# Chemical and Microscopic Characterization of Potato (*Solanum tuberosum* L.) Cell Walls during Cooking

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Cell wall material (CWM) was isolated from noncooked, 5 min cooked, and 15 min cooked potato tissue and accompanying cooking media from the cultivars Irene and Nicola. A mass balance of the material in the different fractions obtained during isolation was made. Chemical compositions of the CWM and cell size distributions of the potato tissues were analyzed. The mealy cooking cv. Irene had more CWM per unit cell surface area than the nonmealy cooking cv. Nicola. These results confirmed observations of the potato cell walls made by transmission electron microscopy. The molar composition of the CWM was comparable for both cultivars. During cooking, for both cultivars relatively more unbranched than branched pectic polysaccharides were solubilized. However, the type of pectin solubilized after 15 min of cooking was different for the two cultivars. This pectin was relatively more branched, more methylated, and more acetylated for cv. Irene than for cv. Nicola.

**Keywords:** *Potato; Solanum tuberosum L.; cooking; texture; cell wall; middle lamella; transmission electron microscopy (TEM)*

## INTRODUCTION

The texture of cooked potatoes is an important quality aspect. One of the factors determining texture is the degradation of cell walls and middle lamellae as a result of heating (Jarvis et al., 1992; Andersson et al., 1994).

In general, cell walls determine the physical properties of plant tissue, which are of importance for the texture of plant products (Tucker and Mitchell, 1993). Cell walls can be presented as a cellulose−xyloglucan network embedded in a pectin matrix. The cell wall strength is established by the cellulose microfibrils, and the pectin matrix acts as a "glue" that holds the microfibrils around one cell and between cells together. The two main types of pectin are linear homogalacturonans and rhamnogalacturonans with neutral sugar side chains attached to the rhamnosyl residues (Carpita and Gibeaut, 1993; Schols, 1995). For potato, this model is supported by the combined microscopic and chemical study of Shomer and Levy (1988). Potato tissue was incubated with pectinase, which resulted in removal of the middle lamella and exposure of the microfibrillar network of the cell wall. Due to this treatment, the volume of the macerate was slightly reduced. In contrast to this, incubation with cellulase resulted in a large reduction of the volumetric tissue construction.

Cooking of potatoes also affects the non-cellulosic matrix. Solubilization of pectic material has been reported (Keijbets, 1974; Moledina et al., 1981; Jaswal, 1991; Marle et al., 1994). Although the polysaccharide structure of noncooked cell walls of single potato cultivars has been extensively studied (Ishii, 1981; Jarvis et al., 1981; Ryden and Selvendran, 1990), the polysaccharide content of cooked potatoes is reported only in relation with dietary fiber research (Englyst and Cummings, 1987, 1990).

In a previous study, 10 potato cultivars, which represented a large part of the diversity in texture types of cooked potatoes, were sensory evaluated (results to be published). Most of the difference in texture was explained on the basis of the difference between mealy and nonmealy (waxy) cooking potatoes. The cultivars Irene (mealy) and Nicola (nonmealy) were representative of this difference in texture. The difference in texture between potato cultivars was further investigated at an ultrastructural level by cryoscanning electron microscopy (Marle et al., 1992). The extent of intercellular contacts and the appearance of cell surfaces were different for mealy and nonmealy cooking cultivars. Based on these observations, middle lamella breakdown, cell wall loosening, and starch gelatinization were supposed to be important factors determining texture. In continuation of these studies, it was decided to investigate the influence of cell walls and middle lamellae in determining texture development. By measuring the solubilization of pectic material during cooking, it was found that the mealy cooking cv. Irene released more pectic material, which was accompanied with more cell sloughing than the nonmealy cooking cultivar Nicola (Marle et al., 1994). More release of pectic material may be the cause or the effect of more cell sloughing. The present study was performed to elucidate whether a difference in composition of cell walls and middle lamellae resulted in the observed difference in pectin release, thereby causing more cell sloughing. Therefore, cell wall material (CWM) was isolated and its composition analyzed. Furthermore, the changes that took place in the cell wall during cooking were visualized by transmission electron microscopy. The mealy cooking cv. Irene and the nonmealy cooking cv. Nicola were used and examined after different time periods during cooking in order to make possible a good comparison between cultivars (with different texture types) during cooking.

## MATERIALS AND METHODS

**Materials.** The potato cultivars Irene and Nicola, mealy and nonmealy cooking respectively, were grown in 1992 on clay

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soil at the experimental station of ATO-DLO in the North East Polder, The Netherlands. Potatoes of size 45−55 mm were stored at 6 °C and 95% relative humidity for 4 months, and samples were taken for experiments.

**Cooking of Potatoes.** About 400 potatoes of each cultivar were randomly selected. Disks of tissue, 16 mm diameter and 4 mm thick, were cut from the internal phloem parenchyma. The disks were randomized, rinsed in demineralized water (4 °C) and blotted with tissue paper before use. A batch of 800 g of disks was directly frozen in liquid nitrogen (noncooked tissue). For cooking, a batch of 1250 g of disks was transferred into 10 L of boiling demineralized water. After either 5 or 15 min, the disks were separated from the cooking medium by sieving (mesh 2.0 mm) and subsequently frozen and disintegrated (DITO SAMA K35) in liquid nitrogen. For the 5 min cooked sample, three batches of 1250 g of disks were combined, while for the 15 min cooked sample, only one batch was used. The cooking media were frozen, freeze-dried, and milled (Retsch-mill). The cooking medium of 15 min cooked tissue of cv. Irene was filtered through a sintered glass filter (D3), yielding a fraction of loose cells, which was also frozen in liquid nitrogen. For the other cooking media this fraction was negligible. Two batches of 400 potatoes were processed for each cultivar.

**Transmission Electron Microscopy (TEM).** Small pieces of noncooked, 5 min cooked, and 15 min cooked potato tissue were directly embedded in a drop of 3% agar solution (Kaláb, 1988). Blocks of tissue embedded in agar were fixed at 4 °C in 2% glutaraldehyde, buffered with 0.2 M cacodylate at pH 7.2, for 16 h. Next, the blocks were washed in cacodylate buffer, postfixed in 1% osmium tetraoxide for 1.5 h, washed in distilled water, dehydrated in a graded series of aqueous ethanol, and embedded in LR White. To obtain more contrast, sections were stained on the grid with 2% aqueous uranyl acetate for 5 min followed by Reynolds lead citrate for 1 min (Hall, 1978). Preparations were examined with a Philips EM 400 transmission electron microscope at 80 kV.

