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Modification of hemicellulose polysaccharides during ripening of postharvest banana fruit

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ABSTRACT

Alcohol-insoluble residues (AIRs) from postharvest banana fruits at five ripening stages were extracted and isolated. The AIR was fractionated with 1 M KOH or 4 M KOH to obtain hemicellulose polysaccharides 1 (HC1) and 2 (HC2), respectively, and their content, molecular-mass, monosaccharide composition and glycosidic linkages were evaluated. HC1 yield decreased significantly from 126.95 to 21.14 mg/g on fresh weight basis during fruit ripening, but HC2 yield increased and then decreased. Concomitantly, the molecular-mass of HC1 and HC2 decreased obviously, indicating that depolymerization occurred. Moreover, the major monosaccharide compositions were identified as glucose and xylose. The GC–MS analysis further revealed that HC1 and HC2 had a 1,4-linked glucose backbone. During fruit ripening, the molar percentage of 1,4-linked Glc*p* residues increased in HC1, but decreased slightly in HC2. Overall, this study indicated that the modification and depolymerization of hemicellulose polysaccharides were responsible for banana fruit softening.

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1. Introduction

Fruit softening involves a coordinated series of modifications of polysaccharide components of the primary cellular wall and middle lamella, resulting in the degradation of the cellular wall structure (Brummell, 2006). The primary cellular wall is a complex network structure composed of various polysaccharides, such as pectin, hemicellulose and cellulose microfibrils (Prasanna, Prabha, & Tharanathan, 2007). Generally, hemicelluloses are attached to cellulose microfibrils by hydrogen bonds and cross-links between cellulose microfibrils (Fujino, Sone, Mitsuishi, & Itoh, 2000). The formation of the cellulose–hemicellulose network probably gives strength (rigidity) to cellular walls (Wakabayashi, 2000). The breakdown of hemicellulosic molecules at the initial stage of fruit softening may partially disrupt the cellulose–hemicellulose network, which, in turn, causes a decrease in the rigidity of cellular walls in fruit tissues (Wakabayashi, 2000).

Giovannoni, DellaPenna, Bennett, and Fischer (1989) reported that *rin* (ripening inhibitor) mutation impairs some aspects of fruit ripening processes, such as softening, polyuronide degradation and level of polygalacturonase (PG). However, when low PG levels in *rin* mutant were transformed to nearly normal levels, polyuronides were extensively degraded and solubilised but inhibition of fruit softening was observed (Giovannoni et al., 1989). Maclachlan and Brady (1994) further indicated that the levels and the molecular-mass of hemicellulose were almost equivalent to those in the wild-type fruit during ripening. Moreover, it was found that the inhibition of the degradation of hemicellulose was associated with the retarded fruit ripening by 1-methylcyclopropene treatment in avocado fruits (Jeong, Huber, & Sargent, 2002) and bananas (Lohani, Trivedi, & Nath, 2004). Thus, it was suggested that the breakdown of hemicellulose polysaccharides could play a more important role during fruit softening.

Up to the present, a wide range of cellular wall pectic modifications have been observed between species. Some studies reported the contribution of hemicelluloses to textural softening in tomato (Maclachlan & Brady, 1994), muskmelon (Coimbra, Barros, Barros, Rutledge, & Delgadillo, 1998) and other fruits (Sakurai & Nevins, 1993). However, the information on the depolymerisation of hemicellulose is relatively limited (Brummell, 2006).

Banana is one of the most consumed fruits over the world. Banana is a climacteric fruit, and as such shows marked physiological changes during ripening (Jiang, Joyce, & Macnish, 1999). Ripening is associated with fruit softening. Recently, more attention has been paid to fruit softening-related enzymes involving cellular wall loosening during banana fruit ripening (Asif & Nath, 2005; Lohani et al., 2004). Unfortunately, the characterisation of

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hemicellulose fractions during ripening of harvested fruit is unclear. The objective of the present study was to investigate the molecular-mass, monosaccharide composition and structures of hemicellulose during banana fruit ripening to elucidate better the fruit softening.

