

## Origin and Development of the Interfascicular Cambium from Residual Meristem in Seed Plants

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### 種子植物 殘存分裂組織으로부터 維管束間形成層의 起源과 發生

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#### ABSTRACT

The origin of the interfascicular cambium from residual meristem can be elucidated by tangential and transverse observation. It is clear that there is structural distinction between interprocambial and interfascicular residual meristem and adjacent parenchyma in both the transverse and tangential view. Consequently, the residual meristem does not convert into parenchyma but, rather, becomes interfascicular cambium. In tangential view, the homogeneous structure of interfascicular residual meristem at an early stage changes gradually into a heterogeneous one at a later stage, with long and short cells from which fusiform and ray initials originate respectively. However, the homogeneous structure of parenchyma adjacent interfascicular residual meristem does not change into a heterogeneous one but remains the same at all stages of development. Therefore, the interfascicular cambium has a direct ontogenetic continuity with the residual meristem, and does not have its secondary origin from differentiated parenchyma. Furthermore, the ontogenetic pattern of the interfascicular cambium is almost the same as that of fascicular cambium.

#### INTRODUCTION

There are contradictory views on the origin of interfascicular cambium. First, this cambium does not have ontogenetic continuity from residual meristem, but differentiates from interfascicular parenchyma (Salisbury and Parke, 1964; Esau, 1977; Cutter, 1978; Little and Jones, 1980; Mauseth, 1988; Buvat, 1989; Fahn, 1990). Second, the cambium has direct ontogenetic continuity from residual meristem (Siebers, 1971a, b, 1972; Soh *et al.*, 1989; Soh, 1991). The former view has been adopted by many plant anatomists, but the latter by only a few. If the future cambium in the interfascicular region is not only structurally different from the adjoining interfascicular parenchyma, but also has its own characteristics, the later view would be correct.

We have found little clear evidence that the future

cambial tissue and its adjoining parenchyma in the interfascicular region are structurally the same. Furthermore, there is also no evidence that the interfascicular cambial cells are directly differentiated from interfascicular parenchyma cells. The first appearance of interfascicular cambium has been claimed to be from the first periclinal division of cells in transverse section (Esau, 1977; Mauseth, 1988; Fahn, 1990). Here, it should be noted that repeated periclinal divisions in the procambium occur before the completion of fascicular cambium differentiation in the stem of seed plants (Soh, 1990). Further, it is necessary to confirm the ontogenetic sequence of interfascicular cambium from the precursor tissue through tangential sections.

Fortunately, some authors recently presented that future cambium in the interfascicular region could be distinguished from the adjoining parenchyma (Siebers, 1972;

Table 1. Cell width of interfascicular residual meristem and its adjoining parenchyma during the growth of *Ricinus communis* hypocotyl measured with 50 cells each in transverse section

Stages(days)	Cell width( $\mu\text{m}$ )	*Parenchyma at cortex side		Interfascicular residual meristem		*Parenchyma at pith side	
Beginning of elongation(1)		15.2	2.1	7.2	1.3	16.2	3.5
During active elongation(6)		30.5	8.5	14.5	3.1	37.7	7.0
End of elongation(11)		42.7	14.1	20.7	5.8	46.5	9.1
After end of elongation(18)		43.2	5.9	17.7	3.1	46.3	13.6

\*Interfascicular parenchyma at 50  $\mu\text{m}$  to the pith and cortex side of the interfascicular residual meristem

Table 2. Cell length of interfascicular residual meristem and its adjoining parenchyma during the growth of *Ricinus communis* hypocotyl measured with 50 cells respectively

Stages(days)	Cell width ( $\mu\text{m}$ )	*Parenchyma at cortex side		Interfascicular residual meristem				*Parenchyma at pith side	
				Long cell	Short cell				
Beginning of elongation(1)		24.1	2.2	23.6	3.1		45.0	12.2	
During active elongation(6)		110.7	27.4	84.5	10.8	38.1	7.5	131.7	13.1
End of elongation(11)		169.0	22.2	155.3	23.4	51.3	13.4	192.5	19.8
After end of elongation(18)		256.7	36.7	235.1	33.6	48.1	14.4	285.2	26.6

\*Interfascicular parenchyma at 50  $\mu\text{m}$  to the pith and cortex side of the interfascicular residual meristem

Cumbie, 1987; Soh and Yang, 1987; Soh *et al.*, 1989; Soh, 1991). Furthermore, the process whereby the fusiform and ray initial of interfascicular cambium originated from residual meristem was traced through tangential view in seed plants (Soh *et al.*, 1989; Soh, 1991). Thus, the present paper briefly reviews the origin and development of interfascicular cambium in some seed plants, mainly in *Ricinus communis* (Soh *et al.*, 1989).