**Isolation of CWM from Noncooked Tissue.** Cold (−20 °C) ethanol was added to frozen tissue (100 g) to a final concentration of 70% (v/v). The suspension was homogenized (Ultra-turrax T25) for 5 min on ice and filtered through a sieve (mesh 90 $\mu$m). Six batches, each obtained from 100 g of frozen tissue, were combined. The residue on the sieve (crude CWM) was suspended in cold (−20 °C) 70% ethanol and disintegrated with a ball mill for 30 min at 4 °C. The suspension was filtered through a sieve (mesh 90 $\mu$m). The residue on the sieve was washed several times with cold 70% ethanol. Washing was continued until hardly any starch grains were observed by a light microscope. The residue was suspended in fresh, cold 70% ethanol and stored in a polythene container at 4 °C (as fraction CWM).

The filtrates were combined and filtered through a GF/C-glass fiber filter (Whatman). The residue, consisting of starch and small fragments of CWM (<90 $\mu$m), was stored in a small amount of 70% ethanol (as fraction starch). An aliquot of the filtrate was stored at 4 °C (as fraction ASS).

**Isolation of CWM from Cooked Tissue.** Frozen tissue (100 g) was homogenized (Ultra-turrax) in demineralized water (150 mL), and after addition of 0.05% sodium azide, the suspension was heated for 1 h in a water bath of 63 °C under gentle shaking. After the suspension cooled to 37 °C, porcine α-amylase was added (Merck art. 16312, 3000 units per 100 g of tissue), and the suspension was incubated for 60 h at 37 °C. Eight batches, each obtained from 100 g of frozen tissue, were combined. The suspension was filtered through a sieve (mesh 90 $\mu$m), and the residue was washed with demineralized water. The walls of intact cells in the residue were disrupted by decompression. For that purpose, the residue was transferred into the stainless steel chamber of the disruption bomb (Parr Instruments) and diluted with some demineralized water. The bomb was pressurized with nitrogen up to 60 atm, and the suspension was equilibrated for 30 min on a magnetic stirrer. Decompression took place by releasing the cells from the bomb, whereby the pressure almost instantly dropped to atmospheric pressure. Subsequently, the released suspension was filtered through a sieve (mesh 90 $\mu$m). The residue was washed with demineralized water (crude CWM) and reincubated with α-amylase (9000 units) for 16 h at 37 °C. Demineralized water was added to a volume of 800 mL, and then the suspension was vigorously mixed for 5 min (Ultra-turrax) and filtered through a sieve (mesh 90 $\mu$m). Mixing and sieving were repeated until hardly any starch was observed in the residue on the sieve by a light microscope. The residue was stored in 70% ethanol in a polythene container at 4 °C (as fraction CWM). The filtrates, containing starch, WSS, and small fragments of CWM (<90 $\mu$m), were combined, freeze-dried, and milled (Retsch-mill) (as fraction starch).

**Isolation of CWM from Cooking Media and Starch Fractions.** Aliquots of the cooking media and starch fractions were each suspended in demineralized water containing 0.05% sodium azide and incubated with α-amylase (300 units/g) for 16 h at 37 °C. The cooking media were filtered (through a GF/C-glass fiber filter) to remove loose cells. Ethanol (100%) was added to the filtrates of the cooking media and to the incubated starch fractions to a final concentration of 70%. After mixing, the samples stood for 3 h at −30 °C. The samples were centrifuged (10 min, 2500*g*) and the residues washed with cold 70% ethanol and centrifuged. The washing (once with 70% ethanol and once with acetone) and centrifugation were repeated. The residues were air-dried.

**Analytical Methods.** *Dry Matter Content.* Samples were predried overnight at 70 °C, and drying was continued for 3 h at 105 °C. Dry matter content was determined on three replicates.

*Starch Content.* Starch content was determined enzymatically using the Boehringer test kit (Mannheim GmbH) on at least two replicates.

*Neutral Sugar and Uronic Acid Content.* All samples were pretreated with 72% $H_2SO_4$ and further hydrolyzed with 1 M $H_2SO_4$ at 100 °C for 2 h. The hydrolysate was filtered through a GF/C-glass fiber filter (Whatman) and neutralized with $BaCO_3$. The mixture was filtered, and 10 $\mu$L of the filtrate was analyzed by HPLC (Pharmacia LKB low-pressure mixer, HPLC pump 2248, and autosampler 2157), equipped with a Carbopack PA1 column (250 mm × 4 mm, Dionex), as described by Stolle-Smits et al. (1995). Non-starch glucose content was determined as the difference between glucose content found by HPLC and that found with the Boehringer test kit. Cellulose content was calculated as the difference between glucose contents found by HPLC in hydrolysates obtained with and without pretreatment with 72% $H_2SO_4$. Each sample was analyzed in duplicate.

Uronic acid content was determined in the filtrate (0.2 mL) using the *m*-hydroxydiphenyl method of Ahmed and Labavitch (1977). Determinations were made on three replicates.

*Number of Methyl Esters and Acetyl Groups.* Methyl esters and acetyl groups were determined by HPLC according to Voragen et al. (1986).

*Cell Size Measurement.* Cell suspensions of noncooked tissue were made as described by Marle et al. (1994). Cell suspensions from tissue cooked for 15 min were obtained by mixing (Ultra-turrax) cooked tissue with demineralized water, and after sieving (mesh 500 $\mu$m) the filtrates were used.

The cell size distribution of a cell suspension was determined using a Coulter Counter (LS130, Coulter Electronics). The cell size distributions were determined on two replicates.

The cell size distribution was used to calculate the specific cell surface area. For each class of cells with a certain diameter ($d_i$) the volume percentage ($v\%_{d_i}$) of the total volume ($V$) was given. With the volume occupied by a class of cells with diameter $d_i$ in a total volume $V$,

$$Vv\%_{d_i} \tag{1}$$

the number of cells, $n_i$, with diameter $d_i$ could be calculated,

$$n_i = 6Vv\%_{d_i}/\pi d_i^3 \tag{2}$$

together with the total cell surface, $A_i$, of all the cells with diameter $d_i$,

$$A_i = 6Vv\%_{d_i}/d_i \quad (3)$$

The total cell surface, $A_{tot}$, per tissue volume $V$ is

$$A_{tot} = \sum 6Vv\%_{d_i}/d_i \quad (4)$$

## RESULTS

**TEM.** TEM visualized the changes in cell walls and middle lamellae of both cultivars during cooking (Figures 1 and 2). The observations give information about the changes taking place in the cell wall structure and also give indications about differences between the cultivars with respect to their cell walls.

