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Changes in the Cell Wall Components of Kiwifruit During Storage in Air or Controlled Atmosphere

M.L. Arpaia[1], J.M. Labavitch, C. Greve, and A.A. Kader
Department of Pomology, University of California, Davis, CA 95616

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Abstract. **Eight-one percent of the harvest firmness in kiwifruit (*Actinidia chinensis* Planch.) was lost during the first 8 weeks of storage in air at 0°C. As softening proceeded, a solubilization of uronic acids and the neutral sugar residues usually associated with pectic polymers (galactose, arabinose, and rhamnose) was detected. No consistent changes were noted in cellulose or the neutral sugars usually associated with hemicelluloses. Starch degradation also occurred coincident with softening. The amount of cell wall components soluble in water following fruit homogenization and the proportion of ethanol-precipitable pectic neutral sugars in this fraction increased during the first 8 weeks of storage. Once the rate of softening slowed (8 to 20 weeks), an equilibrium situation apparently was established between the amounts of the sugars formed in the ethanol-precipitable (i.e., polymeric) and ethanol-soluble fractions, suggesting that digestion of wall components continues after their excision from the insoluble wall matrix. Controlled atmosphere (2% O_2 + 5% CO_2; CA) storage retarded flesh softening relative to that measured in fruit held at 0° in air. A comparison of the changes in the cell wall components of air-stored and CA-stored kiwifruit suggests that, in addition to cell wall degrading processes contributing to fruit softening, starch degradation (possibly causing cell turgor changes) also may be involved in low-temperature softening of kiwifruit. The losses in water-insoluble cell wall pectic neutral sugars and uronic acids in air and CA storage were similar during the first 8 weeks of storage. Once softening slowed in CA, small but consistent reductions in the amount of cell wall turnover were observed as compared to air storage.**

Kiwifruits can be air-stored for 4 to 6 months at 0°C, although extensive flesh softening will occur. Ethylene influences the rate of softening in air storage (4, 5, 18, 21). CA storage (2% O_2 + 5% CO_2) retards softening of kiwifruit at 0° (4–6, 16, 19) as long as ethylene is excluded (4, 5, 16) and CA is established within 1 week of harvest (6).

At the time of commercial maturity, the major carbohydrate in the fruit is starch, which is hydrolyzed during fruit maturation, ripening, or storage (4, 11, 20, 22). The hydrolysis of starch corresponds to the rapid increase in soluble solids content of the fruit (4, 11, 22). Reid et al. (22) reported that, coincident with the hydrolysis of starch during fruit maturation, there is a rapid increase in sucrose, glucose, and fructose in the 'Bruno' cultivar. Fuke and Matsuoka (11) reported for the 'Bruno' and 'Hayward' cultivars that the predominant sugars of ripened fruit were glucose and fructose.

The objective of this study was to follow the changes in the cell wall components of kiwifruit as they soften during air storage at 0°C. We also compared the changes in cell wall neutral sugars and uronides in CA-stored fruit with those seen in air in an attempt to explain the differences in softening patterns.

Materials and Methods

Plant material

Kiwifruit 'Hayward' were harvested during the 1980 (soluble solids content = 7.2%) and 1982 (soluble solids content = 6.9%) seasons from the same commercial planting in Gridley, Calif. and transported to the Pomology Postharvest Research Facility at the Univ. of California, Davis. To minimize decay during storage, the fruit were dipped in a combination of 600 $\mu l \cdot liter^{-1}$ sodium orthophenylphenate and 1125 $\mu l \cdot liter^{-1}$ 2,6-dichloro-4-nitroaniline, adjusted to pH 11.0 (25).

After cooling overnight to 0°C, the fruit were placed in vented polyethylene bags for air storage in a room with low (<0.015 $\mu l \cdot liter^{-1}$) C_2H_4 contamination. In 1980, fruit were also placed in 1.5-m^3 CA storage chambers. A CA of 2% O_2 + 5% CO_2 was attained within 24 hr using a continuous flow system (500 $ml \cdot min^{-1}$). Storage atmospheres were monitored at regular intervals using gas chromatography and maintained within 5% of the desired levels of O_2 and CO_2 and at low C_2H_4 (<0.010 $\mu l \cdot liter^{-1}$) contamination. Relative humidity was maintained at 90–95% in all storage systems.

At periodic intervals (0, 2, 4, 6, 8, 16, and 24 weeks in 1980–81 and 0, 2, 4, 6, 8, 12, and 20 weeks in 1982–83) 25 fruit were removed from storage, warmed to 20°C, and evaluated within 2 hr. Two firmness measurements were taken for each pared fruit using a UC Fruit Firmness Tester with an 8-mm tip, and were averaged to give a mean flesh firmness determination per fruit. Only those fruit whose mean firmness fell within 1 SD of the 25-fruit sample average were used for subsequent analysis. The number of fruit used for analysis consequently varied from 12 to 18.

Cell wall preparation and analysis

Preparation (Fig. 1). Fruit tissue (1 to 5 g) from the outer pericarp (24) was obtained from each pared fruit. The tissue was homogenized in an equal volume of distilled deionized (dd) H_2O for 4 min at 0°C and centrifuged at 4500 × *g* for 10 min at 0°. The supernatant solution plus two dd H_2O washes were combined as the water soluble fraction (WSF). An additional pellet wash, with 80% methanol, which was used to remove chlorophyll, was first evaporated to dryness under a stream of N_2 gas, then redissolved in dd water and combined with WSF. The WSF was stored at −30° until analyzed. The water-insoluble fraction (WIF) was lyophilized, weighed, and stored at 20° in air-tight containers until analyzed.