2. Materials and methods

2.1. Plant materials

Hands of mature green banana fruit (*Musa* spp., AAA group, cultivar 'Brazil') were obtained from a local farm in Guangzhou, China. Fruits were cut into fingers and then dipped for 3 min in 0.1% Sportak® (prochloraz, Bayer) fungicide solution to control the postharvest diseases. The fruits were maintained at 25 ± 1 °C and 90% relative humidity (RH) after air-dried for 3 h at 25 °C. After 0, 10, 15, 17 and 20 days of storage, when fruit ripening reached stages I (mature green), II (green), III (green > yellow), IV (yellow > green) and V (yellow) in peel colour, respectively, 10 fingers of the fruits were sampled and then peeled. The pulp tissues were cut into small pieces, then frozen immediately in liquid nitrogen and finally stored at −80 °C.

2.2. Preparation of alcohol insoluble residue (AIR)

The alcohol-insoluble residue (AIR) was prepared by the method of Vierhuis, Schols, Beldman, and Voragen (2000) with some modifications. The frozen pulp tissues (100 g) were blended for 2 min with 300 ml of 95% (v/v) ethanol using a homogenizer, and then maintained in boiling water for 15 min to inactivate endogenous enzymes. After cooling rapidly in an ice bath, the homogenate was centrifuged for 15 min at 4,000×*g*. The residue was washed sequentially with 200 ml of the mixture solution of chloroform:methanol (1:1, v/v) and 200 ml of acetone. Pulp starch was removed carefully by re-extraction in 90% aqueous Me_2SO until no starch was detected using the KI–I_2 method (Nelson, 1968). The extract suspension was then centrifuged for 15 min at 4,000×*g*. The precipitate phase was collected, washed twice with 70% ethanol at 25 °C, filtered and then dried at 40 °C. The dried powder was considered as the alcohol-insoluble residue and then stored in desiccators.

2.3. Fractionation of hemicelluloses

The separation of hemicelluloses was performed by the method of Methacanon, Chaikumpollert, Thavorniti, and Suchiva (2003) with some modifications. After being eluted sequentially with cold distilled water and 0.5 M HCl to eliminate pectin, the insoluble residues of AIR from banana fruit at different stages were subjected to subsequent extraction with 1 M KOH containing 0.02 M $NaBH_4$ or 4 M KOH containing 0.02 M $NaBH_4$ at 0 °C for 1 h under nitrogen. Each time the extracted polysaccharides were precipitated by adding ethanol to a final concentration of 70%, followed by a dialysis against the corresponding solution, and then lyophilised to obtain 1 M KOH soluble hemicellulose (HC1) and 4 M KOH soluble hemicellulose (HC2), respectively.

2.4. Analyses of monosaccharide compositions

The analysis of monosaccharide compositions was carried out by the method of Yang et al. (2006) with a slight modification. The polysaccharide (10 mg) was hydrolysed for 6 h with 10 ml of 2 M trifluoroacetic acid (TFA) at 120 °C. Derivation was then carried out using the trimethylsilylation reagent. The trimethylsilylated derivatives were loaded onto HP 6890 gas chromatograph (GC) equipped with a HP 5 capillary column (30 m × 0.32 mm) and a flame-ionisation detector (FID), using inositol as the internal standard. The operation was performed using the following conditions: H_2, 30 ml/min; air, 150 ml/min; N_2, 1 ml/min; injection temperature, 230 °C; detector temperature, 230 °C; column temperature programmed from 130 to 180 °C at 5 °C/min, holding for 2 min at 180 °C, then increasing to 220 °C at 5 °C/min and finally holding for 3 min at 220 °C. Sample (0.2 μl) was injected to the GC for the analyses of monosaccharides. Arabinose, xylose, galactose, glucose, rhamnose, mannose, fructose and uronic acid (galacturonic acid) were used as the standards.