Noncooked tissue of cv. Irene seemed to have denser cell walls than noncooked tissue of cv. Nicola. Upon cooking, cell walls of both cultivars expanded, resulting in a less dense and rigid appearance compared to noncooked tissue. The intercellular contact between cells was reduced, which was initiated at the intercellular spaces. After 5 min of cooking, most of the intercellular contact was still intact, and the difference in compactness of the cell walls between both cultivars was still visible. However, the cell walls of cv. Irene seemed to be more expanded than those of cv. Nicola. After 15 min of cooking, the intercellular contact was greatly reduced for both cultivars. Large intercellular spaces were visible between the cells, and small remnants of solubilized cell wall and middle lamellae structures were present. It seemed that more middle lamellae material was solubilized for cv. Irene than for cv. Nicola. In the cell walls of cv. Irene, chainlike structures (parallel with the cell surface) were more clearly visible than in the cell walls of cv. Nicola. Moreover, the cells of both cultivars were still surrounded by cell walls, which had a loose, porous structure, but which were not fractured.

**Isolation of CWM.** Due to the different states in which starch and the middle lamellae were present in noncooked and cooked potato tissue, different isolation procedures were used to isolate CWM from both types of tissue.

The CWM isolated from noncooked potato tissue contained 3.4−7.8% starch. During isolation of CWM, the presence of residual starch was monitored by light microscopy, and it was observed that some large starch grains (diameter >90 $\mu$m) were left in the residue, together with starch grains in some small cells, which were not broken during ball milling. The residual starch content of CWM isolated from cooked potato tissue ranged between 1.4 and 4.7%.

Table 1 shows the distribution of dry matter over the fractions after isolation of CWM from noncooked and cooked potato tissue. In general, the amounts of CWM isolated from cooked potato tissue were slightly higher than those isolated from noncooked potato tissue. (For 15 min cooked tissue from cv. Irene, the sum of CWM and CWM from loose cells was taken.) This was due to the different isolation procedures used. During isolation of CWM from cooked tissue, the cooked cells were easily separated from each other as a result of cell wall loosening during cooking (Marle et al., 1994). Subsequent decompression with the disruption bomb and washing resulted in complete cell walls with one crack and without contents. However, the intercellular contact between uncooked cells remained intact at the applied isolation conditions, and decompression of tissue fragments did not fracture all the individual cells. Therefore, these intact cells were broken by ball milling. This last procedure resulted in a solution with small and large cell wall fragments, from which more CWM ended up in the filtrate during sieving than from the solution with cooked cell walls. Therefore, the amounts of CWM of noncooked and cooked potatoes cannot be compared quantitatively. Comparisons can be made between cultivars for each cooking time and between 5 and 15 min cooked tissues of each cultivar.

The CWM found in the starch fractions originated from cell wall fragments lost during isolation and soluble pectic polysaccharides.

After isolation, the recovery of the cell wall carbohydrates (taking into account all the fractions) at different cooking times was comparable (Figure 3).

In cooked tissue, more cellulose was found than in noncooked tissue. During cooling of cooked potatoes, about 3% of the gelatinized starch is converted into "resistant starch" (Englyst and Cummings, 1990), which is partly measured as "cellulose" during HPLC analysis. However, CWM from cooked tissue contained up to 4.7% starch; 3% of this amount may be resistant starch, which is less than 0.5% of the amount of cellulose present in CWM and therefore negligible. The difference in cellulose content will probably be due to the two isolation methods used, and it can be assumed that the missing part can be found in the starch fractions (which were not analyzed for cellulose).

The amount of cell wall glucose showed a large standard deviation due to the fact that it was calculated as the difference between total glucose and starch glucose. Total glucose and starch glucose were present in large amounts, and their standard deviation was considerable for the small amount of cell wall glucose.

**Cell Wall Composition.** During isolation of CWM, part of the CWM initially present in potato tissue was lost in the starch fraction. For noncooked and cooked tissue respectively, the sugar compositions of CWM and the accompanying starch fraction are shown in the same figures. It is only reliable to draw conclusions on basis of the composition of CWM, if for both cultivars comparable amounts of sugars were lost in the starch fractions during isolation.

Sugar compositions of CWM and starch fractions from noncooked potato tissue of both cultivars are shown in Figure 4. In CWM, all sugars were present in higher amounts for cv. Irene than for cv. Nicola. The composition of the starch fractions differed significantly only for uronic acid and arabinose. Apparently, during the isolation, more arabinose disappeared with the starch fraction for cv. Nicola than for cv. Irene. However, the differences in amounts of arabinose between both cultivars in the CWM as well as in the starch fractions were very small with respect to the differences for the other sugars. Altogether, it is more reliable to conclude that noncooked CWM in situ contained a comparable amount of arabinose for both cultivars. Furthermore, for cv. Irene, more uronic acid disappeared with the starch fraction during isolation than for cv. Nicola. In this case, cv. Irene contained a higher amount of uronic acid in CWM and starch fraction compared with cv. Nicola.

In Figure 5, the sugar compositions of CWM and starch fractions from 5 and 15 min cooked potato tissue are shown, respectively. After 5 min of cooking, all sugars in CWM were still present in higher amounts for cv. Irene than for cv. Nicola. Like in the starch fractions of noncooked tissue, the amount of uronic acid in the starch fractions of 5 min cooked tissue was higher for cv. Irene than for cv. Nicola.