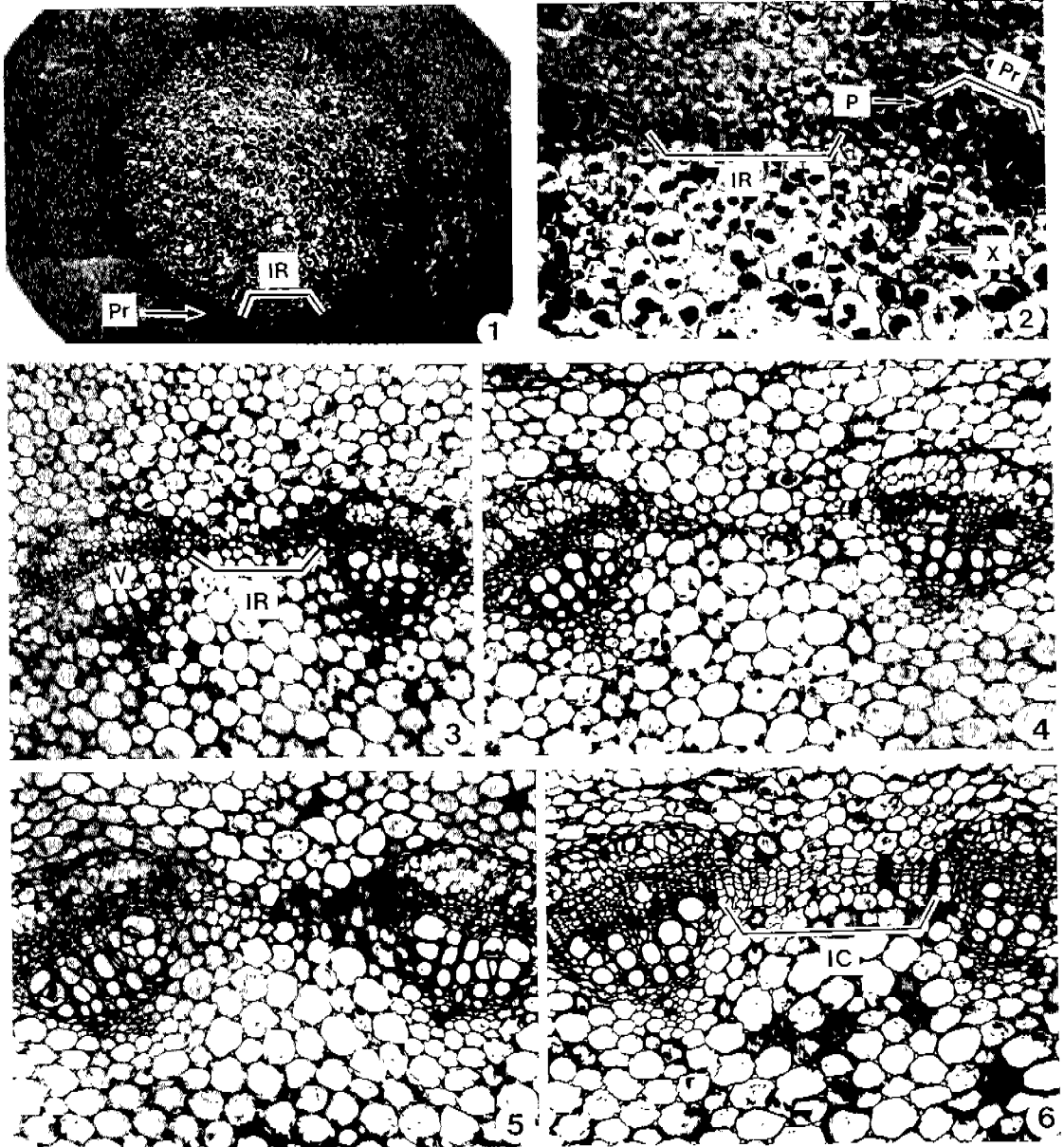
### INTERPROCAMBIAL AND INTERFASCICULAR RESIDUAL MERISTEM

