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Development and Ultrastructure of Interfascicular Cambium in Stem of *Ginkgo biloba* Seedling

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The progressive differentiation of interfascicular cambium from residual meristem in the first internode of *Ginkgo biloba* seedlings was elucidated by light and electron microscopy. The cells of residual meristem were small and homogeneous and heterogeneous in their arrangement but those of the adjacent cortex and pith were large and homogeneous. Some interprocambial residual meristem progressively became elongated and vacuolated during the process of the differentiation. In tangential section, residual meristem composed of long and short cells. The eventual interfascicular cambium had long fusiform initials and short ray initials. Storage materials in the cells progressively disappeared from the interprocambial residual meristem and were absent in early interfascicular cambium. Both the radial and tangential walls of cells of the interprocambial residual meristem were almost the same, but the radial wall became progressively thicker than the tangential wall during differentiation of interfascicular cambium. From these results, it is clear that interfascicular cambium is gradually differentiated from residual meristem.

Keywords : interfascicular cambium, residual meristem, ultrastructure, *Ginkgo biloba* stem

It has been widely accepted that the vascular cambium can be categorized into two groups: one is the intrafascicular cambium which originates through gradual differentiation from procambium; and the other is the interfascicular cambium which develops from interfascicular tissue (Esau, 1977; Fahn, 1982). It is also well known that interfascicular cambium initiates from periclinal divisions of the interfascicular parenchyma cell (Salisbury and Parke, 1964; Gemmell, 1969; Cutter, 1978; Swamy and Krishnamurthy, 1980; Fahn, 1982). But, a recent study, without intervening of the parenchyma, has shed new light in understanding the differentiation of the interfascicular cambium (Soh *et al.*, 1989; Soh, 1991, 1993). The report shows that the interfascicular cambium does not differentiate secondarily and abruptly from the interfascicular parenchyma, but that it differentiates gradually maintaining meristematic continuity with the interfascicular residual meristem.

Also, researchs have been carried out on the ultrastructure of the vascular cambium in relation to seasonal changes (Srivastava, 1966; Srivastava and O' Brien, 1966; Kidwai and Robards, 1969a, b; Robards and Kidwai, 1969a, b; Evert and Deshpande, 1970; Catesson, 1974, 1990). However, there has been little ultrastructural research on the early ontogeny of the vascular cambium. Among the rare references on this topic, are included a study on the ultrastructure of the procambium in *Salix schwerinii* bud (Berggren, 1985) and on the ultrastructure of the vascular meristem of *Botrychium ternatum* (Soh and Kim, 1993; Lee and Soh, 1995). In a cambial cell during growing season, a large central vacuole develops (Robards and Kidwai, 1969; Timell, 1973), wherein storage materials like starch grains and lipid droplets degrade and disappear (Kidwai and Robards, 1969). In contrast while dormant, many small vacuoles appear and storage materials such as starch grains and lipid droplets accumulate (Kruatrachue and Evert, 1977; Riding and Little, 1986; Catesson, 1974, 1990). However, no report can be found about changes in va-

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cuolation and storage material content of vascular meristem cells during the early ontogeny of vascular cambium.

This paper aims to examine the ultrastructure during the early ontogeny of the interfascicular cambium and to determine whether the ontogeny progresses gradually or abruptly. Results will focus on the changes of the nucleus/cell ratio, vacuolation, and storage material content.

MATERIALS AND METHODS

Seeds of *Ginkgo biloba* L. weighing 1.9-2.1 g were chosen for the examination and sown in wet sand for two weeks. After two weeks seeds with radicles of about 2 mm were planted in pots. From these homogeneously germinated seedlings the first internodes of five seedlings were collected and sorted according to growth stage (Table 1) and a portion fixed in FAA solution for light microscope observation (Soh *et al.*, 1988). The fixed materials were embedded in paraffin, then transversely and longitudinally sectioned to 10 μm by a rotary microtome. These sections were triply stained with hematoxylin, safranin and light green (Berlyn and Miksche, 1976).