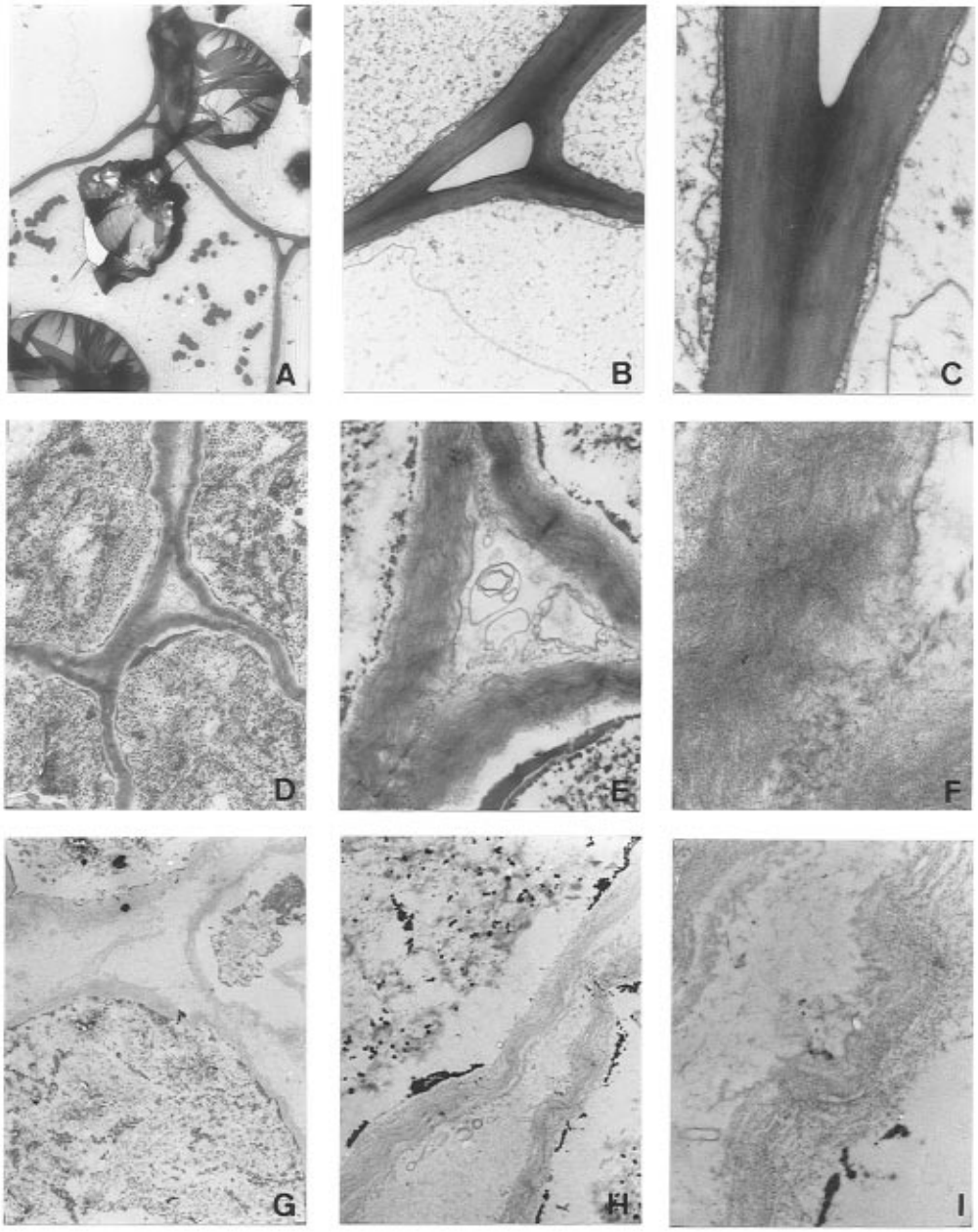


**Figure 1.** TEM photographs of cell walls in noncooked and cooked potato tissue from cv. Irene: noncooked (A) 1000×, (B) 3600×, (C) 13 000×; 5 min cooked (D) 1000×, (E) 3600×, (F) 13 000×; and 15 min cooked (G) 1000×, (H) 3600×, (I) 13 000×.

After 15 min of cooking, the difference in cooking behavior between both cultivars became clear. Pectic polysaccharides (UA + ARA + GAL) were present in higher amounts in CWM of cv. Nicola than in CWM of cv. Irene. In the starch fraction of cv. Irene, higher amounts of uronic acid and arabinose were present as compared with cv. Nicola. For cooked tissue, the pectic polysaccharides in the starch fractions were most probably solubilized in the tissue during cooking, but were at that time hindered sterically from diffusing into the cooking medium. During isolation, these pectic polysaccharides were released in the starch fractions. Therefore, cooked tissue of both cultivars could be compared on the basis of CWM, because this is the CWM that remained insoluble after cooking.

Loose cells and 15 min cooked tissue had comparable molar compositions (data not shown).

The compositions of CWM in the cooking media of both cultivars after 5 and 15 min of cooking are shown in Figure 6. Xylose and mannose were not detected in the cooking media. After 5 min of cooking, uronic acid and galactose appeared in higher concentrations in the cooking medium of cv. Irene. After 15 min of cooking, the difference between both cultivars was more pronounced, because uronic acid, arabinose, and galactose were present in higher concentrations in the cooking medium of cv. Irene. The glucose found in the cooking media (Figure 6) most likely originated from starch and not from cellulose, which is not solubilized upon cooking. Cool storage (24 h at 4 °C) and freeze-drying of the cooking media were favorable for transformation of the solubilized starch into resistant starch (Englyst and Cummings, 1987). Redispersion of this starch was probably not complete under the conditions used during analysis (Englyst and Cummings, 1984).

**Methyl Esters and Acetyl Groups.** During cooking, the degree of methylation (DM) decreased in a comparable way for CWM from both cultivars (Table 2). However, the DM of the CWM dissolved in the cooking

