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Symplastic and Apoplastic Sugar Contents in Gall Tissues and Callus of the Sumac (*Rhus chinensis* MILL.)

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To elucidate the role of cell wall in interaction with gall-inducing organisms, symplastic and apoplastic sugar contents in different shapes of gall tissue of the sumac (*Rhus chinensis* Mill.) were compared with those of the callus. The gall tissues with vascular cylinders, intercellular spaces and callus were fractionated into symplastic [methanol (MeOH), hot water (HW), and starch] fractions and apoplastic [pectin, hemicellulose, trifluoroacetic acid (TFA)-soluble, and cellulose] fractions. Symplastic sugar content of gall tissues was higher than that of callus. In apoplastic (cell wall) fractions, the cellulose content of gall tissues was lower than that of callus, due to large amount of pectin with high ratio of uronic acid (UA) and hemicellulose with low ratio of UA. Analysis of neutral sugar component of the hemicellulosic, TFA-soluble fraction showed that arabinose (side chain) and galactose (backbone) of arabinogalactan were rich in gall tissues and callus. The gall tissues had higher glucose and lower xylose contents than the callus. These results suggest that the structure of cell wall polysaccharides of gall changed during its development with an increase in symplastic sugar contents. The feeding activities occuring in gall by the gall-inducers were discussed.

Keywords: apoplast, cell wall polysaccharide, *Rhus chinensis*, gall tissue, sugar content, symplast.

Association of gall with gall-inducing organisms was recongnized in the earliest cecidological studies. However, it was not clarified until recently that the development and growth of gall were correlated with the feeding activities and nutritional requirements of gall-inducing organisms. It has also been recognized that the development of gall is contingent on the continuous presence of the gall inducer (Mani, 1992).

The sugars of plant cells are classified into two groups, i.e., symplastic and apoplastic sugars. The symplastic sugars in cytoplasm or vacuoles are extensively metabolized during growth and development and the apoplastic sugars (cell-wall polysaccharides) are also extensively metabolized during plant growth and development (Lavavitch, 1982; Taiz, 1984; Masuda, 1990; Sakurai, 1991; Hoson, 1993). Moreover, among apoplastic sugars, cellulose plays an essential role in the regulation of cell shape and rigidity. Massive synthesis of cellulose takes place during plant growth and development, although the mechanism of cellulose synthesis and its underlying regulation remain unclear (Delmer, 1988; Delmer *et al.*, 1993) and in dispute (Okuda *et al.*, 1993). Recently, Albersheim *et al.* (1997) suggested that the structure of cell wall polysaccharides may define its mode of synthesis.

To understand not only the mechanism of cell-wall polysaccharide metabolism but also the role in interaction between gall and aphid, we investigated developmental changes of sugar contents in the gall of elm (*Zelkowa serrata* Makino) by comparing with those changes in the leaf (Yeo *et al.*, 1997). However, the mechanism and the role still remain unclear, because the structural turnover of cell-wall polysaccharide may be tissue- or organ-specific. Undifferentiated callus was characterized by having primary cell walls with low level of cellulose content (Yeo *et al.*, 1995).

Present study was conducted to compare symplastic and apoplastic sugar contents in different gall tissues and callus of *Rhus chinensis*.

MATERIALS AND METHODS

Plant Material and Callus Culture

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Fist- and finger-shaped galls formed on the pinnate of sumac (*Rhus chinensis* MILL.) compound leaf were harvested on September 20, 1997 at Mt. Sungsoo in Chollabukdo, Korea. The fist-shaped gall was induced by *Schlechtendalia chinensis* Bell. and the finger-shaped gall by *Nurudea rosea* Matsumura, respectively (Blackman and Eastop, 1984; Paik, 1972). The aphids were removed from the galls. One gram of gall tissue was immediately weighed and fixed in 10 ml MeOH at 65°C for 15 min, followed by storage at room temperature until use.