Water-soluble fraction. In 1982, ethanol (EtOH) was added

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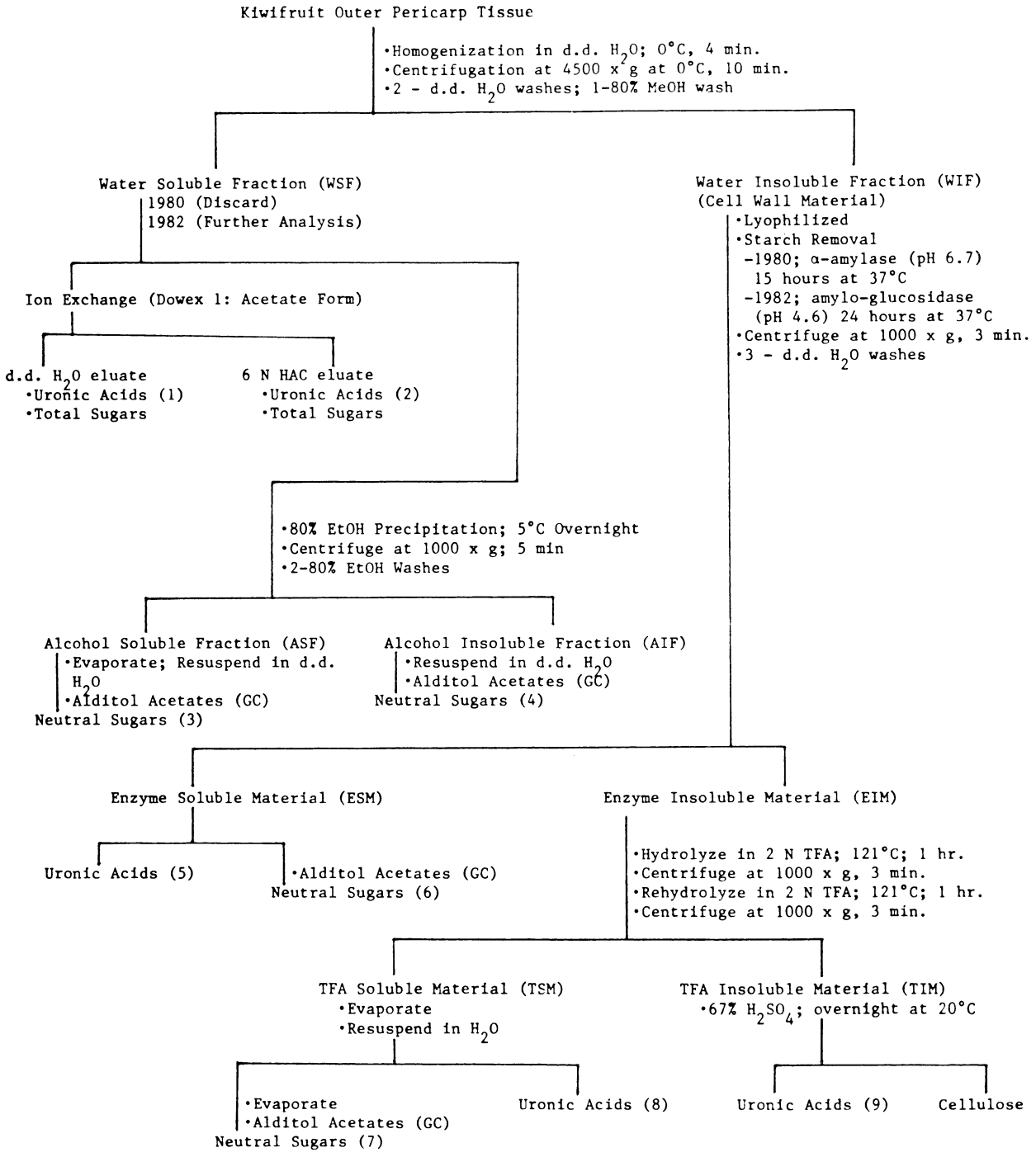
[1]Present address: Batchelor Hall Extension, Univ. of California, Riverside, CA 92521.



Total Water Soluble Uronic Acids = 1 + 2
Total Water Soluble Neutral Sugars = 3 + 4
Total Cell Wall Uronic Acid = 5 + 8 + 9
Total Cell Wall Noncellulosic Neutral Sugars = 6 + 7 (glucose, 7 only)
Starch = glucose in 6 only

Fig. 1. Flow chart of the purification and fractionation of neutral sugars, uronide, starch, and cellulose from kiwifruit pericarp tissue.

to a 2-ml aliquot of the WSF (final ethanol concentration = 80%), 2 drops of 1 N HCl were added, and the preparation was held overnight at 5°C to precipitate polysaccharides. The suspension was centrifuged at 1000× *g* for 5 min and the collected pellet then was washed two additional times in 80% EtOH. The resulting alcohol-soluble fraction (ASF) was evaporated to dryness under a stream of N_2 gas and redissolved completely in dd H_2O. The alcohol-insoluble fraction (AIF) also was redissolved in dd H_2O. Both fractions were analyzed within 3 days.