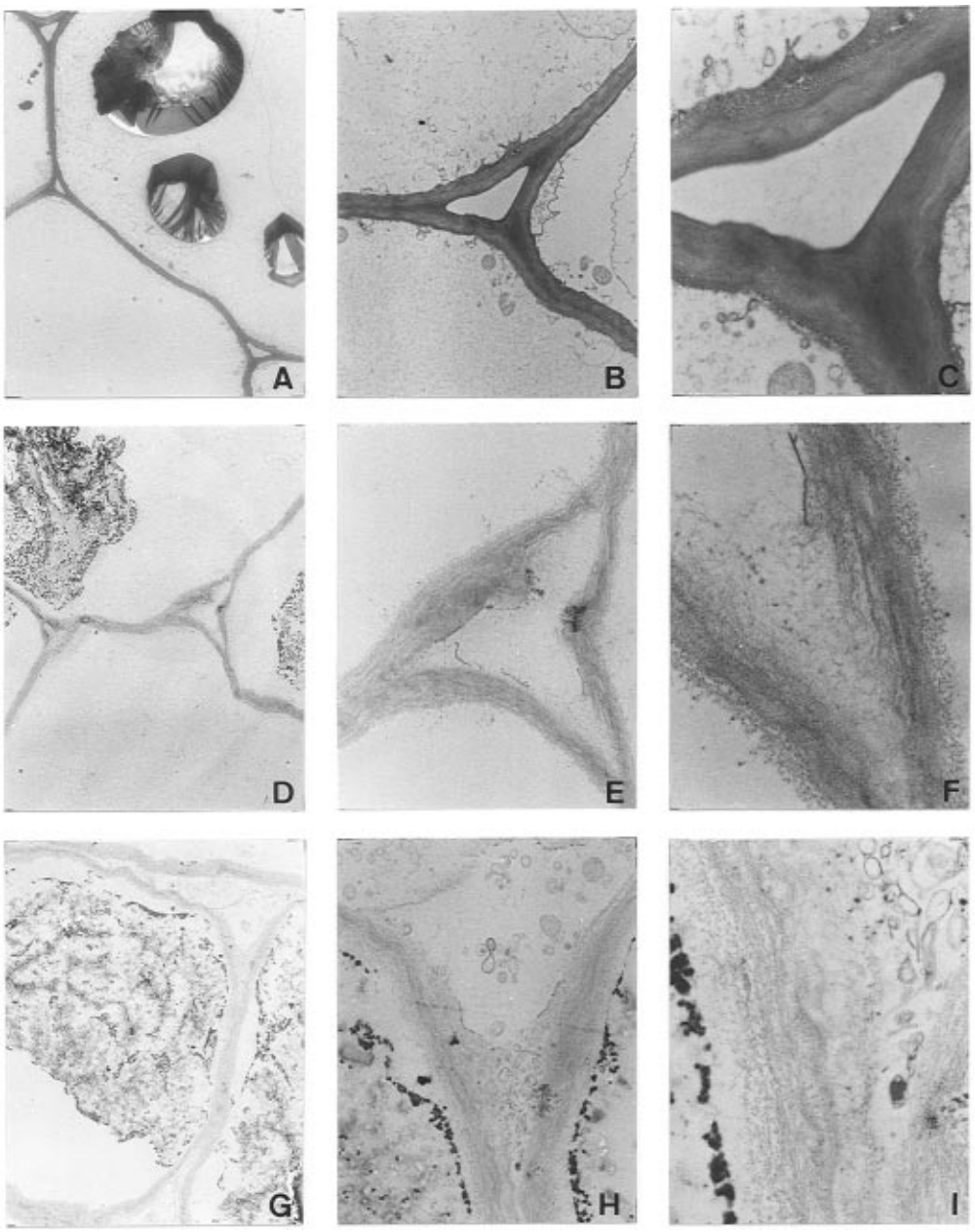


**Figure 2.** TEM photographs of cell walls in noncooked and cooked potato tissue from cv. Nicola: noncooked (A) 1000×, (B) 3600×, (C) 13 000×; 5 min cooked (D) 1000×, (E) 3600×, (F) 13 000×; and 15 min cooked (G) 1000×, (H) 3600×, (I) 10 300×.

**Table 1. Yield of Dry Matter per Fraction for Noncooked and Cooked Potato Tissue (Weight Percentage on Dry Solids Basis)**

| | | | fractions | | | | loose cells | | |
|---|---|---|---|---|---|---|---|---|---|
| cultivar | cooking time (min) | noncooked tissue | CWM | starch + ASS + CWM | starch + WSS + CWM | cooking medium | CWM | starch + WSS + CWM | total |
| Irene | 0 | 100 | 4.0 ± 0.1 | 91 ± 5 | | | | | 95 |
| | 5 | 100 | 4.6 ± 0.3 | | 94 ± 1 | 6.2 ± 0.9 | | 95 | |
| | 15 | 100 | 3.2 ± 0.1 | | 74 ± 1 | 10.1 ± 0.1 | 0.6 ± 0.1 | 16 ± 1 | 104 |
| Nicola | 0 | 100 | 4.4 ± 0.3 | 91 ± 2 | | | | | 95 |
| | 5 | 100 | 5.1 ± 0.3 | | 88 ± 2 | 8.5 ± 0.1 | | | 102 |
| | 15 | 100 | 4.9 ± 0.3 | | 87 ± 3 | 12.3 ± 0.6 | | 104 | |

medium was significantly higher for cv. Irene after 5 and 15 min of cooking.

Noncooked CWM of cv. Irene contained more acetyl groups than CWM of cv. Nicola. After 5 min of cooking, this difference was still present, but prolonged cooking solubilized more acetyl groups for cv. Irene than for cv. Nicola. The numbers of acetyl groups in noncooked and cooked tissue could not be compared due to different isolation methods.

**Cell Size Measurement.** This season, the specific cell surface area was not similar for both cultivars (Marle et al., 1994). The cell size distribution curves were similar in shape to those measured before (Marle et al., 1994), but cv. Irene had its maximum at a cell diameter of 165 $\mu$m and cv. Nicola at a cell diameter of 190 $\mu$m (curves not shown). The specific cell surface areas calculated according to eq 4 were (3.72 ± 0.11) ×