To induce callus for comparison with above gall tissues, young leaves of *Rhus chinensis* were sterilized with 70% ethanol for 30 s and with 1% sodium hypochlorite for 15 min. Five segments at 2×2 mm were excised and innoculated on 20 ml of MS (Murashige and Skoog, 1962) medium (pH 5.8) supplemented with 2.0 mg/l of 2,4-D and 3% sucrose and 0.8% agar in petri dish. They were cultured under white fluorescent light of an intensity of about 15 $\mu Em^{-2}s^{-1}$ and 16/8-h light/dark period at 25±1°C. After one month of culture, the green callus was harvested and washed two times with deionized water and weighed to one gram. The callus was fixed in 10 ml of methanol at 65°C for 15 min and stored at room temperature until use.

Histological Observation

The gall tissue and callus segments were fixed in a fixation solution (FAA; formalin : glacial acetic acid : 50% ethanol = 5 : 5 : 90) for 48 h at room temperature after vaccum infiltration for 10 min. After dehydration through a gradient series of ethanol, the tissue segments were embedded in paraplast. Thin sections (8 μm) were longitudinally cut from the paraplast-embedded tissues with a microtome. The sections were mounted on glass slides coated with gelatin. After removing of paraplast with xylene and rehydration, the sections were stained with a Heidenhain's iron hematoxylin (0.5% in 100% ethanol) and safranine (1% in 50% ethanol) for 5 min. And then, they were dehydrated through a gradient series of ethanol and embedded in a mounting medium (Fisher Scientific).

Fractionation of Symplastic and Apoplastic Sugars

Fractionation was performed by the modified method of Sakurai *et al.* (1987). The samples (one gram FW) in methanol were centrifuged for 10 min at 1,000 g. The supernatant was designated as the symplastic MeOH fraction. The residue was hydrated with deionized water for 10 min and homogenized with motar and pestle. The homogenate was boiled for 10 min to inactivate any glycanase, and then centrifuged at 1,000 g. The residue was washed twice with deionized water. The supernatant was designated as the hot water (HW) fraction. The residue (cell wall material) was treated with 2 ml of 5 units of porcine pancreatic α-amylase (EC 3.2.1.1, Type I-A; Sigma, St. Louis, MO. U.S.A.) in 50 mM sodium acetate buffer (pH 6.5) for 2 h at 37°C and centrifuged for 10 min at 1,000 g. The residue was washed three times with deionized water. The washings were combined with the supernatant and designated as the starch (S) fraction.

Pectic substances were extracted three times, for 15 min each, from the wall with 50 mM EDTA in 50 mM sodium phosphate buffer (pH 6.8) at 95°C. Next, hemicellulosic substances were extracted for 18 h at 25°C with 17.5% NaOH that contained 0.02% sodium borohydride. In a previous study (Yeo *et al.*, 1995), the residue was found to contain appreciable amounts of neutral sugars other than glucose. Therefore, the residue was further hydrolyzed with 2 ml of 2 M trifluoroacetic acid (TFA) for 1 h at 121°C in a screw-capped test tube. The TFA-insoluble fraction was collected by centrifugation (10 min at 1,000 g). The supernatant was designated as the TFA-soluble fraction. The residue was washed twice with deionized water. The washings were combined with the TFA-soluble fraction. The residue (TFA-insoluble) was washed three times, each with 0.03 M acetic acid, ethanol, and a mixture of diethyl ether and ethanol (1 : 1, v/v). The washed residue was dried for one day at 25°C and two days at 40°C. The dried material was designated as the cellulose fraction.

Measurement of Sugar Content

Total sugar content of each fraction was determined by a phenol-sulfuric acid method (Dubois *et al.*, 1956). Before the determination, the cellulose fraction was solubilized in 7.5 M H_2SO_4 for 1 h in ice bath and hydrolyzed with 1 M H_2SO_4 for 1 h at 100°C. Uronic acid contents in each fraction was determined by a *m* -hydroxydiphenyl method (Blumenkranz and Asboe-Hansen, 1973). Total cell wall sugar contents include those of pectin, hemicellulose, TFA-soluble, and cellulose fraction. MeOH, HW, and starch fraction are symplastic fractions. Data from one experiment with triplicated samples are given.