In addition, a 10-ml aliquot of the WSF was applied to a column [8 × 1 cm (i.d.)] of analytical grade Dowex-1 (Bio-Rad AG1-X8; acetate form). The column was washed wiith 20-ml portions of dd H_2O (to elute neutral sugars) and 6 N acetic acid (to elute uronic acids).

Water-insoluble fraction. Starch was removed from the WIF by treatment with either α-amylase (1980) or amyloglucosidase (1982). When α-amylase was used to remove starch, 10 mg of the WIF was suspended in 15 ml of 100 mM K-phosphate (pH 6.7) containing 0.20 mg α-amylase (from porcine pancreas, Sigma). The suspension was incubated at 37°C for 15 hr with constant agitation. The suspension was centrifuged at 1000× *g* for 3 min and then washed three times with 6 ml of dd H_2O. The enzyme-soluble material and water washes were combined (ESM). The volume of the ESM was measured and an aliquot was saved for carbohydrate analysis. The enzyme-insoluble material (EIM) was lyophilized after washing.

In 1982–83, amyloglucosidase (1,4-α-D-glucan glucohydrolase, Sigma) was incubated with the WIF, permitting a comparison of two widely used starch-removal techniques. Fifty milligrams of the WIF was treated with 0.4 mg amyloglucosidase in 6 ml of 100 mM sodium acetate buffer (pH 4.6) for 24 hr at 37°C with constant agitation. Following incubation, the ESM and EIM were handled as described previously.

Carbohydrate analysis—gas chromatography. The neutral sugar contents of the ASF, AIF, and WIF were determined using the methods outlined by Albersheim et al. (3). In 1980 and 1982 a Sigma-3 gas chromatograph (Perkin-Elmer) equipped with a flame ionization detector was used. For the 1980–81 analysis, the gas chromatograph was equipped with dual nickel columns [120 × 3 mm (i.d.)] containing 0.2% ethylene glycol succinate, 0.2% ethylene glycol adipate, and 0.4% silicone XF-1150 on Gas-Chrom P. Nitrogen was the carrier gas; oven temperature was programmed from 150° to 190°C at 1°/min. For the 1982–83 analysis, separation of the neutral sugar alditol acetate derivatives was achieved using a fused silica capillary column [30 m × 0.25 mm (i.d.)] of bonded OV-225 (DB-225, J & W Scientific). The carrier gas was H_2 and the oven was held at 210°. Peak areas were integrated by a Perkin Elmer Sigma-10 Chromatography Data System. All samples were analyzed in duplicate.

Carbohydrate analysis—colorimetric assays. Uronic acids in all soluble fractions (Fig. 1) were determined using the method described by Blumenkrantz and Asboe-Hansen (8). The material remaining insoluble after 2 N trifluoroacetic acid (TFA) hydrolysis (3) was collected by centrifugation, washed in MeOH, and dissolved in 67% H_2SO_4. This solution was assayed for cellulose (27) and uronic acid using a modification of the method of Ahmed and Labavitch (1). After ion exchange chromatography of the WSF, both the water and the 6 N acetic acid fractions were assayed for total sugars by the anthrone method (10). All samples were analyzed in duplicate.

Calculation of total amounts of uronic acids, neutral sugars, and starch. The total amounts of uronic acid, noncellulosic neutral sugar, and starch are expressed as milligrams per gram of fresh weight on the basis of the sums of the designated fractions (Fig. 1). Since the kiwifruit contains considerable amounts of starch at harvest (4, 11, 20, 22) and even after ripening (11) or prolonged storage (4) it may still contain some starch, the total noncellulosic wall glucose is reported only as that amount of glucose measured in the EIM. Starch content of the fruit is determined as the amount of glucose measured in the ESM.

Results and Discussion

Fractionation of uronic acids, neutral sugars, and starch

Uronic acids. The reported values for total WSF uronic acids are the sums of the uronic acids measured in the water and 6 N acetic acid eluates of the Dowex-1 columns. Considerable uronic acid was eluted from the ion exchanger with water; from 30% to 50% of the measured uronic acid was found in the acetic acid fraction. The total cell wall (WIF) uronic acid is reported as the sum of the uronic acids found in the ESM and TFA-soluble (TSM) and -insoluble materials (TIM). There was no difference between air- or CA-stored fruit. In 1980, ≈23% of the total cell wall uronic acids (see Fig. 1) were found in the α-amylase-generated ESM (Table 1). Of the total uronic acids found in the EIM, ≈75% was found in the TIM. When amyloglucosidase was used for starch removal (1982), the ESM contribution towards the total cell wall uronic acid content ranged from 91% in freshly harvested fruit to ≈72% in fruit that had been held in storage for 20 weeks (Table 1). Of the total uronic acid found in the EIM, ≈59% was found in the TIM.

Neutral sugars and starch. The total WSF neutral sugars are reported as the sums of the amounts measured for each monosaccharide in the ASF and AIF. The total sugar values determined by the anthrone method (10) and the sums of individual neutral sugars from gas chromatographic analysis gave similar results. The data in Table 1 are taken from the anthrone colorimetric analysis. As a rule, most of the neutral sugars found in the cell wall (WIF), with the exception of xylose, also were found in alcohol-soluble form (the ASF) in the WSF.