Increased vacuolation by the differentiation of cortex and pith delimits an approximately circular zone, which is a subapical residual meristem, a residuum of apical meristem in the transverse section of shoot tip. Procambial strands differentiate from residual meristem at a relatively later stage. Interposed residual meristems among procambial strands would be called, rather, interprocambial residual meristem, because the meristem is not practically interposed in the interfascicular region but in the interprocambial region. Although the interposed residual meristem among procambial strands has been referred to as interfascicular residual meristem (Sterling, 1946; Larson, 1975, 1982), this term would be better used only

after the primary vascular differentiation within the procambium. For convenience, in this paper, the residual meristem will be developmentally subdivided into three stages: subapical, interprocambial, and interfascicular.

The developmental stages of *Ricinus communis* hypocotyl can be arranged as Table 1 (Soh and Kang, 1989; Soh *et al.*, 1989). Fig. 1 shows an octagonal arrangement consisting of eight procambial strands and interprocambial residual meristem of tangential bands of relatively small cells among the strands in an early stage of the hypocotyl development. Interprocambial residual meristem develops to interfascicular residual meristem during primary vascular differentiation. This meristem is future interfascicular cambium, regarded as 'residue of residual meristem' by Soh *et al.*, (1989) and called 'precambial layer' by Siebers (1971a).

On the other hand, the meristem has been referred to as 'interfascicular parenchyma' by some authors (Gemmell, 1969; Cutter, 1971; Esau, 1977; Fahn, 1990). If the depth of the meristem is not so great, the interfascicular residual meristem will eventually be differentiated into interfascicular parenchyma, after all characteristic vascular bundles of a given stem level completed. However, the interfascicular residual meristem is not considered as parenchyma in *Ricinus communis* hypocotyl and *Ginkgo biloba* internode with relatively wide interfascicu-



Figs. 1-6. Transverse sections of the *Ricinus communis* hypocotyl. Bars=153  $\mu$ m, 49  $\mu$ m (Figure 2). Fig. 1. Eight procambial strands (Pr) and interfascicular residual meristem (IR) among the strands with differentiating xylem (X) and phloem elements (P) in octagonal arrangement at the beginning stage of elongation. Fig. 2. A magnified view of Fig. 1. Fig. 3. Interfascicular residual meristem (IR) between two vascular bundles (V) at the active elongation stage. Fig. 4. Interfascicular residual meristem showing the beginning of periclinal cell divisions adjacent to the vascular bundles at the early stage of the end of elongation. Fig. 5. Interfascicular residual meristem showing radial seriation of cells by periclinal divisions at the later stage of the end of elongation. Fig. 6. An interfascicular cambium (IC) with radial seriations of cells between two fascicular cambia at the stage after the end of elongation.

cular cambium. However, we do not have any information as to whether or not the metaphloem and metaxylem

differentiate just before the initiation of interfascicular cambium by periclinal division of cells. Many authors

lar tissue. This is because the meristem not only has continuity with the residual meristem but also is structurally more similar to the procambium within vascular bundles than to its adjoining interfascicular parenchyma in all stages (Tables 1, 2; Soh and Kang, 1989; Soh *et al.*, 1989; Soh, 1991).

The interprocambial and interfascicular residual meristem is distinguished from the adjoining interfascicular parenchyma in all developmental stages in the transverse section (Figs. 1-5; Tables 1, 2). Such a distinction was also noted by Siebers (1971a) in the transverse view. By comparing the interfascicular residual meristem with the interfascicular parenchyma in tangential view, we can find there is also structural distinction between the two (Figs. 7-14). The parenchyma has a homogeneous structure at all stages of development, but interfascicular residual meristem changes from a homogeneous to a heterogeneous structure, as in the process of procambium development (Soh and Kang, 1989).