Materials collected for electron microscopy were fixed in 2.5% glutaraldehyde solution (0.1 M phosphate buffer, pH 7.0) at 4℃ for just over 4 h and then postfixed in 1% osmic tetroxide. Next, the postfixed materials were washed in buffer solution, dehydrated by ethyl alcohol, exchanged with propylene oxide and then embedded in the epon mixture (Luft, 1961). Finally the materials were sectioned to a 1 μm thickness by an LKB-V ultramicrotome, and stained with toluidine blue for light microscopy. Ultrathin sections were double stained with uranyl acetate and lead citrate and observed by a transmission electron microscope (LEM 2000, Akashi Beam Technology Corporation, Japan). The dimensions of the cells and nuclei were measured by an image analyzer (IBAS 2000, Kontron, Germany).

Table 1. Length of the first internode and leaf appearance during growth of *G. biloba* seedling

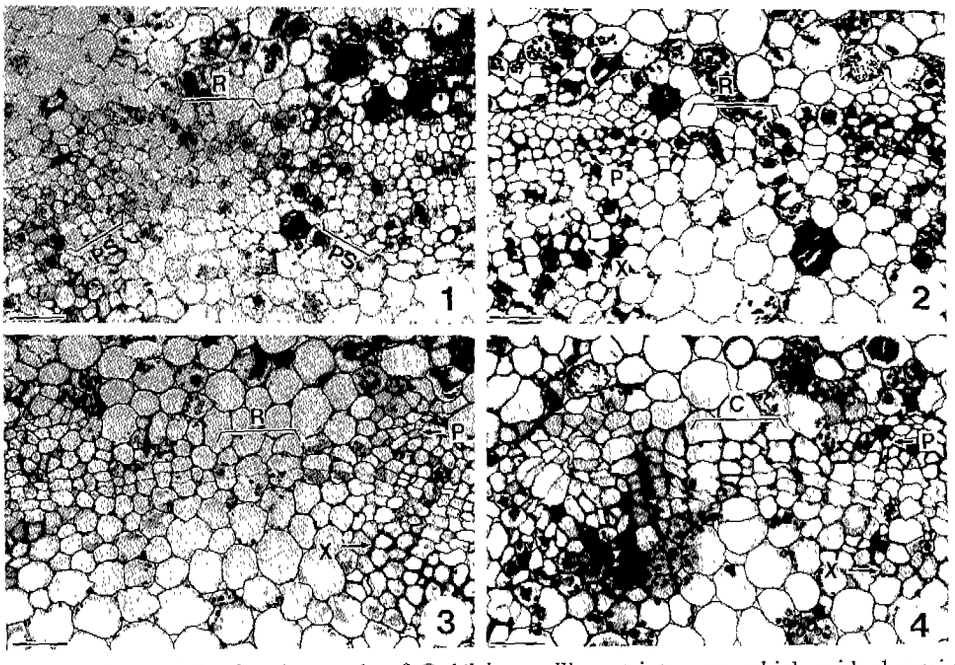
Measurement Stage (days)	1st internode (mm)	Remarks
Interprocambial residual meristem (3)	1.5	1st internode appearing
Early interfascicular residual meristem (6)	4.5	1st internode elongating 1st leaf primordium
Late interfascicular residual meristem (8)	14	1st leaf appearing
Early interfascicular cambium (16)	19	1st leaf unfolding
Mature interfascicular cambium (25)	25	2nd leaf appearing

RESULTS

The differentiation process of interfascicular cambium in the first internode of *G. biloba* seedlings was divided into five developmental stages for convenience: (i) the interprocambial residual meristem stage during which the internodes can be distinguished, (ii) the early interfascicular residual meristem stage during which the elongation of the internodes begins, (iii) the late interfascicular residual meristem stage during which the first leaf appears, (iv) the early interfascicular cambium stage during which the first leaf matures, and (v) the matured interfascicular cambium stage during which the second leaf appears (Table 1).