2.5. Analysis of glycosidic linkage

The analysis of glycosidic linkage was conducted by the method of Kim, Reuhs, Michon, Kaiser, and Arumughama (2006) with minor modification. Briefly, the dried HC1 or HC2 sample (4.0 mg) was dissolved with 2 ml of Me_2SO under nitrogen and then methylated with 1.5 ml of CH_3I and 20 mg of NaOH powder. Partially methylated alditol acetate was prepared from the fully methylated sample by acid hydrolysis with 2 M TFA at 120 °C for 1 h and the reduction of the hydrolysate using $NaBH_4$, followed by acetylation with acetic anhydride. The alditol acetate was analysed by GC–MS (QP2010 Plus), using a EC™-5 capillary column (30 m × 0.25 mm × 0.25 μm). Helium was used as a carrier gas at a constant flow rate of 1 ml/min. The oven conditions included an initial temperature of 80 °C for 2 min, then to 200 °C at 25 °C/min and finally to 270 °C at 10 °C/min. The inlet temperature was kept constant at 260 °C. The mass range used in this study was 29–450 m/z. Peak assignments were made based on the retention time and mass spectra. Inositol was added and then used as an internal standard.

2.6. Gel permeation chromatography

Gel permeation chromatography was performed according to the method of Manrique and Lajolo (2004) with a slight modification. HC1 and HC2 samples were loaded on a 1 × 80 cm column packed with Sepharose 4B resin, and then eluted with 40 mM sodium acetate buffer (pH 5.0) containing 0.1% NaCl and 0.02% NaN_3 at a flow rate of 0.2 ml/min. The molecular-mass calibration curve was obtained using the standard dextrans with the mean molecular weights of 500, 70, 40 and 10 kDa (Pharmacia, Sweden). Various fractions were collected every 10 min and then analysed for the contents of total sugars. The profiles of the molecular-mass distributions of various soluble hemicelluloses were obtained using the molecular weight calibration curve. Blue dextran (the mean molecular weight of 2000 kDa) and glucose were used to test the void volume (V_0) and the total volume (V_t) of the column, respectively.

2.7. Measurement of total sugars content

Contents of total sugars were determined by the method of Dubois, Gilles, Hamilton, Rebers, and Smith (1956). Briefly, HC1 and HC2 samples (500 μl) were incubated for 30 min with 500 μl of 5% (w/v) phenol and 2.5 ml of 98% (v/v) H_2SO_4. The absorbance was recorded at 490 nm. The absorbance value can indicate well the relative content of the total sugars.

2.8. Data handling

Experiments were arranged in a completely randomized design. The data were analysed by SPSS (Version 13.0). One way analysis of variance (ANOVA) and the Tukey's multiple comparisons were carried out to examine any significant difference between the means.

3. Results and discussion

3.1. Yields of hemicellulose fractions

Generally, hemicellulose polysaccharides form the cellulose–hemicellulose network by hydrogen bonds which probably provide strength (rigidity) to plant tissues (Fujino et al., 2000; Wakabayashi, 2000). In this study, the HC1 yield from banana pulp tissues decreased significantly from 126.65 to 21.14 mg/g FW during fruit ripening (Fig. 1A). Similarly, HC2 yield also decreased except at fruit ripening stage II (Fig. 1B). Our previous study indicated that the firmness of harvested banana fruit decreased rapidly during fruit ripening (Duan et al., 2008). Thus, it is suggested that the degradation of hemicellulose polysaccharides is involved in fruit softening. Loss of hemicellulose was reported also in strawberry (Koh & Melton, 2002; Rosli, Civello, & Martinez, 2004), papaya (Manrique & Lajolo, 2004), olive (Vierhuis et al., 2000) and other fruits (Brummell & Harpster, 2001).

3.2. Molecular-mass profile of polysaccharide fractions

The gel permeation chromatograms of HC1 and HC2 from the pulp tissues of banana fruit at different ripening stages are shown in Fig. 2. At fruit ripening stages I, III and V, the total sugar peaks of