For each neutral sugar component of the cell wall (WIF), except glucose, the total of each monosaccharide is reported as the sum of that found in the ESM and EIM. When the WIF had been treated with α-amylase (1980–81), most of each neutral sugar (75% to 92%) was found in the EIM [i.e., remained with the ''starch-free'' cell wall (Table 1)]. When amyloglucosidase was used (1982–83), higher levels of neutral sugars were found in the ESM (range: ≈20% in soft fruit and 58% in firmer fruit).

A comparison of the amounts of neutral sugars and uronic acids found in the ESM when either α-amylase or amyloglucosidase was used for starch digestion indicates that, while both enzymes effectively remove starch, there is extensive removal of other cell wall components as well. This removal was most evident when amyloglucosidase was used (Table 1). In subsequent testing (unpublished data), we have found that amyloglucosidase contains polygalacturonase as well as other polysaccharide-degrading activities (including glucanases), implying that when this enzyme is used in starch analysis great care must be used in evaluating starch content on the basis of solubilized carbohydrate. Furthermore, starch-free cell walls generated by this treatment should be regarded as significantly modified.

Changes in cell wall components during storage in air at 0°C. About 80% of the harvest firmness was lost during the

Table 1. Percentages of uronic acid and neutral sugars found in the enzyme-soluble material (ESM) after starch digestion of the water-insoluble fraction (WIF) of kiwifruit pericarp tissue

Constituent	Weeks at 0°C								
	0	2	4	6	8	12	16	20	24
Uronic acids[z]									
α-Amylase[y] (1980)	18.5	21.8	24.4	23.7	25.4	---	23.2	---	---
Amyloglucosidase (1982)	91.0	90.5	76.5	81.2	73.1	74.5	---	71.8	---
Neutral sugars[x]									
α-Amylase[y] (1980)	15.8	25.4	13.7	8.2	15.7	---	27.7	---	16.7
Amyloglucosidase (1982)	52.8	58.1	53.5	47.6	56.0	32.0	---	19.4	---

[z]As described by Blumenkrantz and Asboe-Hansen (8).
[y]There were no statistical differences between air- and CA-stored fruit. Values reported are the means of duplicates for air and CA fruit.
[x]As described by Dische (10), calculation based on enzyme-soluble carbohydrate, calculated as glucose equivalents.

Table 2. The significance (based on one-way analysis of variance) of treatment effects (0°C storage in air or 2% O_2 + 5% CO_2) on flesh softening and the compositions of the cell wall material (WIF) of kiwifruit pericarp tissue (shown in Fig. 5)

Texture/wall component	Weeks at 0°C					
	2	4	6	8	16	24
Flesh firmness	**[z]	***	***	***	***	***
Cell wall components:						
Uronic acids	NS	NS	†	**	***	–
Galactose	NS	NS	NS	NS	**	†
Arabinose	NS	NS	NS	NS	**	*
Rhamnose	NS	NS	NS	NS	*	*
Xylose	NS	†	NS	NS	NS	NS
Fucose	NS	NS	NS	NS	**	NS
Mannose	NS	NS	NS	NS	NS	NS
Noncellulose glucose	*	NS	NS	NS	NS	NS
Cellulose	NS	NS	NS	*	***	–
Starch	NS	NS	NS	*	**	*

[z]Nonsignificant (NS) or significant at the 10% (†), 5% (*), 1% (**), or 0.1% (***) levels. Data were not taken (–) for cellulose and uronic acids at 24 weeks.

first 8 weeks of storage (Fig. 2A)), and nearly 70% of the cell wall uronic acids (WIF) was lost during the same period (Fig. 2B). For the remainder of the storage period, uronic acid levels in the WIF remained constant. This decrease in wall-bound uronides was mirrored by an increase in water-soluble uronides. Galactose was initially the prevalent neutral sugar found in the noncellulosic portion of the WIF (accounting for ≈35% of the total neutral sugars in this fraction). However, the level of galactose in the WIF declined steadily throughout storage (Fig. 2C). WSF galactose content rose sharply during the first 2 weeks of storage but changed little thereafter. Similarly, there was a general decline in water-insoluble (WIF) arabinose and rhamnose content, which was paralleled by an increase in these sugars in the WSF (Fig. 2 G and H). The xylose content of the WIF fluctuated over the sampling period (Fig. 2F); the amounts present at harvest and after 20 weeks of storage were similar. As a consequence, this pentose was the predominant sugar in the noncellulosic WIF (≈40%) at the last sampling. The data for WIF content of fucose and mannose (Fig. 2 I and J) indicate a decrease in the first few weeks of storage with little change thereafter. These sugars are present in fairly small amounts, however, and so we are not confident that the changes seen are significant.

About a 30% decline was detected in what we report as noncellulosic glucose during the first 8 weeks of storage (Fig. 2D). It is possible that a portion of this decrease represents "starch glucose" remaining with the EIM pellet because of incomplete starch removal. At harvest, we measured >40 mg starch/g fresh weight (Fig. 2E) and <2 mg of "noncellulosic" glucose in the wall fraction (Fig. 2D). If the α-amylase and amyloglucosidase had removed only 95% of the starch, then ≈2 mg of "starch glucose" would have remained with the EIM and subsequently been measured as noncellulosic. Because of our uncertainty about the completeness of starch removal, we cannot be certain that metabolism of wall glucose suggested by the data in Fig. 2D is real. The level of starch fell dramatically during the first 8 weeks of storage, to nearly 10% of its initial value (Fig. 2E). This decline was paralleled by an increase in water-soluble glucose.