Light microscopic structure

In transverse section, as differentiation advanced, the ring shaped residual meristem which continued downward from the shoot apical meristem consisted of densely stained small cells. The cells of interprocambial residual meristem and interfascicular residual meristem were densely stained and then progressively vacuolated. However, the cells of outside cortex and the inside pith of both the interprocambial and interfascular tissue were lightly stained and vacuolated in early stage (Figs. 1, 2). Since the interfascicular residual meristem was subject to periclinal divisions of cells adjacent to the vascular bundle, its cells began to be radially arranged (Fig. 3). But, with progressing cell vacuolation, there was a concomitant reduction of stainability and the diameter of cells became wider. Following this, interfascicular residual meristem underwent active periclinal divisions; thus, the radial diameter got narrower than that in the previous stage and radial rows of three to four cells were formed. Thus the meristem had



Figs. 1-4. Transverse sections of the first internode of *G. biloba* seedling at interprocambial residual meristem stage (Fig. 1), early interfascicular residual meristem stage (Fig. 2), late interfascicular residual meristem stage (Fig. 3), and early interfascicular cambium stage (Fig. 4). Early interfascicular cambium (C) was progressively differentiated from residual meristem (R) of which cells are different from those of cortex and pith in their dimensions. Scale bars represent 50 μm in all figures. R, residual meristem; PS, procambial strand; P, phloem; X, xylem.

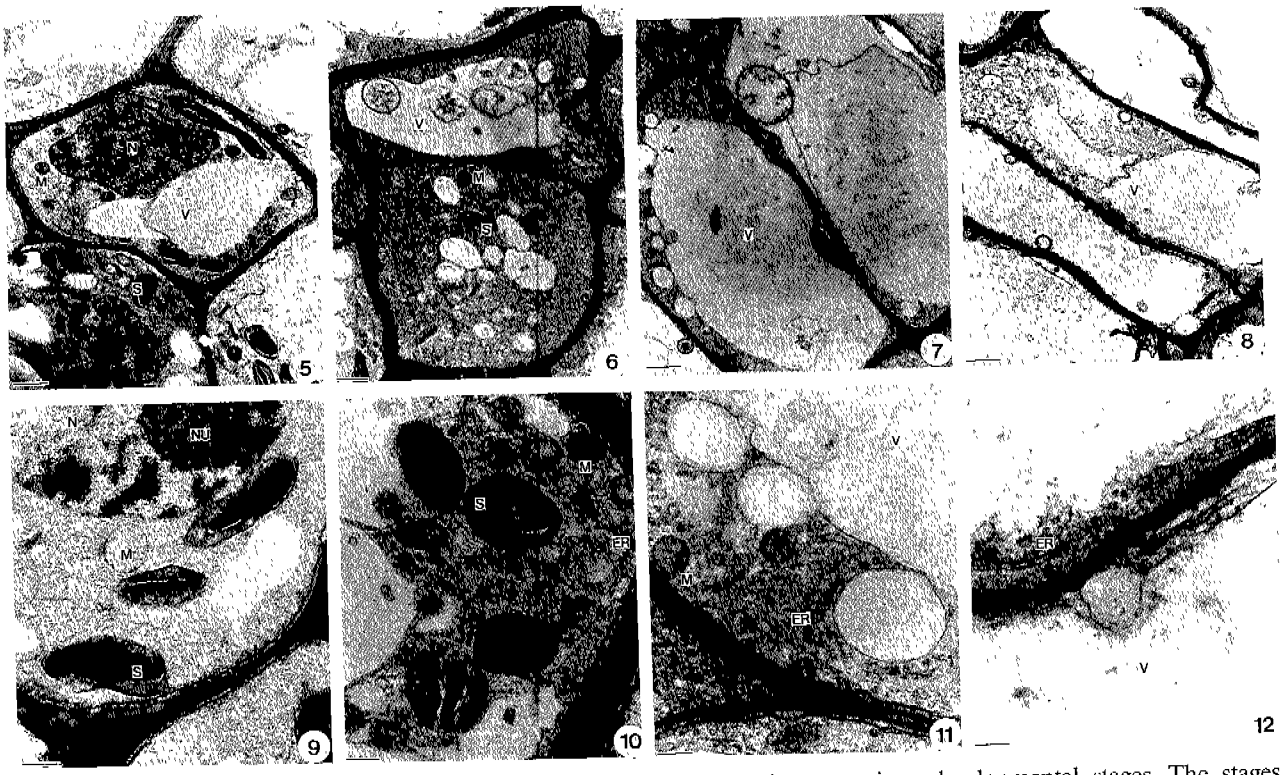
the characteristics of interfascicular cambium (Fig. 4).

