Physicochemical Characteristics of Onion (*Allium cepa* L.) Tissues

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The structure and mechanical properties of onions are important factors affecting their textural quality. The onion bulb consists of several layers of pigmented, papery scales surrounding fleshy storage scales that comprise an upper epidermis, an intermediate parenchyma tissue, and a lower epidermis. The purpose of this study was to examine the chemical composition of cell walls from the papery scales and outer fleshy scales of onion (*Allium cepa* L. cv. Sturon) in relation to their mechanical properties. Cell-wall material (CWM) was prepared from the component tissues and analyzed for its carbohydrate and phenolic composition. The CWMs were rich in uronic acid and glucose, with smaller quantities of arabinose, galactose, and xylose. In the fleshy scales, the lower epidermis contained relatively more galactose-rich pectic polysaccharides, whereas the upper epidermis and the papery scales contained virtually no galactose. Analysis of mechanical properties showed that the order of strength of the tissues was papery scales > fleshy scales, which were in the order lower epidermis > upper epidermis > intermediate parenchyma. The upper epidermis of fleshy scales was stronger in the vertical than the horizontal direction, and both orientations showed negligible notch sensitivity. Cyclohexane-*trans*-1,2-diaminetetraacetate-induced vortex-induced cell separation of the intermediate layer of fleshy scales indicated that calcium cross-linking may play an important role in cell−cell adhesion. A small but significant amount of ferulic acid was found in the walls, predominantly in the thick cuticle of the lower epidermis of fleshy scales. Alkali-labile wall-bound flavonoids were also detected.

Keywords: *Onions; mechanical properties; cell walls; phenolic acids*

INTRODUCTION

Onions are one of the most important vegetable crops grown in Europe and are valued for their flavor and pungency (Fenwick, 1985).

Immature and mature onions are consumed throughout the year, the mature bulbs being cured to dry the skin and develop color. Commercial onion processing results in the production of large quantities of waste, which consists predominantly of the outer pigmented, papery scales together with two outer layers of fleshy scales. It has been shown that the papery and fleshy scales, which have a common origin as leaf bases, differ in physicochemical properties (Ng et al., 1998).

There have been several detailed studies on the cell wall chemistry of onions (Redgwell and Selvendran, 1986; Ng et al., 1998). In contrast, studies on mechanical properties have generally been on whole onions and not usually in the form of engineering properties (Ang et al., 1960; Komochi, 1990; Maw et al., 1996). Hence, there is little definitive information relating the cell-wall chemistry of different onion tissues to mechanical and processing properties. The aim of the present study was to develop a greater understanding of the structural and mechanical characteristics of the papery and fleshy scales in relation to their cell-wall chemistry.

MATERIALS AND METHODS

Materials. Onions (*Allium cepa* L. cv. Sturon), supplied by a local grower (BOPA, Spalding, U.K.), were dissected to provide samples of the dry papery scales and the two outer fleshy scales. The fleshy scales were further dissected into upper epidermis pulled from the concave surface, intermediate parenchymatous tissue, and lower epidermis removed from the convex surface. Samples were immediately frozen in liquid nitrogen and stored at −40 °C prior to chemical analysis.

Unless otherwise stated, all chemicals were of AnalaR quality.

Light Microscopy. Fresh onion material was fixed in 30 g L^{-1} of glutaraldehyde (Agar Scientific Ltd.) in 50 mM cacodylate (TAAB) buffer, pH 7.4, for 3 h. The samples were dehydrated in an ethanol (Fisons) series with three changes in 1000 mL L^{-1} ethanol and then infiltrated with LR White resin (London Resin Co. Ltd., Reading, U.K.). The samples were transferred to gelatin capsules containing fresh resin, which was polymerized for 24 h at 60 °C. Sections, 1−2 μm thick, were cut with glass knives, dried down onto glass slides, and stained with 10 g L^{-1} toluidine blue (Aldrich) in 10 g L^{-1} borax (BDH), pH 11.

Fluorescence Microscopy. Hand-cut transverse sections of fleshy scales were mounted in water or 20 mM NH_4OH (pH 10) and examined in a Leitz Ortholux II microscope with an HBO 50 W mercury arc lamp and an exciter and barrier filter combination with transmission of 340−350 and 430 nm, respectively.

