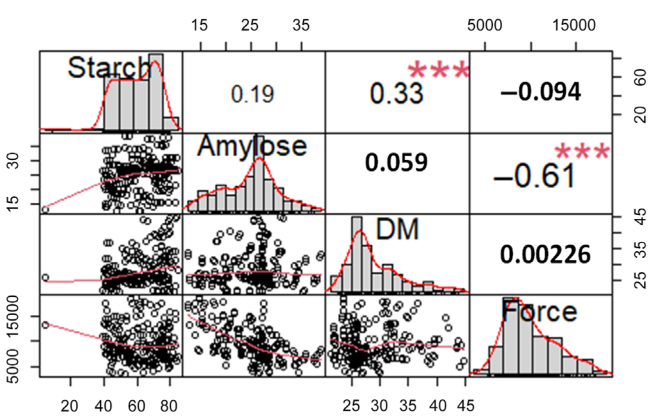

Figure 3. Distribution of amylose (% db), DM (% wb), force (g), area (g. mm), and initial gradient (g mm^{-1}) among 200 genotypes of cassava (NaCRRI population), and correlation analysis. Values indicate the coefficients of correlation (*r*). Asterisks (***) indicate statistically significant correlations ($P < 0.05$).

Fried plantain

For raw plantains and regardless of ripening stage, DM varied from 18.6 to 40.4 g per 100 g WW and total pectin fr0m 0.65 to 3.38 g of GalA per 100 g DW (see Supporting information, Table S5). At the yellow stage (the favoured consumption stage), starch content in fried plantain varied from 17.2 to 55.7 g per 100 g dry solid and GalA between 1.99 and 2.81 g per 100 g dry solid. A large increase of pectin content was observed during ripening of four varieties (Fig. 5a), combined with a slight decrease of DM (Fig. 5b). DM and starch contents agreed with previous values in the literature[33,34,57] whereas total pectin contents were significantly higher than values in the literature,[33,57] possibly as a result of differences in the extraction methods used.

In parallel, three texture attributes (firmness, chewiness, and stickiness) of fried plantain were evaluated. The overall analysis of the data set, regardless of variety and harvest stage, indicated a correlation between DM and two sensorial attributes (positive with firmness and negative with stickiness). However, no correlation between sensorial attributes and pectin content was observed (Table 2; see also Supporting information, Fig. S3).

DISCUSSION

The RTB samples in the present study represent the broadest range of textural properties of cooked products previously examined, and the relationships with physicochemical parameters (DM, starch, amylose, cell wall, pectin and Ca^{2+} content, and PME activity) (Table 3) provide an opportunity to test hypotheses about the biochemical parameters that control such textural variation.

Impact of dry matter, starch, and amylose on cooking properties

Theoretically, hardness should increase with DM of RTB samples because water can plasticize the system. It is largely observed in pasty products, such as in pounded yam,[21] but positive correlations were only found between DM of raw samples and the hardness of boiled yam (as already reported[58,59]) and fried (see Supporting information, Fig. S3) and boiled plantain.[34] No significant correlation was however observed between DM and texture of boiled sweetpotato or cassava; and direct correlation between texture of boiled cassava and DM is indeed rarely observed.[27,60]