Analysis of Neutral Sugar Composition of HW, S and TFA-soluble Fractions

The neutral sugar composition was determined by a gas liquid chromatography (GLC). A portion (3 ml) of each fraction was placed in a screw-capped tube and dried with a stream of filtered air at 50°C. One ml of 2 M TFA contaning 300 μg of *myo*-inositol as an internal standard was added to the tube. The tube was autoclaved for 1 h at 121°C. The hydrolyzed monosaccharides were reduced with sodium borohydride and acetylated with acetic anhydride in the presence of 1-methylimidazole as a catalyst (Blakeney *et al.*, 1983). The acetylated monosaccharides were dissolved in 200 μl of acetone and one μl was introduced into a GLC system (M600D, Young-Lin Instrument Co., LTD, Seoul) equipped with a capillary column (SP-2380, Supelco, Park, Bellefonte, PA, U.S.A.). The column temperature was raised from 180 to 230°C at the rate of 4°C/min. Data from one experiment with three determinations are given.

RESULTS AND DISCUSSION

Aphid Inhabitants in Fist- and Finger-Shaped Galls

Schlechtendalia chinensis inhabited in fist-shaped gall and *Nurudea rosea* in finger-shaped gall formed both on the pinnate of sumac compound leaf (Table 1). *Schlechtendalia chinensis* in fist-shaped gall was either in larval form without wing bud (19%) or with wing bud (77%) at the 2nd generation. *Nuru-*