Mechanical Tests. Specimens were excised from the equatorial region of onion bulbs (Figure 1) in a direction horizontal to the bulb axis. The influence of the orientation of the upper epidermal cells (vertical and horizontal) on mechanical properties was also investigated (Figure 1). Sample thickness was measured using vernier callipers (RS 572-044, 0.01 mm).

Samples of the papery scales and the upper epidermis, intermediate layer and lower epidermis from fleshy scales were tested to failure with a universal testing machine at a cross-head speed of 0.05 mm s^{-1} (Stable Microsystems TA-XT2,

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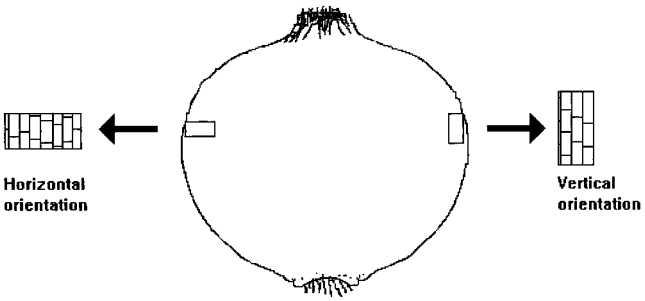

Figure 1. Schematic view of onion bulb showing orientation of samples for mechanical testing.

Godalming, U.K.). Samples approximately 30 mm long and 3 mm wide were edge notched to 1 mm in a purpose-made jig and were glued to stainless steel end plates with an overlap of ~3 mm at each end. The samples were then clamped in the tensile grips of the testing machine, and the tensile strength was calculated from the maximum force and the unnotched cross-sectional area of the sample. A total of 30 samples of each tissue type was tested.

In a separate series of experiments to investigate the effect of notch length on the mechanical properties of the upper epidermis, horizontally and vertically oriented specimens 30 mm long but 9 mm wide were excised and notched in 1 mm increments from 0 to 8 mm. Ten specimens of each notch size were tested as above. Data from this series were expressed as the nominal tensile strength calculated from the maximum force and the cross-sectional area prior to notching.

Vortex-Induced Cell Separation (VICS). Pieces (10 × 10 mm) of papery scales and fleshy scales were sequentially extracted with cyclohexane-*trans*-1,2-diaminetetraacetate (CDTA, Na salt; 0.05 M, Sigma), Na_2CO_3 (0.05 M, BDH) at 1 and 20 °C, and KOH (0.05, 0.1, and 0.25 M; BDH) at 20 °C as described by Parker and Waldron (1995). The extractions were carried out sequentially for 16 h each. In the case of CDTA and Na_2CO_3, failure to induce cell separation was followed by a repeat of the extraction, but for 30 min at 100 °C. Hot extractions were not followed by further extractions. After each extraction, the tendency for cell separation was determined by placing two tissue sections into each of two screw-capped test tubes with 3 mL of water, vortexing the tissue sections for 1 min, and shaking the tubes vigorously 10 times. The following scores (number of plusses) were assigned according to the degree of disruption: (0) each tissue section intact; (1) each tissue section broken into 3−5 clumps; (2) each tissue section broken into 6−7 clumps; (3) tissue sections broken into many clumps, some separate cells; (4) tissue sections disrupted into clumps of ~20−30 cells or less, many separated cells; (5) tissue completely disrupted, many clumps <5−10 cells, mostly single separated cells (total VICS). Intermediate values were apportioned if necessary.

Preparation of Cell-Wall Material (CWM). Samples (10−100 g) of papery scales and fleshy scales were individually blended in 15 g L^{-1} sodium lauryl sulfate (SDS) containing 5 mM $Na_2S_2O_5$ with an Ystral homogenizer (Ystral GmbH, Dottingen, Germany) for 5 min. A few drops of octanol were added to reduce foaming. The homogenate was filtered through a 100 μm nylon mesh (John Stannier and Co., Manchester, U.K.), and the residue was ball-milled (Pascall, 0.5 L pot) at 0 °C in 5 g L^{-1} SDS containing 3 mM $Na_2S_2O_5$ for 2 h at 60 rpm to remove the bulk of the remaining cell contents. After the homogenate had been filtered through 75 μm nylon mesh, the residue was suspended in cold water containing 3 mM $Na_2S_2O_5$, homogenized for 5 min, and refiltered. The procedure was repeated three times until the cell-wall residue was free of intracellular contents as assessed by light microscopy after staining in iodine/potassium iodide. The CWM was stored as a frozen suspension at −20 °C. Prior to extraction of cell-wall phenolics, the CWM was further extracted with hot ethanol to remove any alcohol-soluble phenolics, washed three times with acetone, and then air-dried.