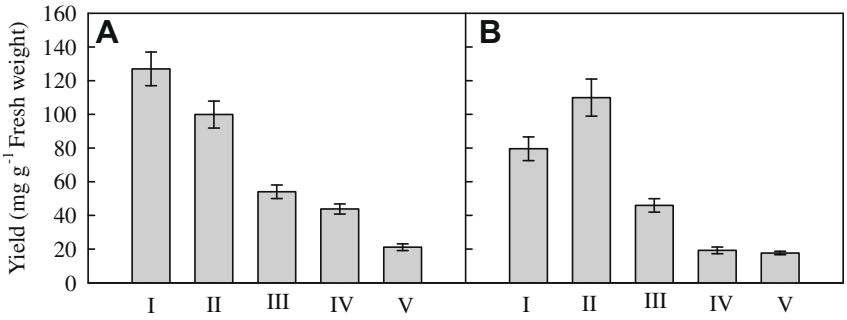

Fig. 1. The contents of 1 M KOH soluble (A) and 4 M KOH soluble (B) hemicellulose polysaccharides from pulp tissues of banana fruit at various ripening stages. The contents were expressed as the yields on fresh weight basis. Data were presented as the means ± standard errors (n = 3). I, Mature green; II, green; III, green > yellow; IV, yellow > green and V, yellow.

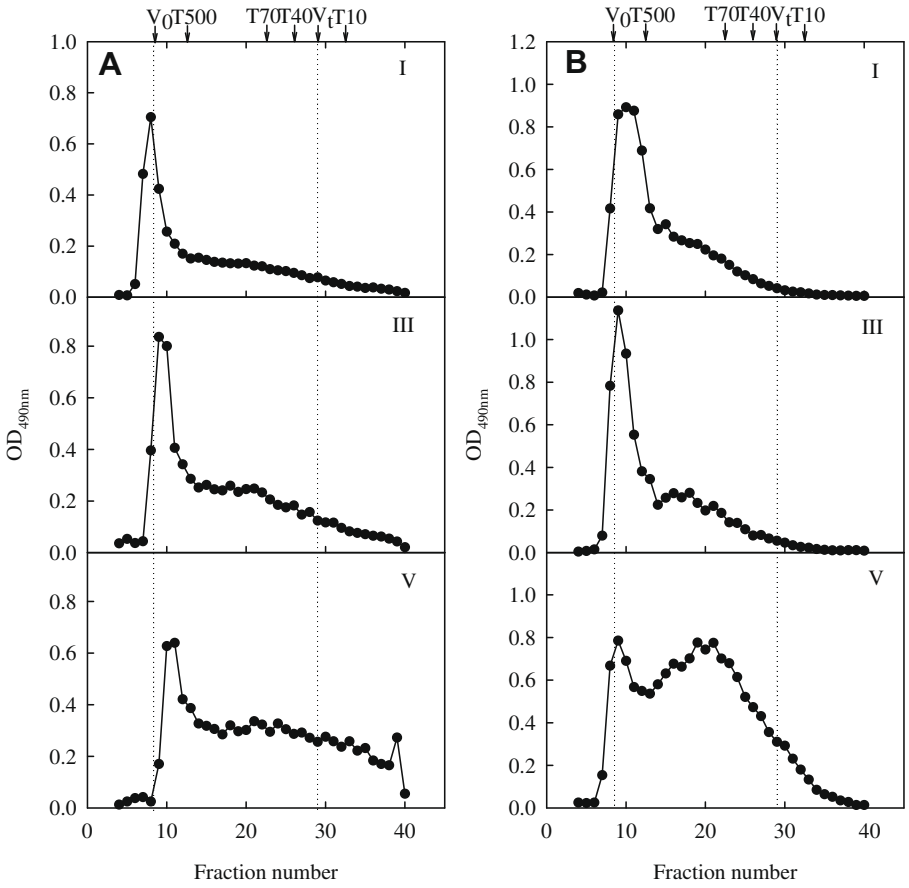

Fig. 2. Molecular-mass distribution of 1 M KOH soluble (A) and 4 M KOH soluble (B) hemicellulose polysaccharides from pulp tissues of banana fruit at various ripening stages. T500, T70, T40 and T10 were the molecular size standards of 500, 70, 40 and 10 kDa whilst V_0 (2000 kDa) and V_t were the void volume and total volume of the column, respectively. I, Mature green; II, green; III, green > yellow; IV, yellow > green and V, yellow.