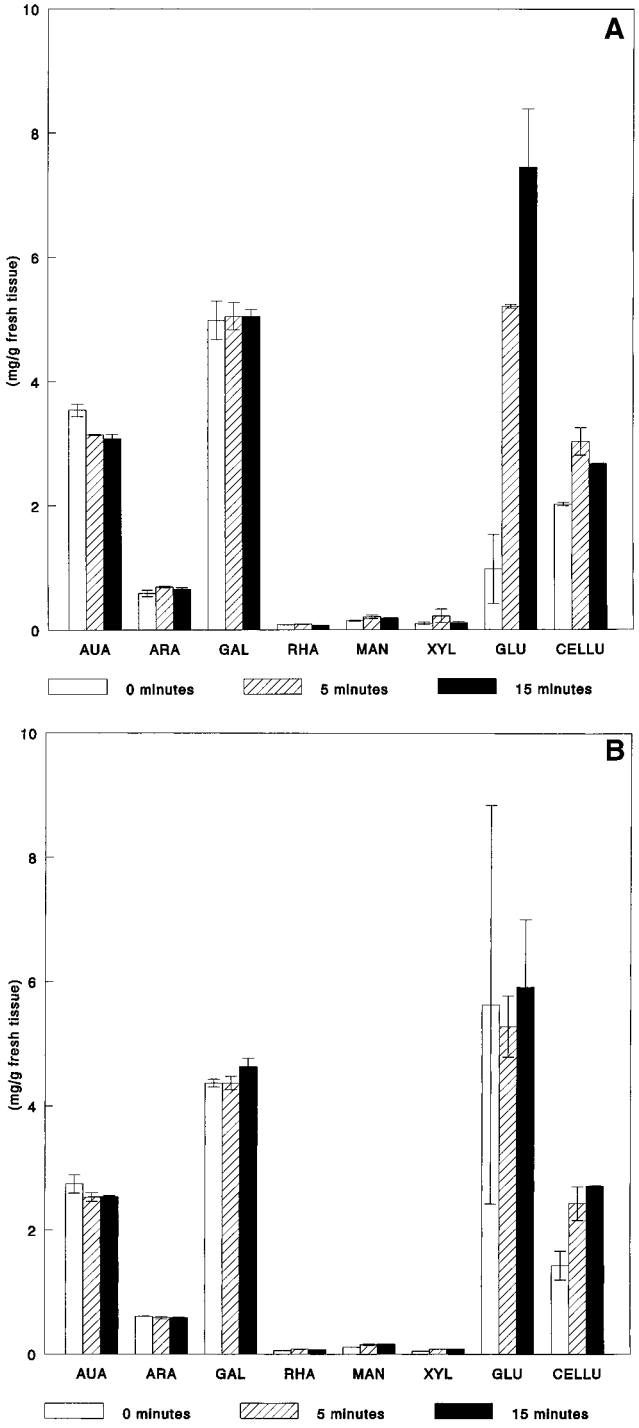


**Figure 3.** Recovery of cell wall polysaccharides for the cultivars (A) Irene and (B) Nicola after 0, 5, and 15 min of cooking. For each sugar residue, the recovery was calculated as the sum of the amounts analyzed in the different fractions (for noncooked tissue, CWM + starch; for cooked tissue, CWM + starch + cooking medium + loose cells).

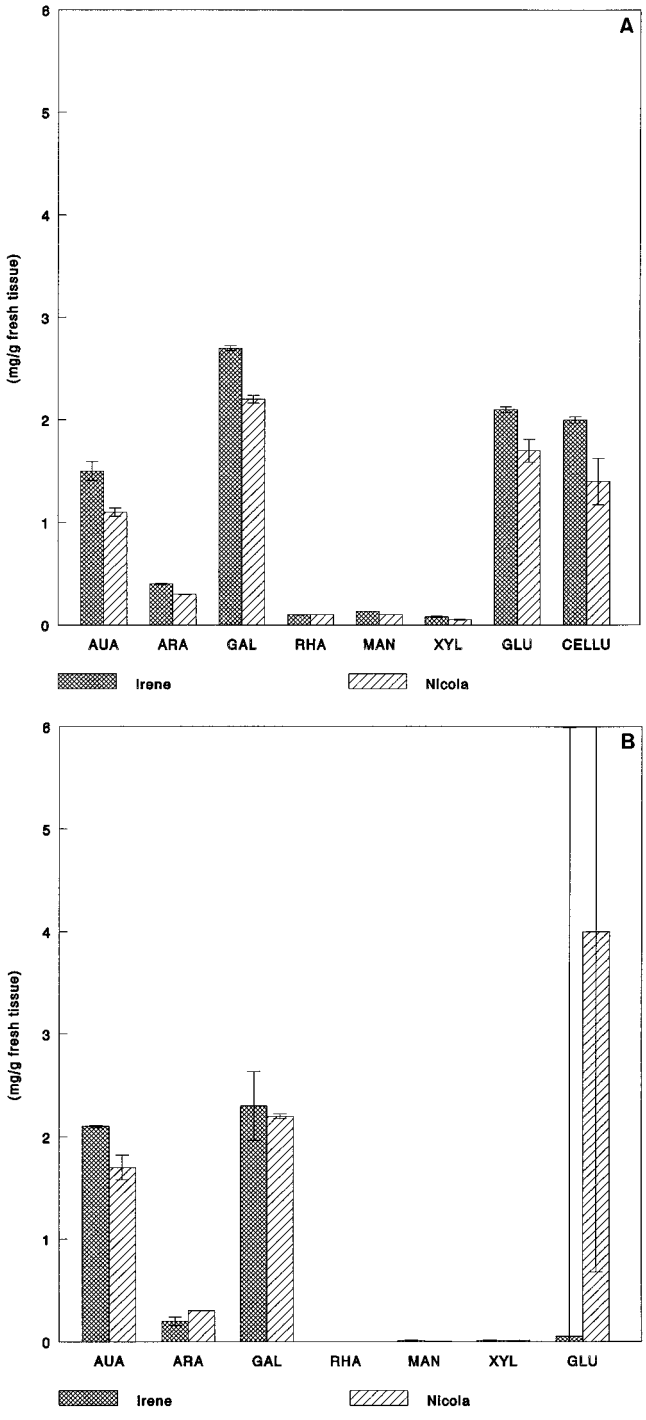


**Figure 4.** Sugar composition of (A) CWM and (B) starch fractions of noncooked potato tissue from the cultivars Nicola and Irene.

$10^4$ $m^2/m^3$ for cv. Irene and $(3.30 \pm 0.05) \times 10^4$ $m^2/m^3$ for cv. Nicola.

## DISCUSSION

Noncooked tissue of cv. Irene contained more CWM than noncooked tissue of cv. Nicola based on fresh weight (Figure 4). However, the amount of CWM per unit cell surface area gives a more reliable comparison, since this amount takes into account the differences in specific cell surface area and dry matter content between the cultivars. The calculated specific cell surface areas were comparable with those found by Hughes et al. (1975).

Table 3 showed that cv. Irene had significantly more CWM per unit cell surface area than cv. Nicola. This higher amount of CWM can make the cell walls of cv. Irene thicker and/or denser than those of cv. Nicola. For example, a potato cell with a diameter of 200 $\mu$m has a cell surface area of $1.3 \times 10^{-7}$ $m^2$. From Table 3, it can be calculated that a cell from cv. Irene contains $2.6 \times 10^{-8}$ g of CWM and a cell from cv. Nicola $2.3 \times 10^{-8}$ g of CWM. Assuming that for both cultivars the cells have an equal cell wall thickness, the difference in density of their cell walls is 13%. On the other hand, assuming that for both cultivars the cells have equal