Sugar Analysis. Cell-wall neutral sugars were analyzed as described previously (Ng et al., 1998). Sugars were released from CWM by dispersing in 720 g kg^{-1} H_2SO_4 (Fisons) for 3 h followed by dilution to 1 M and hydrolyzing for 2.5 h at 100 °C (Saeman et al., 1954). All samples were analyzed in duplicate, and the standard deviations of the data were <2%. Neutral sugars were reduced with $NaBH_4$ and acetylated according to the method of Blakeney et al. (1983) using 2-deoxyglucose (Sigma) as an internal standard. Alditol acetates were quantified by gas chromatography as described in Parr et al. (1997).

Uronic acids were determined colorimetrically according to a modification of the method of Blumenkrantz and Asboe-Hansen (1973) in which samples were dispersed in 720 g kg^{-1} H_2SO_4 for 3 h at room temperature, diluted to 1 M H_2SO_4, and hydrolyzed for 1 h at 100 °C.

Phenolic Acid Analysis. Phenolic acids were extracted and determined as described by Waldron et al. (1996). CWM (1 g) was sequentially extracted with 0.1 M NaOH (1 h; HPLC grade; BDH), 0.1 M NaOH (24 h), 1 M NaOH (24 h), and 2 M NaOH (24 h) under N_2 (O_2-free) at room temperature. The supernatant was filtered (GF-A, Whatman, U.K.) and acidified with HCl (Fisons). *trans*-Cinnamic acid (Sigma; 100 μL, 1 mg mL^{-1} 500 mL L^{-1} methanol) was added to the filtrate as an internal standard and extracted three times with ethyl acetate (Fisons; HPLC grade). The ethyl acetate extracts were combined and dried under a stream of N_2. The sample was dissolved in 500 mL L^{-1} methanol (200 μL; HPLC grade; BDH) and analyzed by HPLC as described in Waldron et al. (1996).

RESULTS AND DISCUSSION

Light Microscopy. Light microscopy of the brown papery scales, sectioned across their long axis, showed them to be 100−150 μm thick and to consist of tightly compressed layers of cells with a shiny outer cuticle (not shown). In contrast, transverse sections of the fleshy scales showed them to be 3−4 mm thick and to consist mainly of thin-walled parenchyma cells with vascular traces, bounded on the upper (concave) side by an epidermis with a thin cuticle and on the lower (convex) side by an epidermis with a thick cuticle. The upper epidermis peeled off easily (Figure 2a, surface view), taking with it several layers of flattened, separated parenchyma cells (Figure 2b, cross-sectional view), similar to the multiple layers described by Komochi (1990). The lower epidermis consisted of a single layer of uniform cells covered by a thick cuticle, all firmly attached to the underlying parenchyma, making it difficult to separate (Figure 2c). However, when peeled off (Figure 2d, surface view), this epidermis was free from any adhering parenchyma cells (Figure 2e, cross-sectional view). The parenchyma cells adjacent to the upper epidermis were large, with substantial intercellular spaces (Figure 2b); those adjacent to the lower epidermis were smaller, with less extensive intercellular spaces (Figure 2c).

Autofluorescence of Onion Cell Walls. Under alkaline conditions only (after infiltration with 20 mM NH_4OH; pH >10), the cell walls of some cells of the fleshy scales emitted a greenish yellow pH-dependent autofluorescence. This was barely discernible in the walls and thin cuticle of the upper epidermis, but distinct in the walls of the lower epidermis, being particularly intense in the thick cuticle (Figure 3). The pH-dependent autofluorescence indicated the presence of cinnamic acid components such as ferulic acid (Waldron et al., 1997a); their presence was confirmed by further chemical analysis (see below). The papery scales emitted virtually no pH-dependent autofluorescence,