Electron microscopic structure

Viewed in a transverse plane, from the interprocambial residual meristem stage during which internodes could be distinguished to the early stage of the interfascicular cambium differentiation during which the first leaf was developed the cell dimensions gradually became larger, whereas the dimensions of the nucleus got smaller (Figs. 5-8). So, the dimensions of the cell nucleus was largest during the interprocambial residual meristem stage and decreased gradually in the following stages (Table 2). In a longitudinal plane, the cell dimensions remained more or less the same at the interprocambial residual meristem stage, but the cells began to be distinguishable between long and short ones from the early interfascicular residual meristem stage (Table 3, Soh *et al.*, 1989; Soh, 1991). Likewise in the transverse plane, the portion that the nucleus occupied in a cell gradually decreased (Table 2). The parenchyma cells located about 40 μm to cortex or pith from the residual meristem had small nuclei even at the interprocambial residual meristem stage, but the dimensions of the nuclei further decreased as differentiation proceeded (Table 4).

Storage materials like starch grains were clearly observed at the interprocambial residual meristem stage. But with progressing differentiation, they were gradually degraded and lost as vacuolation began to take place (Figs. 9-12). Mitochondria and endoplasmic reticula were more frequently observed from the interprocambial residual meristem stage to the late interfascicular residual meristem stage than at the early interfascicular cambium stage or at the matured interfascicular cambium stage.

The thickness of the radial and tangential walls showed no difference at the interprocambial residual meristem stage (Fig. 5), but the tangential wall became gradually thinner than the radial wall from the late interfascicular residual meristem stage to the early differentiation of the interfascicular cambium (Figs. 6-8). This result seems to be attributable to the repetition of periclinal divisions. In the parench-



Figs. 5-12. Transverse sections of the first internode of *G. biloba* seedling at various developmental stages. The stages of Figs. 5-8 and 9-12 are the same as in Figs. 1-4 respectively. Radial wall of cells become progressively thicker than that of tangential wall although both walls of cells at interprocambial residual meristem stage (Fig. 5) are almost same. Storage materials in cells at interprocambial residual meristem (Fig. 9) are progressively disappeared through subsequent developmental stages (Figs. 10-12). N, nucleus; M, mitochondira; V, vacuole; S, starch grain; ER, endoplasmic reticulum; Nu, nucleolus. Scale bars represent 1.3 μm in Figs. 5-7, 1.0 μm in Fig. 8, 0.6 μm in Fig. 9, 0.4 μm in Fig. 10, and 0.2 μm in Figs. 11-12.

Table 2. Changes of cell and nucleus dimension in interprocambial and interfascicular residual meristem and interfascicular cambium of the first internode of *G. biloba* in transverse section

Cell dimension (μm^2) Stage (days)	Cell	Nucleus	N/C (%)
Interprocambial residual meristem (3)	159.78± 7.01	81.74± 7.00	51.16± 3.35
Early interfascicular residual meristem (6)	168.13± 4.47	57.30± 4.11	34.08± 1.93
Late interfascicular residual meristem (8)	254.70± 8.38	45.36± 6.17	17.81± 2.62
Early interfascicular cambium (16)	381.49± 26.21	40.27± 5.43	10.56± 1.78
Mature interfascicular cambium (25)	271.50± 21.40	13.30± 5.44	4.90± 1.11

N/C, Percentage of nuclear area to cell. Data are based on averages from 70 to 100 cells.

yma cells located about 40 μm from the residual meristem to cortex or pith, the thickness of the radial tangential wall remained almost unchanged regardless of the developmental stage.

DISCUSSION

It has been accepted without experimental confirmation that the interfascicular cambium originates from periclinal divisions of interfascicular parenchyma (Salisbury and Parke, 1964; Gemmell, 1969; Cutter, 1978; Swamy and Krishnamurthy, 1980; Fahn, 1982). However, the origin and development of interfascicular cambium has almost the same differentiation pattern as intrafascicular cambium because its differentiation proceeds from the residual meristem maintaining meristematic continuity (Soh, 1993). This conclusion has already been made through light microscopic observations of the seedlings of *Ricinus communis* and *G. biloba* (Soh *et al.*, 1989; Soh, 1991).