HC1 eluted corresponded to the average molecular weights of approximately 1208, 994 and 674 kDa, respectively (Fig. 2A), which suggested an evident depolymerization of HC1 during fruit ripening. Differently, there was an eluted peak corresponding to an average molecular weight of about 994 kDa of HC2 at fruit ripening stages I, III and V (Fig. 2B). The molecular-mass band of HC2 at ripening stage V had a great fractionation range with two peaks eluted, corresponding to the average molecular weights of approximately 994 and 97 kDa. It was suggested that the striking molecular-mass downshift of HC2 was concomitant with the increase in the level of smaller polysaccharide at ripening stage V, but no obvious depolymerization of the HC2 occurred at fruit ripening stages I and III. Downshifts in the molecular-mass of hemicellulose polysaccharides appeared also during fruit softening of papaya (Manrique & Lajolo, 2004), tomato (Sakurai & Nevins, 1993), grape (Yakushiji, Sakurai, & Morinaga, 2001) and pear (Hiwasa et al., 2004; Murayama, Katsumata, Endou, Fukushima, & Sakurai, 2006). Overall, the data obtained in this study further confirmed that the depolymerization of hemicellulose polysaccharides of postharvest fruit was involved in the regulation of the mechanical strength of cellular walls (Wakabayashi, 2000).

3.3. Monosaccharide composition

Fig. 3 shows the molar percentage of monosaccharide in hemicellulose polysaccharides from the pulp tissues of banana fruit at different ripening stages. In HC1 and HC2, the predominant monosaccharides were identified as glucose, followed by xylose, mannose and fructose (Fig. 3A and B). In addition, a trace amount of galactose was found in HC2 at fruit ripening stage V (Fig. 3B). Thus, the hemicelluloses of pulp tissues of banana fruit consisted mainly of xyloglucan-type polysaccharides. Similarly, the high levels of glucose and xylose were observed in the monosaccharide composition of hemicellulose fractions in kiwifruit (Li, Nakagawa, Nevins, & Sakurai, 2006), papaya (Manrique & Lajolo, 2004) and mango (Yashoda, Prabha, & Tharanathan, 2005).

The monosaccharide composition of HC1 fraction remained nearly constant except for a slight change in the molar percentage of mannose and xylose, which fluctuated during ripening of banana fruit (Fig. 3A); this was in agreement with the report of Manrique and Lajolo (2004) in papaya fruit during softening. Vierhuis et al. (2000) also observed that the sugar composition of the hemicellulose-rich fractions in olive fruit changed little throughout the fruit development. However, the molar percentage of glucose and xylose of the HC2 fraction decreased from 71.07% to 58.18% and 21.13% to 13.27% during ripening, respectively, whereas the levels of mannose tended to increase from 4.14 to 14.74% (Fig. 3B). As a consequence of a continuous breakdown of the xyloglucan backbone, an obvious modification of the monosaccharide composition in HC2 occurred during ripening of harvested banana fruit.

3.4. Glycosidic linkage

To further account for the role of modification of hemicellulose polysaccharides in fruit softening, the per-methylated HC1 and HC2 fractions from banana fruit at ripening stages I (mature green) and V (yellow) were hydrolysed, reduced, acetylated, then converted into partially methylated alditol acetate, and finally analysed by GC–MS. According to the different derivative glycosyl residues, the glycosidic linkage types could be estimated (Smith & Harris, 1995). The results of glycosidic linkage of HC1 and HC2 are shown in Tables 1 and 2. Both hemicellulose fractions contained high amount of 2,3,6-Me_3-Glc*p*, which suggested the presence of a long 1,4-linked Glc backbone. Similarly, Yashoda et al. (2005) reported that the major hemicellulosic fractions of unripe mango were determined to be xyloglucan-type with 1,4-linked glucan. In this study, both hemicellulose fractions were branched with a 1,4-linked-glucan backbone at C-3 in the presence of 1,3,4-linked Glc (2,6-Me_2-Glc*p*) and, glucose (2,3,4,6-Me_4-Glc*p*) constituted the non-reducing terminal units of HC1 and HC2 fractions (Tables 1 and 2). Unfortunately, the derivatives of xylose, the second highest compositional monosaccharide of HC1 and HC2,