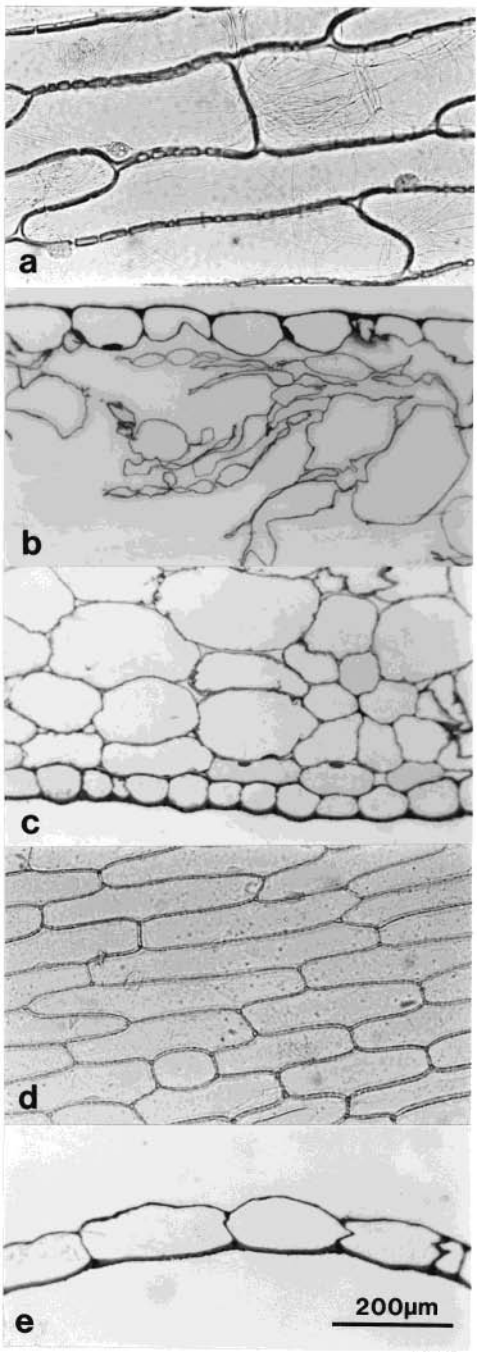

Figure 2. Microscopy of fleshy scales: (a) peel of upper epidermis (surface view), bar = 50 μm; (b) peel of upper epidermis (cross-sectioned) showing adhering parenchyma, bar = 100 μm; (c) section through lower epidermis and underlying tissue, bar = 100 μm; (d) peel of lower epidermis (surface view), bar = 100 μm; (e) peel of lower epidermis (cross-sectioned) showing absence of adhering parenchyma, bar = 200 μm.

and that which could be discerned was very faint, green, and located between the cells (viewed from above).

Mechanical Properties. Tensile strength was measured for the papery scales and the upper and lower epidermal layers and the intermediate tissue from the fleshy scales. When measured in the horizontal orientation, papery scales were found to be stronger than the lower epidermis of the fleshy scales, which in turn was stronger than the upper epidermis (Table 1). Additionally, this upper epidermis was some 4 times stronger than the intermediate tissue of the fleshy scales. The

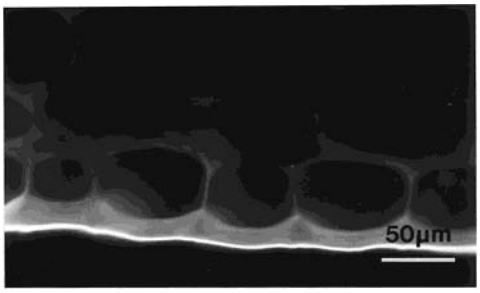

Figure 3. Autofluorescence at pH 10 of lower epidermis of fleshy scale.

Table 1. Tensile Strength of Onion Tissues

sample	orientation	thickness[a] (mm)	tensile strength[a] (MPa)
papery scales	horizontal	0.1 (0.00)	34.8 (3.2)
fleshy scales			
upper epidermis	vertical	0.05 (0.00)	1.55 (0.10)
upper epidermis	horizontal	0.05 (0.00)	0.95 (0.10)
intermediate tissue	horizontal	1.27 (0.17)	0.40 (0.03)
lower epidermis	horizontal	0.01 (0.00)	16.0 (1.0)

[a] Value in parentheses are expressed as the standard deviation.