If the differentiation of interfascicular cambium

Table 3. Changes of cell and nucleus dimension in interprocambial and interfascicular residual meristem and interfascicular cambium of the first internode of *G. biloba* in longitudinal section

Cell dimension (μm^2)	Long cells					Short cells				
Stage (days)	Cells	Vacuole	Nucleus	V/C (%)	N/C (%)	Cells	Vacuole	Nucleus	V/C (%)	N/C (%)
Interprocambial residual meristem (3)	312.95± 19.24	65.87± 11.92	109.14± 10.50	21.05	34.87	312.95± 19.24	–	129.47± 7.41	–	41.37
Early interfascicular residual meristem (6)	1184.31± 39.21	513.03± 36.04	111.93± 7.40	43.31	9.45	682.92± 89.13	143.74± 31.21	118.96± 9.72	21.05	17.42
Late interfascicular residual meristem (8)	1912.00± 94.91	1147.06± 130.86	139.43± 13.56	59.99	7.29	753.50± 43.18	375.81± 34.60	96.97± 14.66	49.88	12.87
Early interfascicular cambium (16)	2838.18± 247.10	1672.75± 138.92	104.62± 11.23	58.94	3.69	764.39± 46.91	422.23± 45.22	102.15± 10.55	55.24	13.36
Mature interfascicular cambium (25)	3484.52± 242.36	2165.20± 434.43	83.63± 13.86	62.14	2.40	846.58± 34.10	429.14± 47.83	80.86± 3.01	50.69	9.55

V/C, Percentage of vacuolar area to cell; N/C, Percentage of nuclear area to cell. Data are based on averages from 70 to 100 cells.

Table 4. Dimensional changes of cell, nucleus and vacuole in parenchyma locating about 40 μm from residual meristem to cortex or pith during ontogeny of interfascicular cambium in transverse section

Cell dimension (μm^2)	Cortex					Pith				
Stage (days)	Cells	Vacuole	Nucleus	V/C (%)	N/C (%)	Cells	Vacuole	Nucleus	V/C (%)	N/C (%)
Interprocambial residual meristem (3)	618.44± 55.67	36.92± 3.52	97.92± 6.82	5.97	15.39	361.34± 15.92	43.21± 1.63	99.32± 10.05	11.96	18.41
Early interfascicular residual meristem (6)	805.26± 41.39	68.87± 3.99	94.30± 7.68	8.55	10.47	409.16± 24.56	161.48± 25.04	86.25± 7.86	39.47	16.69
Late interfascicular residual meristem (8)	1218.4 ± 68.88	924.46± 179.47	81.68± 5.77	75.87	5.97	785.88± 69.95	694.80± 135.69	89.96± 14.21	88.41	5.86
Early interfascicular cambium (16)	1608.2 ± 94.47	1181.95± 169.89	79.42± 12.99	73.50	3.56	884.08± 27.31	762.23± 83.87	77.67± 13.10	86.22	5.02
Mature interfascicular cambium (25)	1916.2 ± 53.41	1448.45± 241.86	80.67± 9.62	75.59	2.69	949.90± 52.91	770.73± 72.79	56.46± 6.10	81.14	4.42

V/C, Percentage of vacuolar area to cell; N/C, Percentage of nuclear area to cell. Data are based on averages from 70 to 100 cells.

is completed by the first periclinal division of the interfascicular parenchyma cell (Fahn *et al.*, 1972), there must have been an abrupt differentiation. However, in the differentiation process of the interfascicular cambium in *G. biloba*, changes in the dimensions of both cell and nucleus in both transverse and longitudinal planes took place gradually from the interprocambial residual meristem to the early interfascicular cambium (Table 2). The same observation was made from the longitudinal observation of the differentiation processes of fusiform initials and ray initials from long and short cells of the residual meristem (Table 3). The area of the nucleus of the residual meristem cell was smaller than that of the nucleus of the cortex or the pith cell. A similar observation was noted in *Ricinus communis* as well (Siebers, 1972).