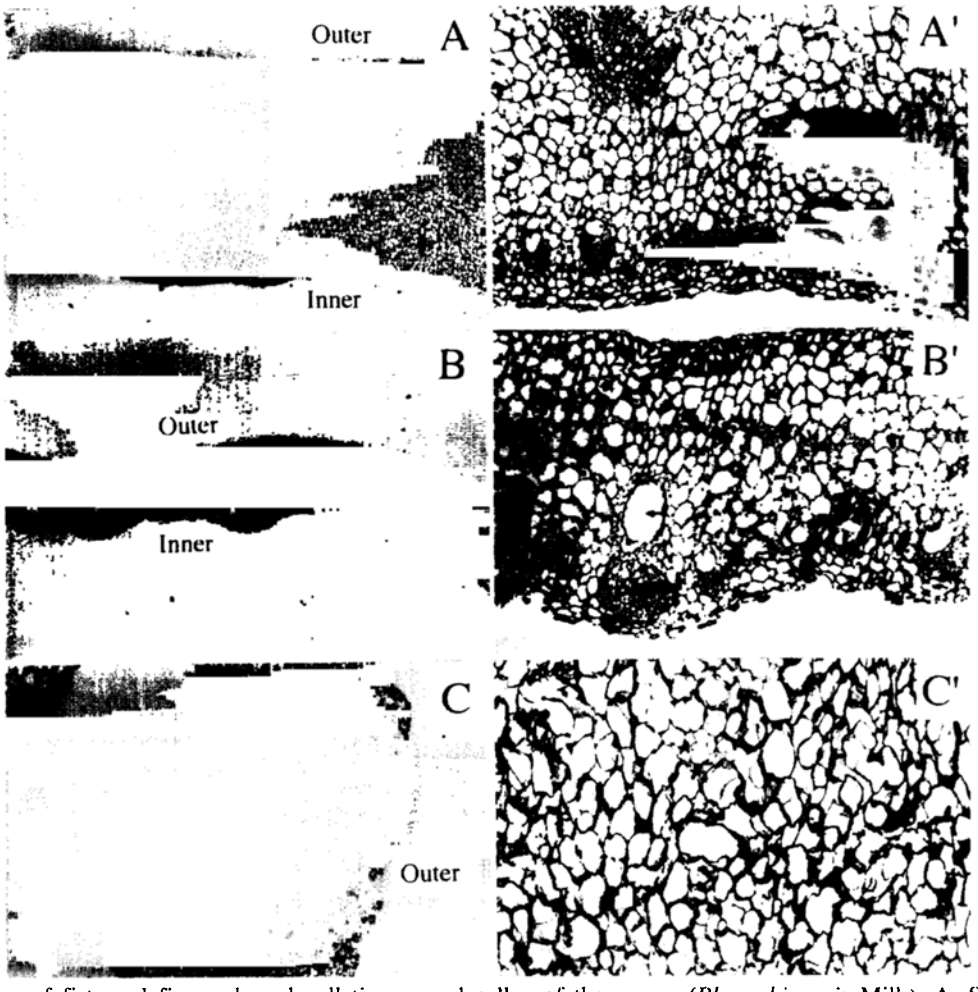

Fig. 1. Anatomy of fist- and finger-shaped gall tissues and callus of the sumac (*Rhus chinensis* Mill.). A; Section of fist-shaped gall tissue induced by an aphid, *Schlechtendalia chinensis* (x 31), (A+; x 250), B; Section of finger-shaped gall tissue induced by an aphid, *Nurudea rosea*, (x 31), B'; (x 250), C; Section of callus (x 31), C'; (x 250), which was derived from young leaf of the sumac on solid MS medium supplemented with 2.0 mg/l of 2,4-D for one month. Large arrows represent vascular cylinders and small arrows represent intercellular gas spaces.

dea rosea in finger-shaped gall was also either in larval form with wing bud (92%) or alatae emigrant (6%) of the 2nd emigrant generation. These findings suggest that feeding activity in fist-shaped gall is actively proceeding, while that of finger-shaped gall is ending.

Anatomical Observation of Gall Tissues and Callus

Fist-shaped gall tissue was wider than finger-shaped gall tissue. The vascular cylinder and intercellular gas space (lacunae), serving primarily to transport nutrients and O_2 to aphid, were developed in the inner part of both gall tissues (Fig. 1A, A' and B, B'). Thus, existence of vascular cylinder and intercellular gas space in the inner part are considered to be prerequisites for suvival of the aphids. The cortical cells of gall tissue were smaller than these of callus. Vascular cylinder and intercellular gas space were not developed in callus derived from sumac compound leaf during one month culture (Fig. 1C, C').

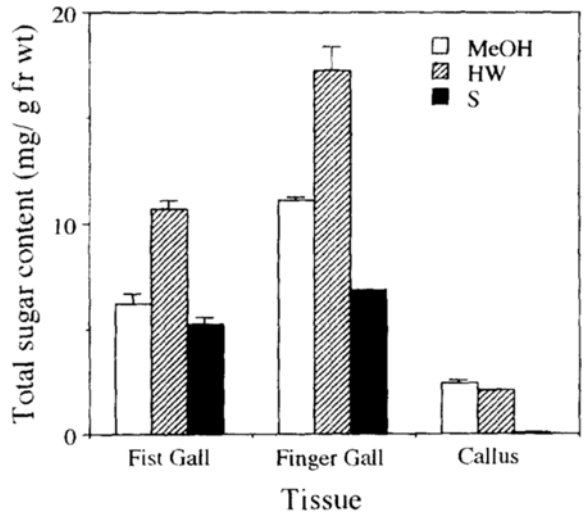

Fig. 2. Total sugar content of symplastic (MeOH, HW, and S) fractions of the fist- and finger-shaped gall tissues and callus of the sumac. MeOH, methanol fraction; HW, hot water fraction; S, starch fraction. Vertical bars indicate SEs of triplicates.