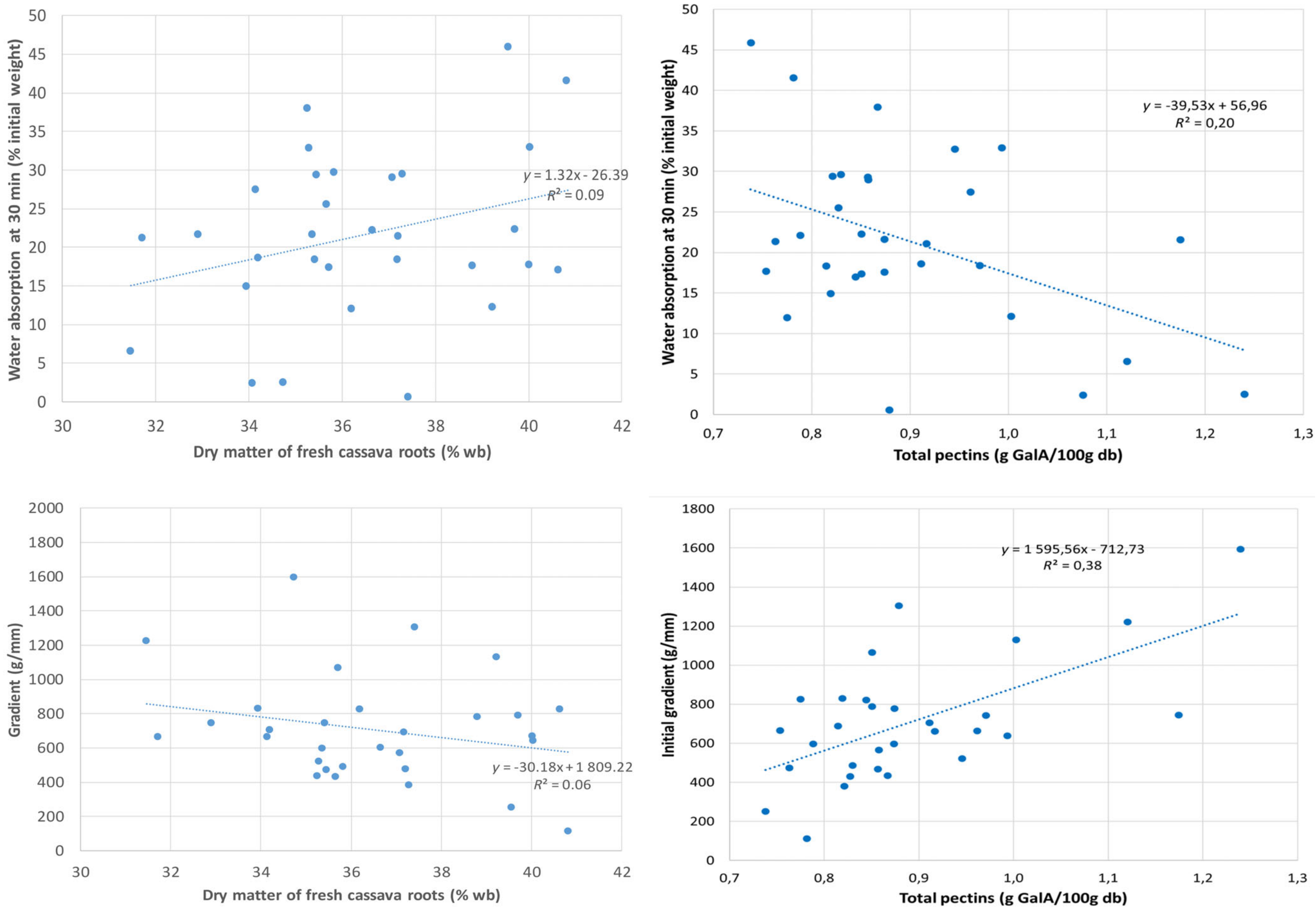

Figure 4. Effect of dry matter and total pectin content of fresh cassava roots on cooking quality parameters water absorption and gradient among 29 genotypes of cassava (CIAT population). Each point represents the average of each genotype across three MAPs (9, 10, and 12 months), or two MAPs (9 and 12 months) when Ca^{2+} is measured.

Starch is the major component of most fresh RTBs, except for ripe plantain (Table 3), but no clear correlation was found between DM and starch or amylose contents for sweetpotato, yam (Table 1) or cassava (Fig. 3), as already reported.[60-62] However, there was a positive correlation between starch content and DM for plantain at the yellow ripening stage ($r^2 = 0.87$, $n = 7$), as already