In the interprocambial residual meristem cell, the radial and tangential walls had the same thickness at the beginning, but as the differentiation advanced the tangential wall gradually became thinner than the radial one (Figs. 5-8). When the thicknesses of the radial and tangential walls of the cortex or the pith which was located about 40 μm from the residual meristem were compared at each differentiation stage, almost no difference was found from the residual meristem to the early differentiation of the interfascicular cambium. This phenomenon will support the fact that the interfascicular tissue differed from parenchyma and had characteristic of meristem. The tangential wall of cambial cells was observed to be thinner in the vascular cambium of active season samples than in those of the dormant season (Srivastava, 1966).

Almost no vacuolation took place in the interprocambial residual meristem cells. Very small vacuoles, if any, were found in them. But in its differentiation process through the interfascicular residual meristem to the interfascicular cambium, vacuolation was observed to take place by degrees (Figs. 5-8). In contrast to apical meristems, the vascular cambium cells have characteristics of vacuolation (Catesson, 1990). It has already been observed in many other plants that the vascular cambium in its active season has a large central vacuole (Srivastava, 1966; Kidwai and Robards 1969a, b; Evert and Deshpande, 1970).

There were storage materials such as starch grains in the interprocambial residual meristem cells. These storage materials were distributed in small amounts in the interfascicular residual meristem. They gradually degraded and almost fully depleted as the differentiation of the interfascicular cambium took place (Figs. 9-12). There is little research on the distribution of storage materials in the differentiation process of the interfascicular cambium. However, it has been reported that in many plants, there are great differences in the distribution of storage materials depending on whether the vascular cambium was active or dormant (Srivastava, 1966; Kidwai and Robards, 1969b; Catesson, 1974, 1990). In the rhizome of *Botrychium ternatum*, many storage materials were degraded and lost in the vascular cambium during the active season where they had been previously observed in dormant vascular cambium (Lee and Soh, 1995). It has already been reported as well, that storage materials accumulated to a great extent in dormant vascular cambium could not be seen in the active cambium of seed plants (Kidwai and Robards, 1969; Kruatrachue and Evert, 1977; Riding and Little, 1985; Catesson, 1990). On the other hand, there was no significant difference in the distribution of storage materials in the cortex and pith during the process of differentiation.

As has been examined so far, the differentiation process of the interfascicular cambium from the interprocambial residual meristem through the interfascicular residual meristem advanced gradually and showed the same tendencies as found in the previous light microscopic research (Soh, 1991). Therefore it can be concluded that the origin and development of the interfascicular cambium is the same as that of the intrafascicular cambium and that the interfascicular cambium is differentiated gradually from interfascicular residual meristem rather than abruptly from the interfascicular parenchyma.

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은행나무 幼植物의 줄기에서 維管束間 形成層의 發生과 微細構造

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적 요

은행나무 유식물의 제1절간에서 잔존분열조직으로부터 유관속간 형성층의 점진적 분화를 광학 및 전자현미경적으로 밝혔다. 잔존분열조직세포는 크기가 작고 균일 배열 또는 비균일 배열을 하고 있지만 그에 인접하고 있는 피층 및 수의 세포는 크기가 크고 균일 배열로 일관되어 있었다. 전형성층속간 잔존분열조직세포는 점진적으로 그 칫수가 커지면서 액포화가 진행되었다. 결국 유관속간형성층은 분화가 진행되면서 방추형시원세포와 방사조직시원세포를 갖추게 되었다. 잔존분열조직세포내에 저장물질은 점차로 유관속간형성층의 분화가 진행되면서 분해 소실되어 갔다. 전형성층속간 잔존분열조직세포의 방사 및 접선벽의 두께는 거의 같으나 유관속간형성층의 분화가 진행되면서 접선벽의 두께가 방사벽보다 얇게 나타났다. 이와 같은 결과로부터 유관속간형성층은 잔존분열조직으로부터 점진적으로 분화되는 것이 분명했다.

주요어 : 유관속간 형성층, 잔존분열조직, 미세구조, 은행나무줄기

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