Total Sugar Content of Symplastic (MeOH, HW, and S) Fractions

In MeOH fraction, the total sugar content of finger-shaped gall tissue (11.1±0.2 mg/g FW) was higher than that of fist-shaped gall tissue (6.2±0.4 mg). The sugar content of callus was the least (2.4± 0.2 mg) (Fig. 2). The content of MeOH fraction in finger-shaped gall was similar to that (12~13 mg) of mature gall tissue of elm tree (Yeo *et al.*, 1997). MeOH fraction contains mono- and oligosaccharides such as glucose, fructose, and sucrose (Wakabayashi *et al.*, 1991). The content of HW was also the highest in finger-shaped gall and the least in the callus. The starch content of both gall tissues was much higher than that of callus (Fig. 2).

In HW fraction, UA contents were 11.9±0.03 mg/ g FW for fist-shaped gall and 13.2±0.55 mg for finger-shaped gall, while only 1.5±0.14 mg for callus. The low content of UA implied the low pectin content in the callus. The ratio of UA to total sugar in fist-shaped gall (1.12) was higher than that of finger-shaped gall (0.76) and callus (0.74). The high ratio of uronic acid content in the fist gall suggests that the gall tissue had cells with younger primary cell wall than finger gall and callus.

The neutral sugar components of HW fraction were determined by GLC (Table 2). There were nearly no differences in the neutral sugar composition (%) between the two different shapes of gall tissues. However, glucose content of gall tissues (83.9 and 85.1%) was higher than that of callus (35.3%), while arabinose (side chain residue) and galactose (backbone) content of gall tissues were lower than those of callus. Xylose content of both gall tissues (0.6 and 0.0%) was much lower than that of callus (9.1%). Fincher and Stone (1983) reported that HW fraction contains not only poly-

Table 1. *Schelechtendalia chinensis* in fist-shaped gall and *Nurudea rosea* in finger-shaped galls formed on the pinnate of the sumac (*Rhus chinensis* Mill.)

Aphid	Fundt atrix	2nd generation		
		Larva without wing bud	Larva with wing bud	Alatae emigrant
Schlechtendalia chinensis in fist-shaped gall	4	19	77	0
Nurudea rosea in finger-shaped gall	2	0	92	6

The aphids in each gall harvested on September 20, 1997 were investigated (n=100).

Table 2. Neutral sugar composition of HW (hot water) fractions in two different shapes of gall tissues and callus of the sumac (*Rhus chinensis* Mill.)

Tissue	Neutral sugar (%)						
	Rha	Fuc	Ara	Xyl	Man	Gal	Glc
Fist-shaped gall	1.1	nd	4.7	0.6	1.8	8.0	83.9
Finger-shaped gall	0.4	nd	3.4	nd	0.9	10.3	85.1
Callus	1.0	nd	18.6	9.2	1.7	34.2	35.3

Rha, rhamnose; Fuc, fucose; Ara, arabinose; Xyl, xylose; Man, mannose; Gal, galactose; Glc, glucose; nd, not detected.

saccharides of non-cell wall components such as starch, but also cell wall component such as arabinogalactan. Arabinose and galactose may be derived from arabinogalactan.

Total Sugar Content of Apoplastic Fractions

There were little differences in total sugar contents (mg/g FW) between fist- and finger-shaped gall tissues (Fig. 3). However, the total cell wall (T) content of gall tissues (ca. 20 mg) was 4 times higher than that of callus (ca. 5 mg) (Fig. 3, upper panel).

The cellulose content of fist-shaped (23%) and finger-shaped (18%) gall tissues was lower than that of callus (30%), while pectin was rich in both gall tissues (Fig. 3, lower panel). The cellulose content was similar to those in barley calli (19.6%) and suspension-cultured cells (17.9%) (Yeo *et al.* 1995), in *Vinca rosea* suspension cells (26%) (Takeuchi and Komamine, 1978), in sycamore suspension cells (23%) (Talmadge *et al.*, 1973), and in elm gall tissues at early developmental stages (16~21%) (Yeo *et al.*, 1997). These results suggest that cell walls of gall tissue consist of primary walls with less cellulose and more pectin.