results also indicate that the tensile strength of the upper epidermis was greater in the vertical than the horizontal orientation, but by a factor of <2. It is interesting that Ang et al. (1960) found that the force to break divided by compressive displacement was greater for whole onions when tested horizontally than vertically. Modeling foams with anisotropic cells gives the result that the fracture toughness ratio in two directions is proportional to $R^{1.5}$, where R is the foam cell aspect ratio (Huber and Gibson, 1988). Figure 2a indicates $R > 4$ and therefore $R^{1.5} > 8$. The observed anisotropy in strength, which is proportional to the fracture toughness ratio for a given notch size, is considerably lower than this figure, although Huber and Gibson (1988) also observed a weaker dependence on R in their experimental data. However, it should be noted that this model considers foams of identical cells and does not include turgor effects.

Notch sensitivity of selected onion tissues was also investigated. According to linear elastic fracture mechanics, a notch-sensitive material will show a rapid fall in its nominal strength proportional to the inverse square root of notch size [e.g., Purslow (1989)] (Figure 4). Notch insensitivity is marked by a linear decrease of nominal strength to zero as notch size expressed relative to sample width increases to unity. Changing the notch size in the upper epidermal layers of horizontal and vertical orientation showed negligible notch sensitivity (Figure 4). Vincent (1990) found that grasses were notch insensitive and fruit skins from apple, tomato, and grape were moderately notch sensitive. The tensile strengths of 9−15 MPa recorded for tomato skins in a tensile test (Voisey et al., 1970) were similar to those obtained for the lower epidermis of fleshy onion scales. The tensile strengths of the upper epidermis and intermediate tissue of fleshy scales are comparable with values of 0.35 MPa for raw potato (Waldron et al., 1997a) and 0.5−1.5 MPa for carrot (McGarry, 1995).

It is important to note that the moisture contents of the papery scales and the fleshy scales were approximately 21.0 and 57.9% (wet weight basis), respectively.

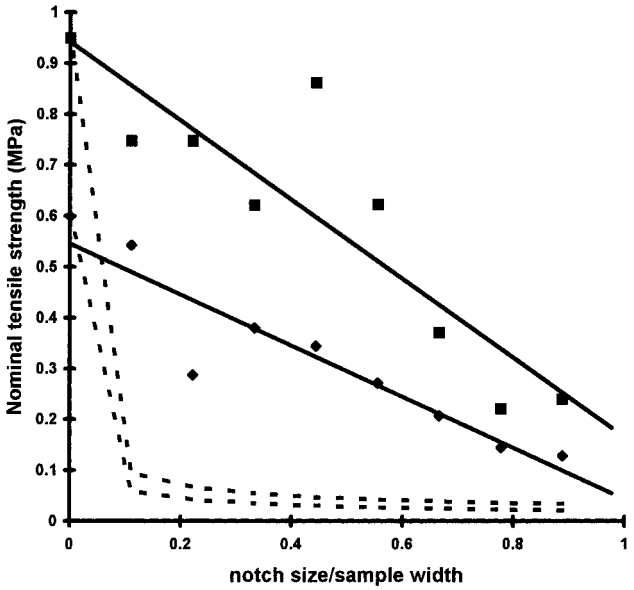

Figure 4. Effect of notch size relative to sample width on nominal tensile strength of upper epidermis: (■) vertical orientation; (◆) horizontal orientation. Notch sensitive predictions are shown (- - -).

Table 2. Effect of Sequential Extraction of Tissue Pieces on the Ease of Cell Separation (VICS)

	papery scales	fleshy scales	upper epidermis	intermediate tissue	lower epidermis
water	-----	-----	-----	-----	-----
+ heat	-----	-----	-----	-++++	-----
CDTA	-----	---++	----+	-++++	-----
+ heat	+++++	+++++	+++++	+++++	+++++
Na_2CO_3-1	-----	-----	-----	+++++	-----
+ heat	+++++	+++++	+++++	+++++	+++++
Na_2CO_3-2	----+	-++++	----+	+++++	-----
+ heat	+++++	+++++	+++++	+++++	+++++
50 mM KOH	----+	-++++	----+	+++++	-----
100 mM KOH	----+	-++++	---++	+++++	----+
250 mM KOH	+++++	+++++	+++++	+++++	+++++