The cellulose in kiwifruit cell walls was defined to be that carbohydrate that remained insoluble following 2 N TFA treatment of the EIM. It is composed predominantly of glucosyl residues, but because it was measured with a colorimetric procedure and not GLC, we do equate it to an amount of glucose. While the data show fluctuation, they do suggest a small proportional loss of this important cell wall component (Fig. 2D).

All neutral sugars found in the WSF at harvest (Fig. 2) were essentially EtOH-soluble (Fig. 3). The ratio of EtOH-precipitable to EtOH-soluble sugars for all neutral sugars except glucose

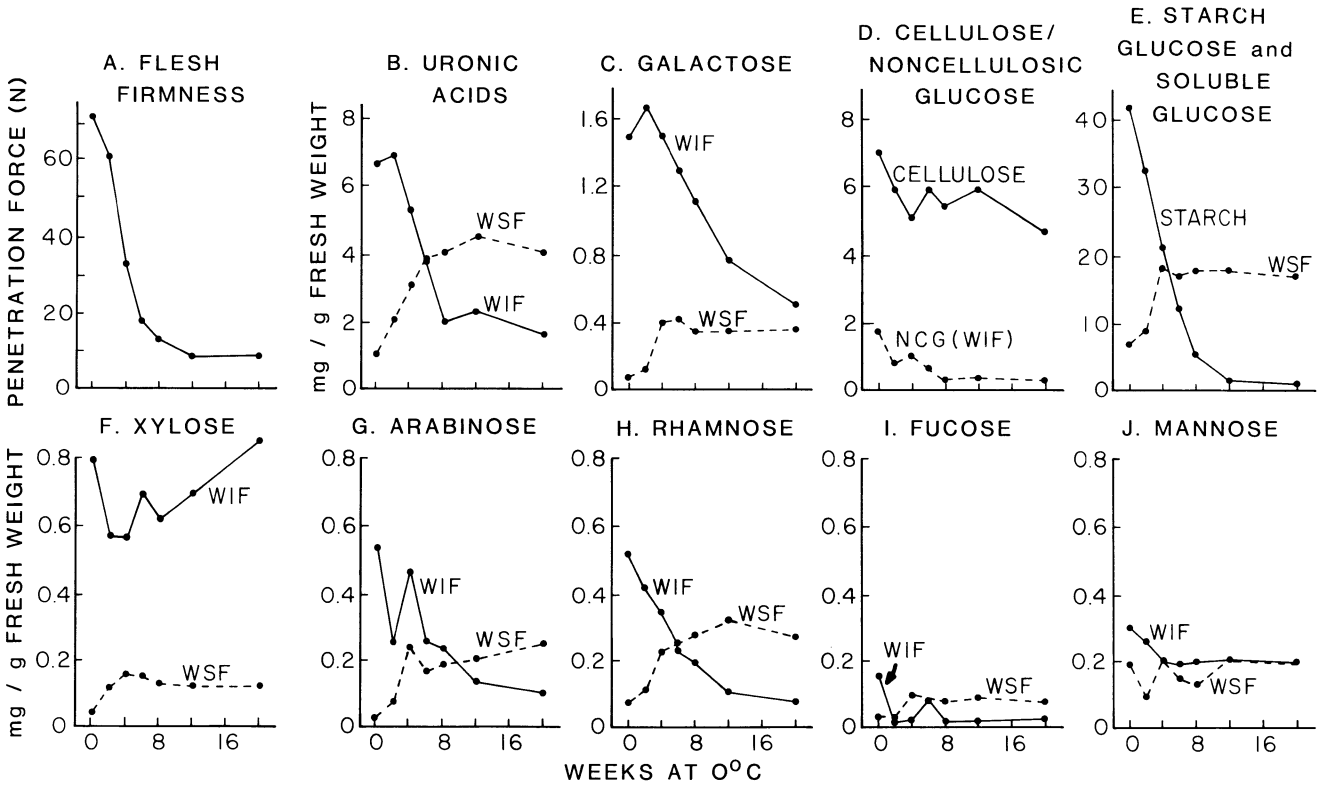


Fig. 2. Changes at 0°C in flesh softening (Newtons) and the carbohydrate composition (milligrams per gram of fresh weight) of the water-soluble fraction (WSF) and cell wall material (water-insoluble fraction, WIF) of kiwifruit pericarp tissue. (**A**) flesh firmness, (**B**) uronic acids, (**C**) galactose, (**D**) cellulose and noncellulosic glucose, (**E**) starch and water-soluble glucose, (**F**) xylose, (**G**) arabinose, (**H**) rhamnose, (**I**) fucose, and (**J**) mannose.