### INITIATION OF INTERFASCICULAR CAMBIUM

In the transverse section, cells of interfascicular residual meristem at an early stage are smaller than adjoining parenchyma cells and dispose randomly. In a later stage, the cells divide periclinally and are arranged in radial files (Figs. 4 and 5). Thus, the periclinal division in interfascicular residual meristem is delayed to compare with that in procambium within vascular bundles (Soh and Kang, 1989; Soh *et al.*, 1989). After a few repeated divisions, the meristem becomes interfascicular cambium in *Ricinus communis* hypocotyl and *Ginkgo biloba* internode (Figs. 5, 6; Soh, 1991). Thus, the first periclinal division in the interfascicular region can be analogous to the initiating layer that will appear within a procambial strand in the elongating terminal shoot of *Populus deltoides* (Larson, 1976, 1982). The initiating layer becomes metacambium with the tangential continuity of radially aligned cells by periclinal divisions and then develops into cambium. However, the first periclinal cell division was described as the initiation of interfascicular cambium by Fahn *et al.* (1972), without justifying the cambial initials in the results.

The tangential sections show that the interfascicular residual meristem with long and short cells at a later stage gradually differentiates into fusiform and ray initials of interfascicular cambium, respectively (Figs. 11-14). Thus, this differentiation pattern is similar to that of *Acer*

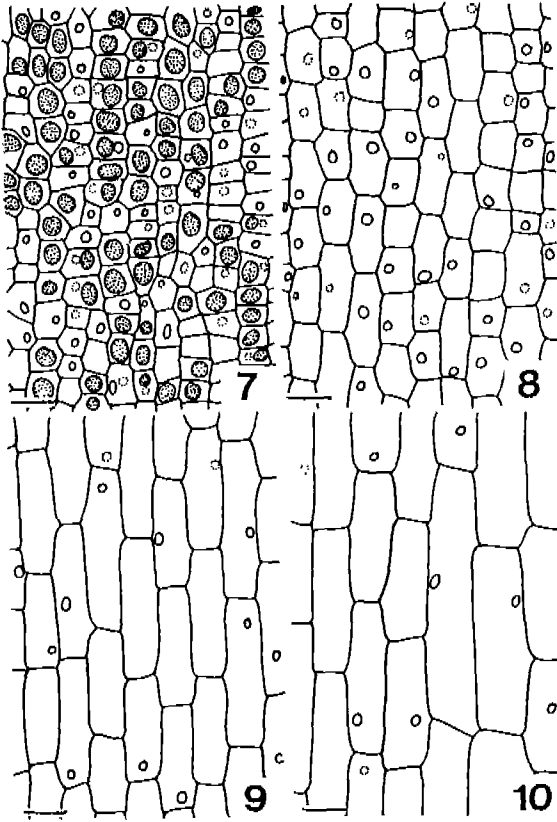
and *Ginkgo* (Catesson, 1964; Soh, 1991). However, the interfascicular tissue of *Hoheria* and *Aristolochia* differentiates exclusively into ray initials (Butterfield, 1976; Schnettke, 1977).

From the above results, it is beyond suspicion that on the contrary to the common view, the interfascicular cambium originates from a predetermined tissue at an early stage of development but not from interfascicular parenchyma. Hara (1972) suggests that the whole cambium, interfascicular and fascicular, might be destined to be differentiated even at an early stage of stem development. Some authors have reached the conclusion that the interfascicular cambium has a direct ontogenetic continuity with the residual meristem (Siebers, 1971a, b, 1972; Soh *et al.*, 1989; Soh, 1991). Therefore, the interfascicular cambium does not have its secondary origin from differentiated parenchyma but is determined at the procambial stage (Lang, 1965). Consequently, the present study does not correspond to the opinion that the residual meristem is converted into parenchyma, which in turn differentiates into interfascicular cambium (Esau, 1977; Swamy and Krishnamurthy, 1980), and that cambium have double origins (Catesson, 1974).