Vortex-Induced Cell Separation (VICS). To obtain information on the chemical nature of cell adhesion in onion tissue, papery scales and fleshy scales were extracted with a variety of procedures originally designed for the sequential extraction of cell-wall polymers (Table 2) (Parker and Waldron, 1995). The papery scales did not show VICS after extraction in cold or hot water or cold CDTA (a chelator of Ca^{2+}; Table 2). The upper and lower epidermal layers of the fleshy scales behaved similarly. However, VICS of these tissues could be obtained after extraction with hot CDTA. In contrast, the parenchyma cells of the intermediate tissue separated relatively easily in hot water and also in cold CDTA. These results indicate that cell−cell adhesion in all of these tissues involves calcium cross-linked pectic polysaccharides and showed that the adhesion is particularly strong in the epidermal layers of the fleshy scales and in the papery scales. However, cell adhesion is not limited by thermally stable cross-links such as those found in sugar beet and Chinese water chestnut (Parker and Waldron, 1995; Waldron et al., 1997a,b). This is of particular interest in relation to the papery scales, which fail to soften even after long periods at 120 °C (Ng et al., 1998). The synergistic effect of the heat and CDTA in causing cell separation in the papery scales probably reflects the tight nature of the cross-linking of the polymers in the cell walls, requiring both thermal degradation of pectic polymers and the removal of calcium. It is quite possible that the thermal degradation of the pectic polymers is modulated by the degree of ionic cross-linking.

Carbohydrate Composition of Cell-Wall Materials (CWM). Onion tissues were prepared as CWMs as discussed under Material and Methods. On a fresh weight basis, the yield of CWM from the papery scales was very much higher than that from the fleshy scales (Table 3). The CWM of the latter contained mainly uronic acid, glucose, arabinose, and galactose with minor quantities of xylose and mannose. In contrast, the papery scales contained virtually no galactose as indicated by a high uronic acid/neutral sugar (arabinose + galactose) ratio (UA:NS). These results were consistent with those published for onion tissues (Ng et al., 1998) in which similar variation existed in cell-wall composition among tissues.

Because the intermediate parenchyma tissue provides the main component of the fleshy scales, its carbohydrate composition was, not surprisingly, broadly similar (Table 3). However, the upper epidermal layer exhibited much lower levels of cell-wall galactose than the intermediate and lower epidermal layers, demonstrating considerable heterogeneity in composition between tissues within an individual scale.

Phenolic Composition of CWM. Recent studies on the ester-linked phenolic components of Chinese water chestnut cell walls highlight their possible role in influencing the textural properties (Waldron et al., 1997a; Parr et al., 1997). Our earlier observation that certain onion cell walls exhibited considerable pH-dependent autofluorescence (see above) suggested the presence of simple phenolics. These were released by saponification and quantified by HPLC. Protocatechuic acid was the most abundant phenolic component in the papery scales and was not detected in the other tissues (Table 4); its presence may be related to resistance to smudge and neck rot diseases (Link et al., 1929; El-Waziri et al., 1978). The CWMs of both papery and fleshy scales contained small quantities of ferulic acid. However, there was no detectable diferulic acid, consistent with the induction of VICS in hot CDTA (see above). The phenolic components in the fleshy scales were highest in the lower epidermis, which is on the outside of the scale. It is known that 4-hydroxybenzoic acid may act as a pathogen-related elicitor in defense response (Schnitzler et al., 1992) and that peroxidative

Table 3. Carbohydrate Composition of Onion CWM

	yield	carbohydrate (mol %)								total	ratio
	(% CWM)	Rha	Fuc	Ara	Xyl	Man	Gal	Glc	UA	(μg mg^{-1})	UA:NS
papery scales	41	1	tr	1	4	2	2	44	47	806	16
outer fleshy scales	2	1	1	2	3	1	13	30	49	796	4
upper epidermis	6	2	1	2	5	2	2	31	55	830	14
intermediate tissue	2	1	1	2	5	2	14	30	45	803	3
lower epidermis	9	1	1	2	5	2	9	21	59	856	5

Table 4. Total Esterified Phenolic Acids of Onion Scales

phenolic acid	esterified phenolic acids (ng mg^{-1} CWM)			
	papery scales	fleshy scales	upper epidermis	lower epidermis
protocatechuic acid	70.6			
p-hydroxybenzoic acid	2.2	1.3		0.3
vanillic acid	4.1	1.7	0.3	2.6
p-hydroxybenzaldehyde		0.7	0.4	0.2
trans-coumaric acid	0.6			4.8
vanillin		0.6	0.4	0.6
trans-ferulic acid	0.4	1.3	0.7	5.8
cis-ferulic acid		1.0		0.8

cross-linking of ferulic acid forms part of the response to wounding and pathogenic attack (Waldron et al., 1997a).