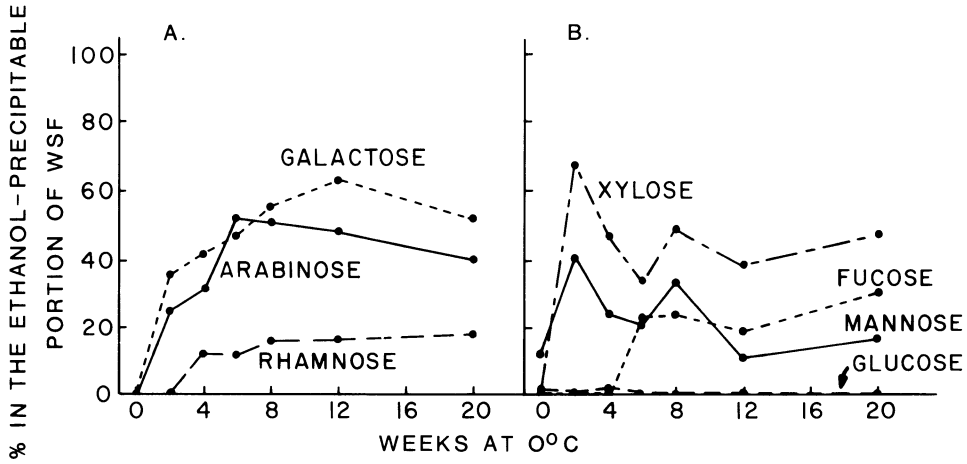


Fig. 3. The proportion of each neutral sugar component in the WSF found in the 80% alcohol-insoluble fraction (AIF) following increasing durations of 0°C storage. (**A**) "pectic" sugars, (**B**) "hemicellulosic" sugars.

increased during the first 2 to 8 weeks of storage, corresponding with the period of rapid flesh softening (Fig. 2A). The increase in the WSF glucose (Fig. 2E) probably is due to starch hydrolysis. Other studies (4, 11, 22) have shown that there is a rise in soluble solids content coincident with starch disappearance. The predominant sugars of ripened kiwifruit have been found to be glucose, fructose, and sucrose (11, 22). Because the level of EtOH-precipitable glucose (Fig. 3B) did not increase during storage, we presume that starch degradation proceeds rapidly and involves no accumulation of relatively high-molecular-weight (i.e., EtOH-precipitable) intermediates.

The patterns of change in those WSF neutral sugars usually most closely associated with pectic polysaccharides (arabinose, galactose, and rhamnose; ref. 26) were similar (Fig. 3A). After the period of substantial flesh softening (0 to 8 weeks), the proportions of these sugars that were EtOH-precipitable (i.e., in the AIF) remained fairly constant. This constancy suggests the existence of an equilibrium situation between wall turnover (i.e., appearance of these sugars in AIF) and total polymer digestion (i.e., accumulation in ASF, signifying, presumably, further metabolism following excision from the wall). This equilibrium however, was not reached until ≈80% of the softening had occurred and the majority of uronic acid (Fig. 2B), galactose (Fig. 2C), arabinose (Fig. 2G), and rhamnose (Fig. 2H)

solubilization had taken place. These cell wall components exhibit similar changes in terms of wall solubilization and the pattern of EtOH insolubility, which suggests a structural association analogous to that described by Talmadge et al. (26) for cultured sycamore cells. Changes in the proportions of xylose, fucose, and mannose, sugars that are normally the primary components of dicot hemicelluloses (19), in the EtOH-precipitable form also were similar to one another (Fig. 3B) but differed from the pattern of change observed for the "pectic" sugars.

A comparison of the components of the WIF as a function of flesh firmness for 1980–81 and 1982–83 illustrates that the patterns of change in the WIF are similar, although the specific quantities of wall components differed for some of the neutral sugars (glucose and xylose), uronic acids, and cellulose (Fig. 4). The pectic polysaccharides (represented by their presumed components—rhamnose, arabinose, glactose, and uronic acids) exhibited similar declines during fruit softening (Fig. 4 A–D) in both years. In general, there was a substantial decline in the amount of these neutral sugars detected in the WIF after fruit firmness had fallen below 18 to 27 N or after ≈80% of the flesh softening had occurred. The level of uronic acids found associated with the WIF declined as fruit softening progressed for both seasons, although higher levels were detected in 1980–81 (Fig. 4D). A decline in cellulose levels associated with ripening was not detected in either year (Fig. 4E). The solubilization of pectic polysaccharides and uronides evident here agrees with reported changes associated with ripening and storage in pears (2, 9, 28), apples (7, 14), tomato (13), strawberry (15), asian pear (29), and previous reports on kiwifruit (12, 23).

There were no consistent changes observed in fucose, xylose, or mannose (Fig. 4 F, G, and H) over the two years. The levels of noncellulosic glucose (Fig. 4I) measured during the two storage seasons also differed. We feel that this difference is due primarily to the enzyme used in starch digestion. In 1980–81, the α-amylase used may not have given complete digestion of the massive amounts of starch initially present (first sampling dates). The decline in starch was parallel in both years (Fig. 4J).

The loss in firmness at 0°C was retarded partially by CA storage (Fig. 5A). CA-stored fruit generally show an initial period of softening during the first 4 to 8 weeks of storage (4, 6, 19). This initial softening usually parallels the decline in flesh firmness in air-stored fruit. There was little difference noted between air and CA in any of the WIF neutral sugars, uronic acids, cellulose, or starch levels for the 2-, 4-, or 6-week sampling periods that corresponded to this initial softening (Table 2).

The decline in WIF uronic acids paralleled the flesh softening, but, after 8 weeks, the CA-stored fruit maintained consistently increased levels of uronic acids (Fig. 5B) and the presumably associated neutral sugars galactose (Fig. 5C), arabinose (Fig. 5G), and rhamnose (Fig. 5H). There were no consistent differences observed in the other noncellulosic neutral sugars (Fig. 5 D, F, I, and J). Fruit held in CA retained higher levels of cellulose after 8 and 16 weeks of storage (Fig. 5D). The decreases in starch content in the two treatments paralleled each other during the initial stages of softening; however, after 6 weeks, CA-stored fruit retained two to four times higher levels of starch (Fig. 5E).