### COMPLETION OF INTERFASCICULAR CAMBIUM

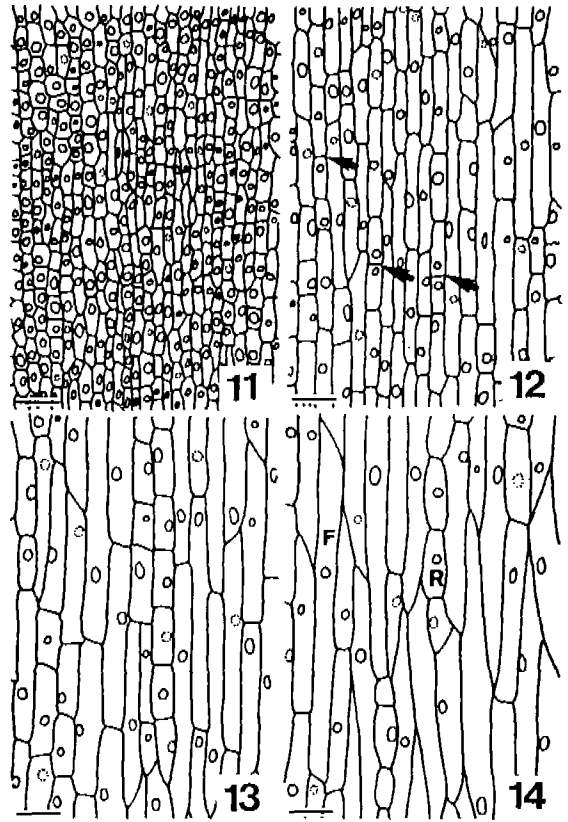
The interfascicular cambium is completed after a few repeated periclinal cell divisions in *Ricinus* (Fig. 6). As seen in the transverse section, the interfascicular residual meristem tissue does not have the cambial characteristic just after the occurrence of the first periclinal cell division, because the end walls of long cells and the arrangement of short cells of the meristem differ from the structure of the fusiform and ray initials of interfascicular cambium in the tangential section of *Ricinus* hypocotyl and *Ginkgo biloba* internode (Figs. 5 and 13). In a series of studies on interfascicular cambium development, Siebers (1971a, b, 1972) identified cambium initiation only in the transverse view. Therefore, it is not clear whether the interfascicular cambium in his figures has acquired cambial characteristics (Siebers, 1971a; Figs. 4 and 5).

The fascicular cambium acquires its characteristic features after several repeated periclinal divisions in the procambium in many plants (Esau, 1965; Cumbie, 1967; Fahn *et al.*, 1972; Soh, 1972, 1974a, b, 1990; Larson, 1974, 1982). Those repeated periclinal divisions of procambium contribute the differentiation of metaphloem and metaxylem, and then the procambium is differentiated into vas-



Figs. 7-10. Tangential sections of the interfascicular parenchyma 50  $\mu\text{m}$  from interfascicular residual meristem and cambium to pith side, with a homogeneous structure composed of cells with transverse end walls in *Ricinus communis* hypocotyl. Bars = 49  $\mu\text{m}$ . Fig. 7. Interfascicular parenchyma composed of almost uniform cells with dotted storage substances in hypocotyl at the beginning of elongation. Fig. 8. The stage during active elongation. Fig. 9. The stage at the end of elongation. Fig. 10. The stage after the end of elongation.

have described the immediate production of secondary vascular elements from the first periclinal division of interfascicular residual meristem cells without the production of primary vascular elements (Siebers, 1972; Siebers and Ladage, 1973; Saks *et al.*, 1984). Furthermore, the root cambium acquires its typical structure with two types of initials in *Ginkgo biloba* and *Acer saccharinum* after a few repeated periclinal cell divisions (Soh *et al.*, 1988, 1991). Additionally, the procambium showing a few periclinal cell divisions in *Populus* roots was described as the metacambium but not cambium by Sundberg (1983). In addition, the ontogenetic pattern of the interfascicular



Figs. 11-14. Tangential sections of interfascicular cambium in *Ricinus communis* hypocotyl of the same stages in Figs. 7-10. Bars = 49  $\mu\text{m}$ . Interfascicular residual meristem with homogeneous structure is composed of relatively short cells with transverse end walls (Fig. 11), shows initial transformation from a homogeneous to heterogeneous structure with relatively long and short cells (arrow: transverse division, Fig. 12), and shows a distinct heterogeneous structure (Fig. 13). And then the meristem differentiates into interfascicular cambium with distinct fusiform initials (F) with tapering end and ray initials (R) with transverse end walls (Fig. 14).

cambium derived from the interfascicular residual meristem is almost the same as that of fascicular cambium derived from the procambium within vascular bundles in *Ricinus* hypocotyl (Figs. 11-14; Soh and Kang, 1989; Soh *et al.*, 1989; Soh, 1991).