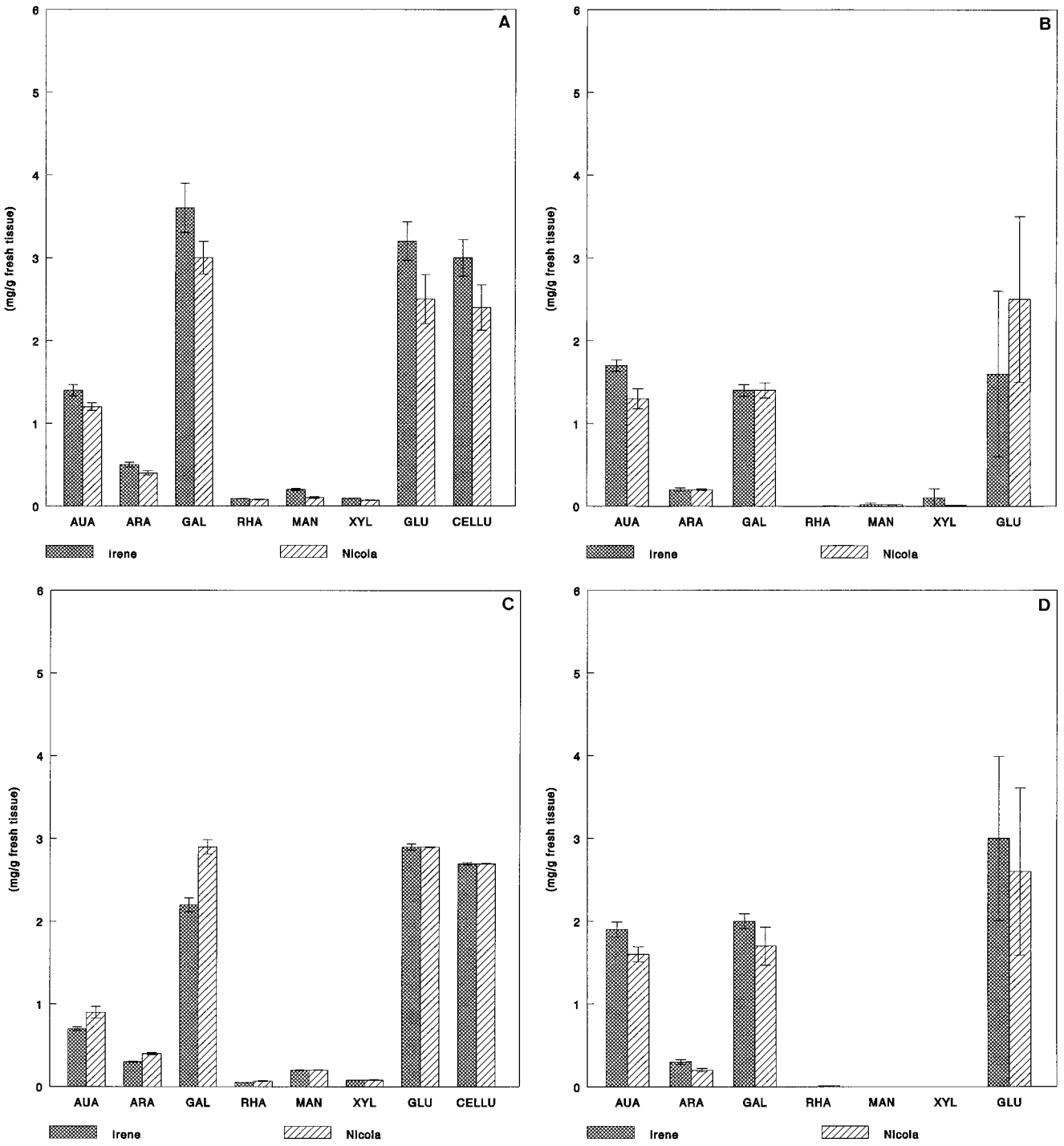


**Figure 5.** Sugar composition of (A) CWM and (B) starch fractions of 5 min cooked potato tissue and sugar composition of (C) CWM and (D) starch fractions of 15 min cooked potato tissue from the cultivars Nicola and Irene.

cell wall densities, and that for cv. Nicola the cell wall thickness is 1 $\mu$m (Figure 2), it can be calculated that the cell wall thickness for cv. Irene is 1.13 $\mu$m. The difference in thickness of the cell walls of both cultivars is 13%.

These results agree with the observations made by TEM, which suggested that cv. Irene had denser cell walls. A difference in cell wall thickness $\leq$13% is difficult to observe. Nevertheless, the molar compositions of CWM of both cultivars were comparable (data not shown).

During cooking, middle lamellae were solubilized and cell walls became looser in structure, as shown by observations with TEM (Figures 1 and 2) of both cultivars. After 15 min of cooking, middle lamella breakdown seemed to be more complete for cv. Irene than for cv. Nicola. Quantification of these observations was given by the chemical characterization of the isolated CWM.

The two cultivars behaved in different ways (Figures 5 and 6) upon cooking. For cv. Irene, significantly more uronic acid, galactose, and arabinose were solubilized. Quinn and Schafer (1994) found that neutral sugars coeluted with uronic acid during ion-exchange chromatography of potato pectic material, indicating that, in potato cell walls, neutral sugars are present as side chains of acid polymers. Therefore, the ratio of ARA + GAL to uronic acid was calculated to obtain information about the type of the solubilized pectic polysaccharides (Table 4). The ratio decreased for CWM during cooking,