It has been demonstrated clearly (5, 19) that a certain degree of softening always will occur when kiwifruit are placed in CA storage. A biphasic softening pattern for kiwifruit has been proposed (4). The results reported here suggest that, indeed, the initial stages of softening in both air and CA storage may be influenced as much by starch hydrolysis and consequent cell turgor changes as by solubilization of the cell wall components. Transmission electron microscopy of kiwifruit pericarp tissue in freshly harvested fruit and softened fruit (air storage for 6 to 8

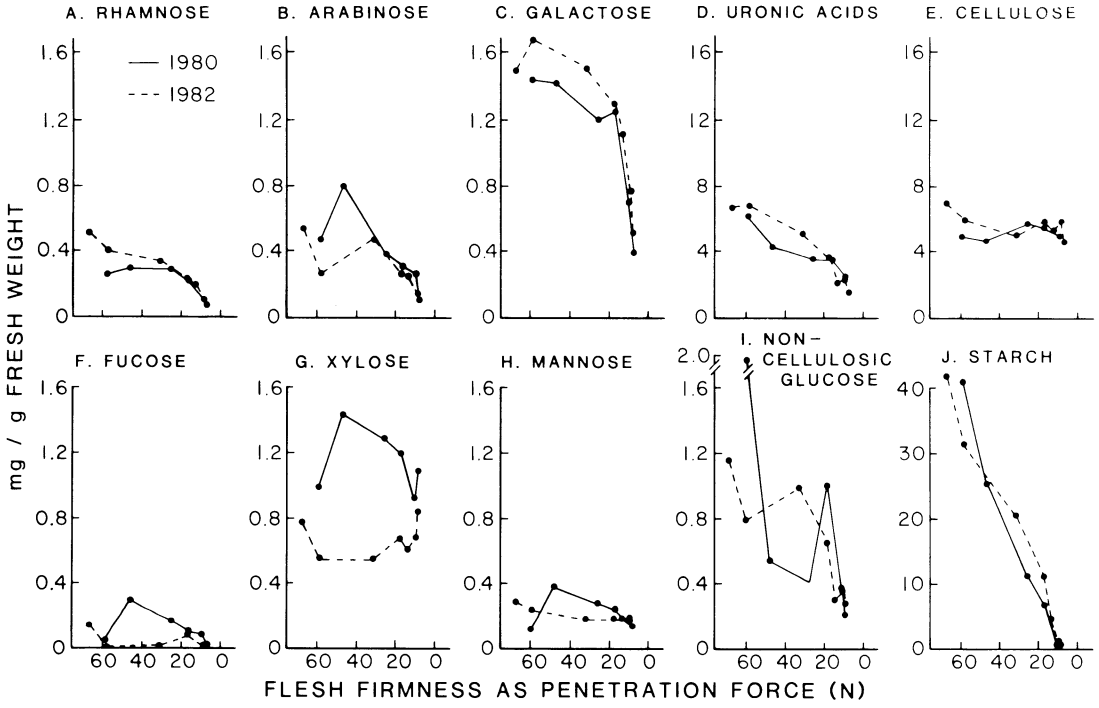


Fig. 4. Changes in the composition (milligrams per gram of fresh weight) of the cell wall material (WIF) during softening of kiwifruit pericarp tissue during two seasons of storage in air at 0°C (**A**) rhamnose, (**B**) arabinose, (**C**) galactose, (**D**) uronic acid, (**E**) cellulose, (**F**) fucose, (**G**) xylose, (**H**) mannose, (**I**) noncellulosic glucose, and (**J**) starch.