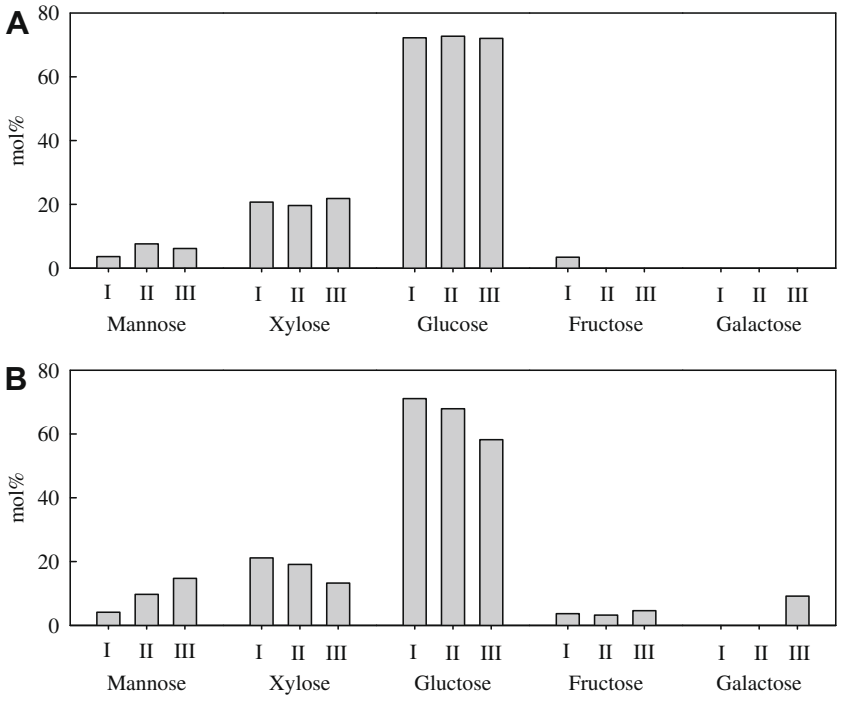

Fig. 3. The monosaccharide compositions of 1 M KOH soluble (A) and 4 M KOH soluble (B) hemicellulose polysaccharides from pulp tissues of banana fruit at various ripening stages. I, Mature green; II, green; III, green > yellow; IV, yellow > green and V, yellow.

Table 1
The glycosidic linkage of 1 M KOH soluble hemicellulose polysaccharide (HC1) from pulp tissues of banana fruit at ripening stages I (mature green) and V (yellow).

Glycosyl linkage		Mol%		Sugar derivatives
		I	V	
Mannose	1,6-	11.41	14.88	2,3,4-Me_3-Man*p*[a]
	1,3,6-	1.86	Not detected	2,4-Me_2-Man*p*
Glucose	1-	11.06	10.02	2,3,4,6-Me_4-Glc*p*
	1,4-	70.02	73.35	2,3,6-Me_3-Glc*p*
	1,3,4-	5.64	1.75	2,6-Me_2-Glc*p*

[a] 2,3,4-Me_3-Man*p* meant 1,5,6-tri-*O*-acetyl-2,3,4-tri-*O*-methymannitol whilst *f* and *p* represented furanose and pyranose, respectively.

Table 2
The glycosidic linkage of 4 M KOH soluble hemicellulose polysaccharide (HC2) from pulp tissues of banana fruit at ripening stages I (mature green) and V (yellow).

Glycosyl linkages		Mol%		Sugar derivatives
		I	V	
Mannose	1,2,6-	6.52	11.77	3,4-Me_3-Man*p*[a]
Glucose	1-	8.48	9.67	2,3,4,6-Me_4-Glc*p*
	1,6-	4.2	1.92	2,3,4-Me_3-Glc*p*
	1,4-	77.02	76.65	2,3,6-Me_3-Glc*p*
	1,3,4-	3.78	Not detected	2,6-Me_2-Glc*p*

[a] 2,3,4-Me_3-Man*p* meant 1,5,6-tri-*O*-acetyl-2,3,4-tri-*O*-methymannitol whilst *f* and *p* represented furanose and pyranose, respectively.

have not been identified by GC–MS, which needs to be investigated further.