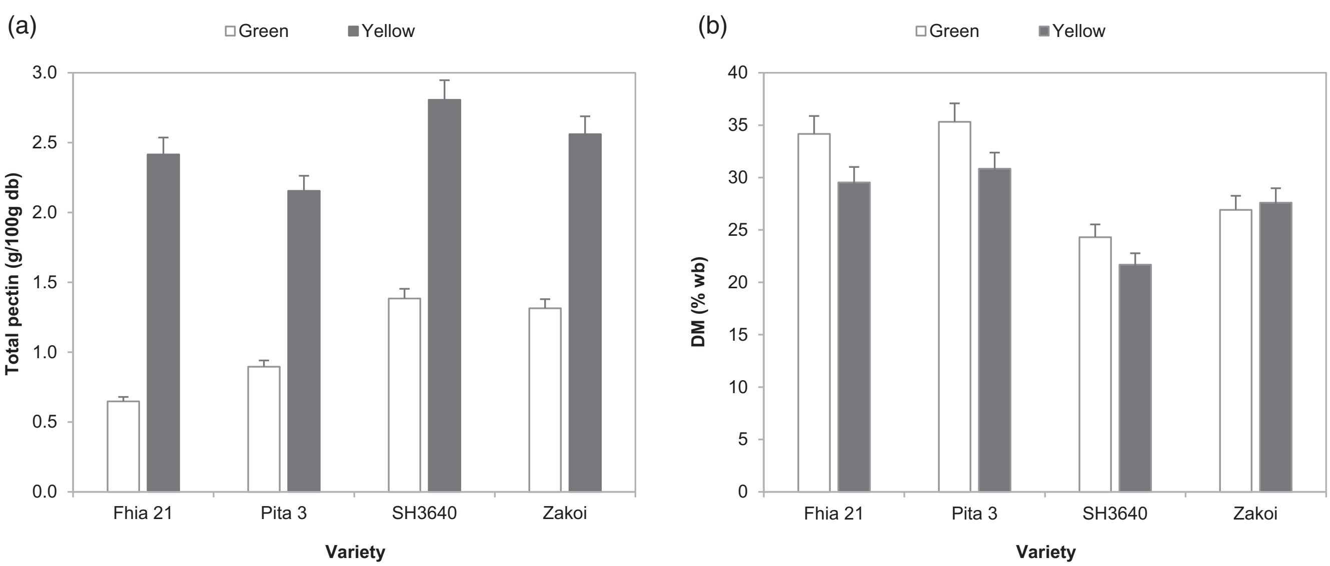

Figure 5. Total (a) pectin content (GalA equivalent) and (b) dry matter (DM) of fresh plantains from different varieties taken at green and yellow ripening stages.

Table 2. Pearson correlation between texture attributes and biochemical parameters ($n = 17$ samples) in fried plantain

Texture attributes and chemical analysis results	Texture attributes of fried plantain				Total pectin (GalA g per 100 g db)	
	Firmness	Stickiness	Chewiness	DM	Fresh plantain	Fried plantain
Firmness_fried plantain	**1 (0.00)**					
Stickiness_ fried plantain	−0.465 (0.60)	**1 (0.00)**				
Chewiness_fried plantain	**0.617 (0.00)**	0.068 (0.00)	**1 (0.00)**			
DM (% wb)	**0.898 (0.00)**	**−0.554 (0.02)**	0.341 (0.18)	**1 (0.00)**		
Total pectin_fresh plantain (GalA g per 100 g db)	−0.349 (0.20)	−0.216 (0.48)	−0.521 (0.07)	**−0.561 (0.01)**	**1 (0.00)**	
Total pectin_ fried plantain (GalA g per 100 g db)	−0.088 (0.78)	−0.342 (0.28)	−0.212 (0.51)	−0.213 (0.51	**0.685 (0.04)**	**1 (0.00)**

Note: Values in bold are statistically significant ($P < 0.05$) and the probability levels are given in parenthesis. Data used were collected from 17 samples of fried plantain (aloco) obtained from seven varieties including Bi-gt and Bi-yt: Aloco from Bita 3 variety taken at the yellow tip green and yellow tiger stage; Co-y and Co-yt: Aloco from Corne 1 variety taken at the yellow and yellow tiger stages; Fh-y and Fh-yt: Aloco from FHIA 21 variety taken at the yellow and yellow tiger stages; Sh-gt, Sh-y and Sh-yt: Aloco from SH3640 variety taken at the yellow tip green, yellow and yellow tiger stages; Pi-gt, Pi-y and Pi-yt: Aloco from Pita 3 variety taken at the yellow tip green, yellow and yellow tiger stages; Sa-gt and Sa-y: Aloco from Saci variety taken at the yellow tip green and yellow stage; Za-y, Za-gt and Za-yt: Aloco from Zakoi variety taken at the yellow and yellow tiger stages.