Interestingly, in addition to the typical wall phenolics quantified in Table 4, the lower epidermis also contained significant quantities of less-well characterized phenolics. Prominent among these were a group of compounds showing the characteristic UV spectra of flavonoids (results not shown). Flavonoids have in the past been reported from the walls of gymnosperms (Strack et al., 1988), but this is apparently the first report from angiosperms. Onion bulbs are known to be rich in flavonoids [e.g., Price et al. (1997)]. Flavonols with UV spectra similar to those of quercitin monoglycosides were detected in small amounts, but the major peak was tentatively identified on the basis of its retention time and characteristic UV spectrum as quercitin 3,4′-diglucoside. Other peaks detected showed UV spectra similar to that of the highly characteristic 8−5′-linked dehydrodiconiferyl alcohol (data not shown), although they were much more hydrophilic. Possibly they represented conjugates. It should be noted that both flavonols and dehydrodiconiferyl alcohol are potentially bifunctional and may serve to cross-link polysaccharide chains in the absence of significant amounts of dehydrodiferulic acids.

GENERAL DISCUSSION

The structure and mechanical properties of plant-based foods are dependent, largely, on the cell wall (Van-Buren, 1979; Waldron et al., 1997a). Our previous investigation focused on the carbohydrate composition of all walls of onions (Ng et al., 1998). In that study, it was demonstrated that the carbohydrate compositions were similar in the varieties assessed, but substantial variation existed between tissues. The present study extends these observations and shows that there are further differences in carbohydrate and phenolic chemistry between the cell walls of tissues in a single bulb scale. Furthermore, there are marked differences in the mechanical properties between papery and fleshy scales and between the different tissues within a scale.

Carbohydrate analysis showed that the papery scales and the upper epidermis of the fleshy scales contained virtually no galactose compared with the intermediate tissue and the lower epidermis. The lack of long galactan side chains (Redgwell and Selvendran, 1986) probably increases the degree of calcium cross-linking between pectin molecules, resulting in modification in functional and mechanical properties (Banker and Dara, 1982; Guillon and Thibault, 1987, 1990). In previous studies on the cell-wall chemistry of onion tissues, it has been demonstrated that the papery scales contain higher levels of the CDTA-extractable pectic polymers than the fleshy scales, consistent with higher levels of calcium cross-linked polysaccharides (Ng et al., 1998). This may contribute to the higher tensile strength of papery scales when compared with that of fleshy scales. It is known that the tensile "strength" of papery scales, expressed as a force, varies considerably among cultivars and growing sites and is positively correlated with thickness, which may play an important role in the cracking and sloughing resistance of onion bulbs (Komochi, 1990).

CONCLUSION

The above studies have demonstrated the following:

(1) The tensile strength of the papery scales was greater than that of the tissues (internal, upper and lower epidermis) of fleshy scales. The upper epidermis of fleshy scales was weaker in the horizontal than the vertical direction, and both orientations showed negligible notch sensitivity.

(2) The differences between the chemical and mechanical properties of the papery and fleshy scales indicate developmental changes that may relate to the loss of galactose side chains.

(3) Thermally induced softening of tissues is retarded by calcium cross-linking of pectic polysaccharides involved in cell−cell adhesion, particularly when the degree of galactan branching has been developmentally reduced.

(4) Although the levels of simple phenolic compounds in the cell walls are low, there are significant quantities of wall-bound flavonoids that could provide a further basis for peroxidative cross-linking in the cell wall.

ABBREVIATIONS USED

CWM, cell-wall material; CDTA, cyclohexane-*trans*-1,2-diaminetetraacetate; Rha, rhamnose; Fuc, fucose; Ara, arabinose; Xyl, xylose; Man, mannose; Gal, galactose; Glc, glucose; UA, uronic acid; UA:NS, uronic acid/neutral sugar (galactose + arabinose) ratio; tr, trace; TFA, trifluoracetic acid; VICS, vortex-induced cell separation.

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