During banana fruit ripening, the molar percentage of 1,4-linked Glc*p* and 1,6-linked Man*p* in HC1 increased from 70.02% to 73.35% and 11.41% to 14.88%, respectively, whereas the amount of terminal Glc (2,3,4,6-Me_4-Glc*p*) and 1,3,4-linked Glc*p* decreased obviously. Concordantly, 1,3,6-linked Man*p* residues disappeared at fruit ripening stage V. Conversely, the 1,4-linked Glc*p* residues in the HC2 fraction exhibited a slightly decrease tendency but the terminal Glc*p* residues increased, which was coincidence with the monosaccharide composition and the breakdown of the xyloglucan backbone. Tong and Gross (1988) reported a significant change in the glycosidic linkage composition of hemicellulose fraction extracted by 8 M KOH during tomato fruit ripening.

In conclusion, in terms of the variations in content, molecular-mass downshift, monosaccharide composition and glycosidic linkage, this study indicated that the modification and depolymerization of hemicellulose polysaccharides in the cellular walls of harvested banana fruit were responsible for fruit softening during ripening.

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References

Asif, M. H., & Nath, P. (2005). Expression of multiple forms of polygalacturonase gene during ripening in banana fruit. *Plant Physiology and Biochemistry, 43*, 177–184.

Brummell, D. A. (2006). Cell wall disassembly in ripening fruit. *Functional Plant Biology, 33*, 103–119.

Brummell, D. A., & Harpster, M. H. (2001). Cell wall metabolism in fruit softening and quality and its manipulation in transgenic plants. *Plant Molecular Biology, 47*, 311–340.

Coimbra, M. A., Barros, A., Barros, M., Rutledge, D. N., & Delgadillo, I. (1998). Multivariate analysis of uronic acid and neutral sugars in whole pectic samples by FT-IR spectroscopy. *Carbohydrate Polymers, 37*, 241–248.

Duan, X. W., Cheng, G. P., Yang, E., Yi, C., Ruenroengklin, N., Lu, W. J., et al. (2008). Modification of pectin polysaccharides during ripening of postharvest banana fruit. *Food Chemistry, 111*, 144–149.

Dubois, M., Gilles, K. A., Hamilton, J. K., Rebers, P. A., & Smith, F. (1956). Colorimetric method for determination of sugars and related substances. *Analytical Chemistry, 28*, 350–356.

Fujino, T., Sone, Y., Mitsuishi, Y., & Itoh, T. (2000). Characterization of cross-links between cellulose microfibrils, and their occurrence during elongation growth in pea epicotyl. *Plant and Cell Physiology, 41*, 486–494.

Giovannoni, J. J., DellaPenna, D., Bennett, A. B., & Fischer, R. L. (1989). Expression of a chimeric polygalacturonase gene in transgenic *rin* (ripening inhibitor) tomato fruit results in polyuronide degradation but not fruit softening. *Plant Cell, 1*, 53–63.

Hiwasa, K., Nakano, R., Hashimoto, A., Matsuzaki, M., Murayama, H., Inaba, A., et al. (2004). European, Chinese and Japanese pear fruit exhibit differential softening characteristics during ripening. *Journal of Experimental Botany, 55*, 2281–2290.

Jeong, J., Huber, D. J., & Sargent, S. A. (2002). Influence of 1 -methylcyclopropene (1-MCP) on ripening and cell wall matrix polysaccharides of avocado (*Persea americana*) fruit. *Postharvest Biology and Technology, 25*, 241–256.

Jiang, Y. M., Joyce, D. C., & Macnish, A. J. (1999). Extension of the shelf life of banana fruit by 1-methylcyclopropene in combination with polyethylene bags. *Postharvest Biology and Technology, 16*, 187–193.

Kim, J. S., Reuhs, B. L., Michon, F., Kaiser, R. E., & Arumughama, R. G. (2006). Addition of glycerol for improved methylation linkage analysis of polysaccharides. *Carbohydrate Research, 341*, 1061–1064.