noted.[63] Although starch or amylose were not directly correlated with the texture of boiled sweetpotato (see Supporting information, Table S3) or yam (Table 1), amylose content was negatively correlated with hardness of boiled cassava (Fig. 3). This negative correlation between amylose content and hardness cannot be explained by lower cassava starch swelling with amylose.[64] The role of starch or amylose on the texture of boiled RTB may also be masked by the more prominent role of other components and, indeed for sweepotato, amylose was a variable for predicting texture within a two-variables model (Fig. 1).

Starch-degrading enzymes can modulate the role of starch. For example, β-amylase plays a key role in starch degradation during plantain ripening[65] and may also be active during plantain cooking lowering firmness through reducing starch-swelling potential. In fried plantain, β-amylase is rapidly inactivated by the high temperatures reached during frying, but may have a greater impact on texture when cooking at lower temperatures.[3,16] β-amylase activity appeared to influence pasting properties of sweetpotato flours through hydrolysis of starch chains (see Supporting information, Table S3), but no effect on firmness of boiled sweetpotato was found in this set of samples. Because β-amylase primarily catalyzes the hydrolysis of linear glucan chains of starch[66] such as in amylose, the relationship between amylose content and firmness may also be modulated by differential β-amylase activity and preferential hydrolysis of amylose during sweetpotato cooking. Indeed, the positive impact of amylose on the firmness of cooked sweetpotato may be related to lower cell separation as a result of lower starch swelling, in turn caused by lower amylose content.

Impact of pectin on cooking properties

A direct correlation between pectin content and textural properties was found for boiled yam and cassava. For the latter, the Ca^{2+} content of raw roots was he most significant variable for predicting texture after boiling, and boiling with added calcium ions reduced WA (see Supporting information, Fig. S2), which clearly implicates pectins in determining cooking properties. In plantain, some biochemical traits linked to pectin structure, such as levels of PME activity (Table 3), were also correlated with textural properties. Sweetpotato, yam, and plantain exhibited various levels of PME activity (Table 3). Sweetpotato firmness was not predicted by PME activity in the investigated genotypes, probably because of the very low activity, whereas the high level of PME in plantain suggested that it could have a greater impact on cooking behaviour. This would be in line with the positive relationship previously observed between PME activity and optimal cooking time of potatoes.[11,12]

Overall, this indicated that different mechanisms of pectin modification during cooking were at play in these different crops. In yam, the mechanism of texture development (and thickening of cell walls) during cooking[21] is unlikely to be connected with endogenous enzymatic activities during cooking because no PME activity was detected. PME, however, could play a role during

Table 3. Overall biochemical characteristics of studied raw crops

Raw crop	CW (% db)	GalA (% db)	Starch (% db)	DM (% wb)	Amylose content (%)	PME activity (pmol s^{-1} g^{-1} db)
Sweet potato	7–14	0.2–4.8	56–72	30–42	11–14	0.51–2.92
Yam	3–13	0.6–3.2	45–83	26–45	2–35[67,68]	0
Cassava	2–5[32,69]	0.7–1.2 (0.56[69])	69–80[70]	20–45	0–40	NA
Plantain (yellow stage)	5–11	1.5–2.4	17–56	20–40	20–27[39,65]	2.4–5.6 × 10^5

Note: For seven yams and plantain, cell walls were extracted using the corresponding SOP[71] and PME activity were determined as described previously.[72]
Abbreviations: CW, cell wall content; DM, dry matter; GalA, galacturonic acid content; NA, not available; PME, pectin methylesterase.

boiling of plantain by demethylating pectins, which could then strengthen the cell–cell adhesion in the middle lamella through cross-linking with calcium ions, resulting in cell wall thickening and a firmer texture.