Uronic Acid (UA) Content of Non-Cellulosic (Pectin, Hemicellulose, and TFA-soluble) Fractions

In pectin fraction, the UA contents of fist- and finger-shaped gall tissues were ca. twice higher than the content of callus (Fig. 4). The combined content of hemicellulose and TFA-soluble fractions in finger-shaped gall (3.8±0.17 mg/g FW) was nearly twice higher than that of fist-shaped gall (2.2±0.14 mg) and callus (2.1±0.20 mg) (Fig. 4). These results suggested that pectin and hemicellulose of gall tissues had more galacturonan than those of callus. In pectin fraction, the ratio of UA to total sugar content of fist-shaped gall (0.74) was similar to that of finger-shaped gall (0.74). That of callus was 2.14 and the higher ratio could not be explained at the moment.

Neutral Sugar Composition of TFA-soluble Fractions

In order to elucidate the turnover in structure of

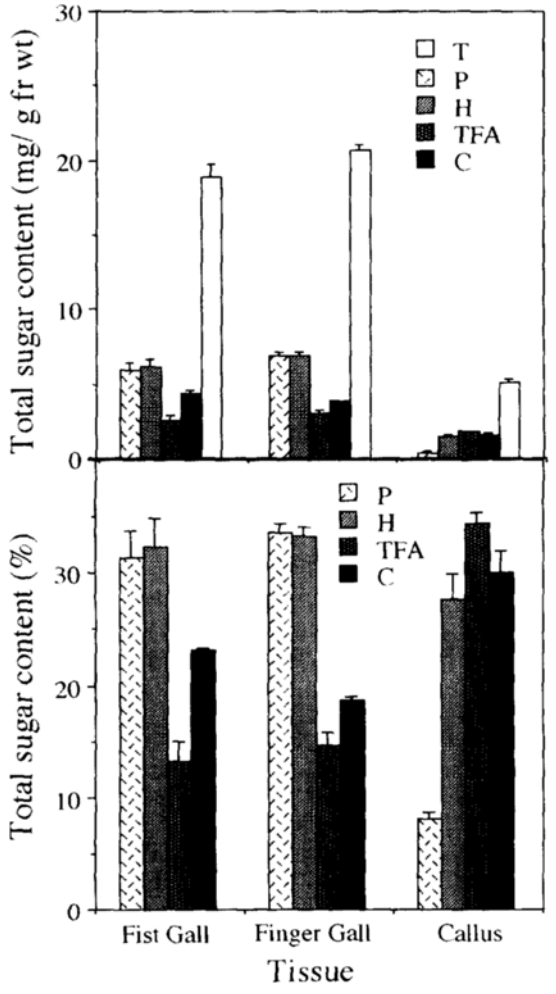

Fig. 3. Total sugar content and percentages of total sugar of apoplastic (cell-wall) fractions of the fist- and finger-shaped gall tissues and callus of the sumac. T, total cell-wall fraction; P, pectin fraction; H, hemicellulose fraction; TFA, trifluoroacetic acid-soluble fraction; C, cellulose fraction. Vertical bars indicate SEs of triplicates.

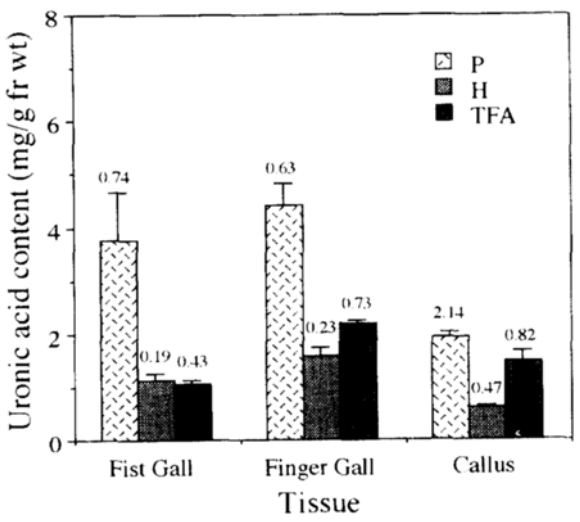

Fig. 4. Uronic acid (UA) content of non-cellulosic fractions of fist- and finger-shaped gall tissues and callus of the sumac. Numbers on histograms of each fractions indicate the ratio of UA content to total sugar contents. P, pectin fraction; H, hemicellulose fraction; TFA, trifluoroacetic acid-soluble fraction. Vertical bars indicate SEs of triplicates.