Koh, T. H., & Melton, L. D. (2002). Ripening-related changes in cell wall polysaccharides of strawberry cortical and pith tissues. *Postharvest Biology and Technology, 26*, 23–33.

Li, X. J., Nakagawa, N., Nevins, D. J., & Sakurai, N. (2006). Changes in the cell-wall polysaccharides of outer pericarp tissues of kiwifruit during development. *Plant Physiology and Biochemistry, 44*, 115–124.

Lohani, S., Trivedi, P. K., & Nath, P. (2004). Changes in activities of cell wall hydrolases during ethylene-induced ripening in banana: Effect of 1-MCP, ABA and IAA. *Postharvest Biology and Technology, 31*, 119–126.

Maclachlan, G., & Brady, C. (1994). Endo-1,4-β-glucanase, xyloglucanase, and xyloglucan endo-transglycosylase activities versus potential substrates in ripening tomatoes. *Plant Physiology, 105*, 965–974.

Manrique, G. D., & Lajolo, F. M. (2004). Cell-wall polysaccharide modifications during postharvest ripening of papaya fruit (*Carica papaya*). *Postharvest Biology and Technology, 33*, 11–26.

Methacanon, P., Chaikumpollert, O., Thavorniti, P., & Suchiva, K. (2003). Hemicellulosic polymer from Vetiver grass and its physicochemical properties. *Carbohydrate Polymers, 54*, 335–342.

Murayama, H., Katsumata, T., Endou, H., Fukushima, T., & Sakurai, N. (2006). Effect of storage period on the molecular-mass distribution profile of pectic and hemicellulosic polysaccharides in pears. *Postharvest Biology and Technology, 40*, 141–148.

Nelson, O. (1968). The waxy locus in maize II. The location of the controlling element alleles. *Genetics, 60*, 507–524.

Prasanna, V., Prabha, T. N., & Tharanathan, R. N. (2007). Fruit ripening phenomena – an overview. *Critical Reviews in Food Science and Nutrition, 47*, 1–19.

Rosli, H. G., Civello, P. M., & Martinez, G. A. (2004). Changes in cell wall composition of three *Fragaria* × *ananassa* cultivars with different softening rate during ripening. *Plant Physiology and Biochemistry, 42*, 823–831.

Sakurai, N., & Nevins, D. J. (1993). Changes in physical properties and cell wall polysaccharides of tomato (*Lycopersicon esculenturn*) pericarp tissues. *Physiologia Plantarum, 89*, 681–686.

Smith, B. G., & Harris, P. J. (1995). Polysaccharide composition of unlignified cell walls of pineapple (*Ananas comosus* (L.) Merr.) fruit. *Plant Physiology, 107*, 1399–1409.

Tong, C. B. S., & Gross, K. C. (1988). Glycosyl-linkage composition of tomato fruit cell wall hemicellulosic fractions during ripening. *Physiologia Plantarum, 74*, 365–370.

Vierhuis, E., Schols, H. A., Beldman, G., & Voragen, A. G. J. (2000). Isolation and characterisation of cell wall material from olive fruit (*Olea europaea* cv koroneiki) at different ripening stages. *Carbohydrate Polymers, 43*, 11–21.

Wakabayashi, K. (2000). Changes in cell wall polysaccharides during fruit ripening. *Journal of Plant Research, 113*, 231–237.

Yakushiji, H., Sakurai, N., & Morinaga, K. (2001). Changes in cell-wall polysaccharides from mesocarp of grape berries during veraison. *Physiologia Plantarum, 111*, 188–195.

Yang, B., Wang, J. S., Zhao, M. M., Liu, Y., Wang, W., & Jiang, Y. M. (2006). Identification of polysaccharides from pericarp tissues of litchi (*Litchi chinensis* Sonn.) fruit in relation to their antioxidant activities. *Carbohydrate Research, 341*, 634–638.

Yashoda, H. M., Prabha, T. N., & Tharanathan, R. N. (2005). Mango ripening – chemical and structural characterization of pectic and hemicellulosic polysaccharides. *Carbohydrate Research, 340*, 1335–1342.