Moreover, the loss of pectin content observed after plantain frying, possibly related to the decrease of firmness, may be the result of β-elimination reaction. This reaction occurs on methylated pectin at pH higher than 4.5 and is increased at temperatures > 80 °C. Such pectin degradation during cooking would agree with the middle lamellae dissolution observed during boiling.[33] This nonenzymatic hydrolysis of pectin could therefore be a driver of softening in fried plantain.

Interaction between starch, pectins, and water absorption

Starch is a major contributor to DM of raw samples in major RTBs (see above) but pectins could also contribute to textural differences as they have a higher water retention capacity than nongelatinized starch (maximum native starch water content of approximately 45% wb) and raw RTB had a moisture content of 55–80% (Table 3). A negative correlation was observed between pectins and DM content of fresh samples for raw plantain and cassava, but not for yam and sweetpotato. Interactions with other compounds, such as amylose, cell walls, lignins and soluble sugars (or a different pectin structure) may explain this discrepancy between RTB crops.

In the present study, the hardness of cooked samples increased with the DM of raw samples for yam and plantains only (see above). This common behaviour could be explained by different mechanisms. The DM of raw plantain is the main driver of firmness after cooking (Table 2; see also Supporting information, Fig. S3) with starch playing a major role in increasing firmness (see above) and pectin content influencing texture in a opposite fashion by increasing water content (Fig. 5). In yam, however, both pectin and DM content seemed to increase hardness in cooked tubers independently of starch content (Fig. 2 and Table 1). Moreover, hard cooking yam varieties absorb more water and release less soluble DM after cooking compared to mealy yam varieties.[27] This behaviour may be a result of the higher content of low-methylated pectin in hard cooking yam varieties leading to a preferential WA by pectins (rather than pectin solubilization) and strengthening cell walls through calcium bridges. Kouadio *et al.*[27] showed that WA is the main parameter determining cooking quality (hard *versus* mealy cooking) of cassava and yam, even though they exhibit different behaviours. The lower WA observed for hard cooking cassava (Fig. 4; see also Supporting information, Fig. S2) was influenced by higher calcium fixation, which is also known to increase firmness. Despite the particularly high starch and low CW content in cassava (Table 3), pectins played a major role through their WA capacities. By contrast, sweetpotato cooking behaviour appeared also to be driven by WA capacity but mainly through its starch/amylose swelling properties (see above).

Furthermore, the observed decrease of firmness and stickiness of fried plantain after ripening (see Supporting information, Table S5) may be linked to both pectin solubilization and starch degradation commonly observed during ripening.[57] These phenomena may underly the acceptability of fried plantain as preliminary studies have identified the optimum consumption at the yellow ripening stage.[53]

The development of new SOPs and access to diverse RTB samples with wide ranges of cooking properties and biochemical characteristics has allowed the present study to confirm tendencies previously suggested and identified new and specific relations between biochemical characteristics and cooking behaviour. Nevertheless, additional studies are necessary to unravel the combined and synergistic impact of starch and pectin metabolism on the cooking properties of RTB crops. Also, obtaining genotypes with highly contrasting compositions and textural/cooking behaviours could lead to a better understanding of the determinants and main reactions in play during cooking. Finally, this would help the breeders to target traits for the development of new RTB varieties with good consumer acceptability.

AUTHOR CONTRIBUTIONS

TT, AR-S, CM, MT and DD were responsible for conceptualization. TT, AR-S, SA, DR and EN were responsible for data curation. AR-S, CM, SA, DM-A-M, MT, HAK, EN and ASDN&N were responsible for formal analysis. DD was responsible for funding acquisition. SA, KM, HAK and DR were responsible for investigations. AR-S, CM, HAK, TT, MT and DM-A-M were responsible for methodology. DD was responsible for project administration. DR, MN, JLM, HAK and NA were responsible for resources. AR-S, CM and DM-A-M were responsible for supervision. AR-S, CM, SA, DM-A-M, MT, TT and EN were responsible for writing the original draft. AR-S, CM, SA, HAK, ASDN&N, GMcD, DM-A-M, MT and DD were responsible for reviewing and editing.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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