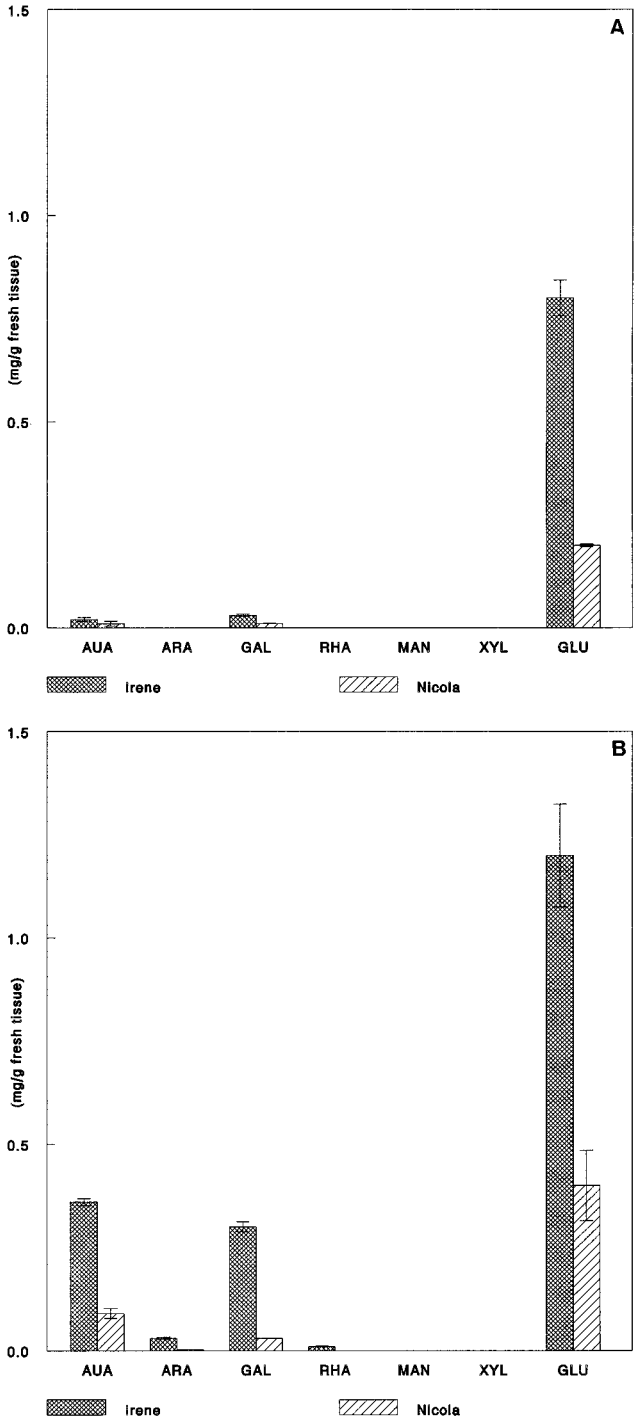


**Figure 6.** Sugar composition of CWM solubilized into the cooking media during (A) 5 and (B) 15 min of cooking of potato tissue from the cultivars Nicola and Irene.

which suggests that relatively more unbranched than branched pectic polysaccharides were solubilized. Concurrently, the CWM solubilized in the cooking medium was highly methylated (Table 2). Highly methylated, unbranched pectin may originate from the middle lamella (Ryden and Selvendran, 1990) but is also found throughout the whole cell wall (Carpita and Gibeaut, 1993). Certainly this type of pectin is the most easily solubilized, because the depolymerization reaction of pectin according to the $\beta$-eliminative mechanism results in cleavage of the pectin chain next to a methyl esterified uronic acid residue (Keijbets, 1974). Furthermore, neutral sugar side chains will be entangled in the pectin matrix depending on their size and conformation,

**Table 2. DM (Mol % of Uronic Acid Content) and Acetyl Groups (mg/g Fresh Tissue) of CWM of Cooked and Noncooked Potato Tissue and of CWM Released in the Cooking Media for Cultivars Nicola and Irene**

| fraction | cultivar | cooking time (min) | DM | acetyl groups |
|---|---|---|---|---|
| CWM | Irene | 0 | 49 ± 2 | 0.21 ± 0.01 |
| | | 5 | 44 ± 1 | 0.28 ± 0.01 |
| | | 15 | 44 ± 2 | 0.17 ± 0.01 |
| | Nicola | 0 | 53 ± 3 | 0.16 ± 0.01 |
| | | 5 | 49 ± 1 | 0.22 ± 0.01 |
| | | 15 | 45 ± 1 | 0.20 ± 0.01 |
| cooking medium | Irene | 5 | 82 ± 5 | nd |
| | | 15 | 61 ± 5 | nd |
| | Nicola | 5 | 67 ± 13 | nd |
| | | 15 | 27 ± 6 | nd |

**Table 3. Calculation of the Amount of Cell Wall Material per Unit Cell Surface Area for Cultivars Irene and Nicola**

| | cv. Irene | cv. Nicola |
|---|---|---|
| dry matter (%) | 23.87 ± 0.05 | 18.01 ± 0.27 |
| specific gravity[a] ($10^3$ g/m$^3$) | 1097 ± 0.5 | 1068 ± 2.6 |
| cell surface area ($10^4$ m$^2$/m$^3$ tissue) | 3.72 ± 0.11 | 3.30 ± 0.05 |
| cell wall material[b] (g/$10^3$ g fw) | 7.0 ± 0.1 | 5.5 ± 0.2 |
| cell wall material[c] ($10^3$ g/m$^3$) | 7.7 ± 0.2 | 5.9 ± 0.2 |
| cell wall material/cell surface area ($10^{-1}$ g/m$^2$) | 2.1 ± 0.1 | 1.8 ± 0.1 |

[a] Calculated according to Simmonds (1977). [b] Uronic acid and neutral sugars. [c] Cell wall material (g/m$^3$) = cell wall material (g/$10^3$ g) × specific gravity.

**Table 4. Molar Ratio of ARA + GAL to Uronic Acid in CWM, Loose Cells, and Cooking Media of Cultivars Nicola and Irene**

| fraction | cultivar | cooking time (min) | UA:ARA + GAL[a] |
|---|---|---|---|
| CWM | Irene | 0 | 1.0:2.3 (0.2) |
| | | 5 | 1.0:3.3 (0.5) |
| | | 15 | 1.0:4.2 (0.3) |
| | Nicola | 0 | 1.0:2.6 (0.1) |
| | | 5 | 1.0:3.1 (0.3) |
| | | 15 | 1.0:4.1 (0.5) |
| loose cells | Irene | 15 | 1.0:3.9 (0.8) |
| cooking medium | Irene | 5 | 1.0:1.5 (0.1) |
| | | 15 | 1.0:0.8 (0.0) |
| | Nicola | 5 | 1.0:1.1 (0.0) |
| | | 15 | 1.0:0.4 (0.0) |

[a] The standard deviation is given in parentheses.

thereby counteracting solubilization (Carpita and Gibeaut, 1993).

For CWM solubilized in the cooking medium, the ratio of ARA + GAL to uronic acid was higher for cv. Irene than for cv. Nicola. Rhamnose was only found in the cooking medium of cv. Irene after 15 min of cooking. Furthermore, Table 2 shows that, after 15 min of cooking, cv. Irene had a higher DM than cv. Nicola. Also, the number of acetyl groups of CWM of cv. Irene was reduced between 5 and 15 min of cooking (Table 2). On basis of the results given above, it can be concluded that, after 15 min of cooking, the solubilized pectic polysaccharides were more branched, more methylated, and more acetylated for cv. Irene than for cv. Nicola.

In conclusion, the composition of CWM isolated from noncooked tissue was comparable for the mealy cv. Irene and the nonmealy cv. Nicola. However, for cv. Irene, more CWM per unit cell surface area was present than for cv. Nicola. At the same time, it was found that, for both cultivars, different types of pectic polysaccharides were solubilized during cooking. Since this observation could not be explained by a difference in composition of CWM, more research is necessary to elucidate the

influence of cell walls and middle lamellae on texture development. Information concerning differences in pectin structure between both cultivars will be obtained from examination of the pectic and xyloglucan fractions of CWM from both cultivars. The results will be dealt with in a following paper.

## ABBREVIATIONS USED

CWM, cell wall material; ASS, alcohol-soluble solids; WSS, water-soluble solids; UA, uronic acid; ARA, arabinose; CELLU, cellulose; GAL, galactose; GLU, glucose; MAN, mannose; RHA, rhamnose; XYL, xylose.

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