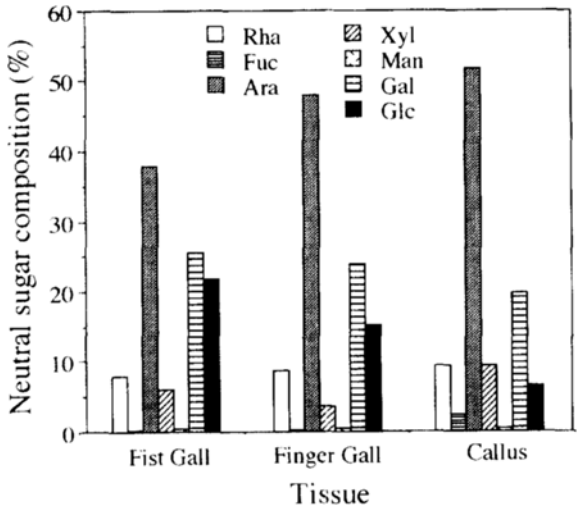

Fig. 5. Neutral sugar composition (%) of the TFA fraction of fist- and finger-shaped gall tissues and callus of the sumac. Rha, rhamnose; Fuc, fucose; Ara, arabinose; Xyl, xylose; Man, mannose; Gal, galactose; Glc, glucose.

hemicellulose, the monosaccharide component of TFA-soluble factions of gall tissues and callus was analyzed by GLC (Fig. 5). The hemicelluloses consist of rhamnose, fucose, arabinose, xylose, mannose, galactose, and glucose. Arabinose was high level (38~50%), followed by galactose (20~25%). Xylose of finger-shaped gall was at the lowest level (4%). Glucose level of fist-shaped (20%) and finger-shaped (13%) gall tissues was higher than that of callus (6%). By constrast, fucose level of callus was higher than those of gall tissues. The level of other components did not vary in all three tissues.

Because the hemicellulose of three tissue cells contained high level of arabinose, probably a component of arabinogalactans, it could be concluded that all tissue cells have primary walls. Hemicelluloses are more complex polysaccharides than pectins, including several distinct species of polysaccharides, such as xyloglucans, arabinogalactans, glucomanans, and glucans. The results also supported that all the cells with primary walls have rich arabinogalactans and glucans. Kikuchi *et al.* (1996) reported that carrot callus contained arabinose and determined the increase in arabinose branching chain of arabinogalactan by methylation analysis. They proposed the increased side chains of arabinose of arabinogalactan participitate in the cell adhesion. We detected high level of arabinose, followed by galactose, suggesting the first elongation of arabinose side chain on the galactan backbone and increase in arabinogalactan content. The glucose component in the hemicelluloses is considered to be 1,3:1,4-β-glucan (Sakurai, 1991). The level of 1,3:1,4-β-glucan in *Gramineae* have been reported to be high in young leaves, coleoptiles, and stem, while low in old tissues (Buchala and Wilkie, 1971). The high level of fucose in callus suggest that callus has consipicous xyloglucan because fucose is a specific sugar component of xyloglucan (Sakurai, 1991). The precise rules of arabinogalactan, 1,3:1,4-β-glucan, and xyloglucan polymers need further structural analysis such as methylation.

In summary, mature gall tissue cells had primary cell walls, like callus with less cellulose. But the gall cells had much higher pectin component than callus and there was non much difference of apoplastic sugar content between fist- and finger-shaped gall tissues. It is, therefore, apparent that the turnover in the structure of pectin polysaccharides during maturation of gall tissues is related to the feeding activity by aphids, the gall-inducers.

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