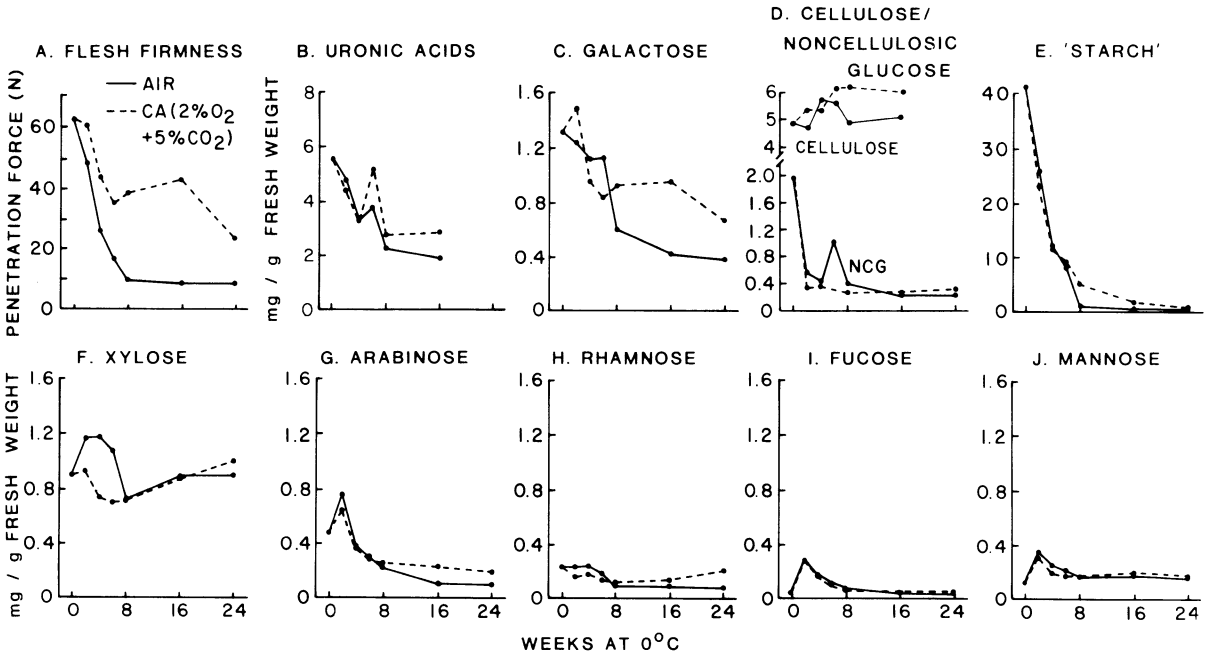


Fig. 5. Effect of storage at 0°C on flesh softening (N) and the composition (milligrams per gram of fresh weight) of the cell wall material (WIF) of kiwifruit pericarp tissue stored in air or 2% O_2 + 5% CO_2 (CA). (**A**) flesh firmness, (**B**) uronic acids, (**C**) galactose, (**D**) cellulose and noncellulosic glucose, (**E**) starch, (**F**) xylose, (**G**) arabinose, (**H**) rhamnose, (**I**) fucose, and (**J**) mannose.

weeks at 0°C) showed differences in amyloplast size (M.L.A., unpublished data). After the initial stage of softening, we were able to detect minor but consistent differences (Table 2) in the levels of uronic acids (Fig. 5B), galactose (Fig. 5C), arabinose (Fig. 5G), and rhamnose (Fig. 5H), suggesting that differences in cell wall digestion are also responsible for at least a portion of the fruit softening that continues in air storage.

In conclusion, we have demonstrated that changes in the level of cell wall components associated with low-temperature softening of kiwifruit follow the general trends observed during normal ripening in other fruits (2, 7, 13–15, 28, 29). Consistent patterns of change were largely restricted to wall components containing uronic acids, galactose, arabinose, and rhamnose, and thus suggest pectin metabolism. Because the data show an accumulation of these "pectin-component sugars" in both high- and low-molecular-weight water-soluble form, we suggest that pectins are excised from the wall as polymers that are subsequently degraded further. It is remarkable that this process proceeds at 0°C.

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Effects of Maturity, Harvest Date, and Storage Time on Postharvest Quality of Red Raspberry Fruit

Thomas M. Sjulin[1] and JoAnn Robbins[2]

Western Washington Research and Extension Center, Washington State University, Puyallup, WA 98371

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Abstract. **'Meeker' red raspberry (*Rubus idaeus* L.) fruit harvested at three maturity stages [inception (IN), red ripe (RR), and processing ripe (PR)] on four harvest dates at weekly intervals were held 0, 3, 6, and 9 days at 0°C and 90–95% RH. Fruit retention strength, firmness, and titratable acidity decreased with increasing maturity, while berry weight, total anthocyanin concentration, pH, and postharvest rot incidence increased. Fruit were darker visually with increasing maturity when compared to color standards. Soluble solids differences among stages of maturity were not consistent for all harvest dates. During storage, fruit at all stages of maturity increased in pH, total anthocyanin concentration, and postharvest rot incidence, but decreased in titratable acidity and darkened visually. The rate of increase in anthocyanin concentration and visual darkening was greater for IN and RR fruit than PR fruit. Total anthocyanin concentration accounted for 85% of the variation in visual darkness. Changes in red hues during storage, and differences in red hues among stages of maturity, were not consistent for all harvests and were not related to total anthocyanin concentration. Firmness increased during storage for the first harvest date, but decreased for the remaining three harvests. Berry weight, firmness, and titratable acidity decreased for all stages of maturity with later harvest dates, while postharvest rot incidence increased. This decrease in berry weight was greater for RR fruit than IN or PR fruit. Harvest date affected pH and rate of weight loss of all maturity stages and fruit retention strength of IN and RR fruit, but not PR fruit. Total anthocyanin concentration increased with later harvest dates of PR fruit, but did not change in IN or RR fruit. Soluble solids decreased linearly with harvest date in IN and PR fruit, but changed nonlinearly in RR fruit.**

Several factors limit the storage life of cultivated red raspberry fruit, including postharvest rot, loss of firmness, and darkening (7, 17, 19). Harvesting at an earlier stage of horticultural maturity (25) than the optimum for processing or immediate fresh use long has been recommended for extending the storage life of red raspberry fruit (13). Current recommendations for fresh-market storage and shipping are to use fruit that "have just turned pink" (23), or "firm" rather than "very ripe" fruit (24), or fruit that have just developed 100% red surface color (17). However, few studies have examined the effect of maturity on quality and storage life of red raspberry. Harvesting fruit at the "pink" stage of maturity delays postharvest rot development when compared to fruit at "normal" maturity (21). Berry weight and soluble solids increase with horticultural maturity up to processing ripe, then decrease at overripe (12, 20). Anthocyanin concentrations continue to increase with maturity (15). Titrat-

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[1]Assistant Horticulturist. Present address: Driscoll Strawberry Associates, 404 San Juan Rd., Watsonville, CA 95076.
[2]Agricultural Research Technologist III.