### ACROPETAL DIFFERENTIATION OF INTERFASCICULAR CAMBIUM

In the transverse section, the periclinal divisions of

cells in the interfascicular region begin adjacent to those in the vascular bundles and advance across the interfascicular region of *Ricinus communis* hypocotyl (Figs. 4 and 5). Such divisions have been commonly described in much of the literature (Priestly, 1928; Esau, 1965; Fahn *et al.*, 1972). Further, many authors state that the stimulus for the initiation of interfascicular cambium appears to arise in the fascicular cambium (Steeves and Sussex, 1972; Phillips, 1976). In addition, there is evidence given by cytochemical experiments that the activity of carboxylesterase, an enzyme marker, appears first in the cells adjacent to the vascular bundles and then spreads the interfascicular tissue from both sides of the bundles (Rana and Gahan, 1983; Gahan, 1988). Gahan (1988) stated from experimental evidence that the signal for the initiation of the interfascicular cambium emanates from adjacent fascicular cambium.

However, except for experiment by Rana and Gahan, the evidence that an inductive factor arising from the vascular bundle acts on interfascicular region depends on mostly deduction from the developmental sequence. And wounding experiments show that there is no special organizing stimulus which is responsible for the initiation of interfascicular cambium as a separate entity from the vascular bundle (Fahn *et al.*, 1972). Furthermore, Siebers (1972) demonstrated, on the basis of culture experiments with hypocotylary tissue of *Ricinus*, that the interfascicular cambium was developed from its isolated embryonic interfascicular tissue independently from the fascicular tissue. Therefore, there is confusion in interpreting whether the initiation of interfascicular cambium is influenced from adjacent vascular tissue or determined at shoot tip.

Although these two contradictory views are based on experimental evidence, there are more fundamental points. First, it is necessary to consider that the gradual differentiation of interfascicular cambium occurs acropetally, so that transverse effect from adjacent vascular tissue could be less important than the downward inductive factor from shoot tip. Thus, the initiation of interfascicular cambium may depend on the age of the tissue which reacts to the inducing stimuli coming from the shoot tip. Second, during vascular tissue differentiation, procambium in vascular bundles has two roles: vascular tissue production by repeated periclinal divisions and cambial ontogeny by anticlinal (transverse) division of short cells and elongation of some cells. However, only cambial ontogeny without the production of primary vascular tissue occurs in the interfascicular region. Thus, cambial onto-

geny can be noticed only in a tangential section because structural changes in the course of the ontogeny are mainly cell elongation and transverse division. Even though the carboxylesterase activity was not detected in the interfascicular region (Gahan, 1988), it might be due to the less active periclinal cell division while active periclinal division occur in procambium in vascular bundles.

In tissue block culture, mixed tissue blocks that were half interfascicular and half fascicular did not show a more pronounced development of interfascicular cambium as compared with tissue blocks containing only interfascicular tissue (Siebers, 1971b). Recently, it was reported that hydroxyproline-rich glycoproteins examined at the protein and the mRNA levels by tissue print immunoblots are specifically present in the cambium tissue of a developing soybean stem (Ye and Varner, 1991). Hydroxyproline-rich glycoprotein mRNAs are localized in interfascicular tissue as well as fascicular tissue from first to sixth internode and cannot be detected in pith parenchyma. After cambium cells are differentiated into secondary phloem and secondary xylem, there are no detectable hydroxyproline-rich glycoprotein mRNAs in differentiated tissues, indicating that hydroxyproline-rich glycoprotein genes are no longer expressed. These results suggest that interfascicular cambium is programmed at an early stage of residual meristem and will be acropetally differentiated through its predetermined course. Furthermore, the results that the ontogenetic course of interfascicular cambium is structurally traced from the residual meristem will be the most clear evidence for this suggestion (Figs. 11-14). If the initiation of both interfascicular and fascicular cambia occurs simultaneously, there will be no inductive factor arising from fascicular cambium.

Some authors have said that the fascicular cambium precedes the interfascicular one (Philipson *et al.*, 1971; Esau, 1977). On the other hand, the fascicular cambium in *Ricinus* epicotyl does not precede the interfascicular cambium (Fahn *et al.*, 1972).

## CONCLUSION

For convenience, the residual meristem is developmentally subdivided into three stages: subapical, interprocambial, and interfascicular. The differentiation of interfascicular cambium with fusiform and ray initials from residual meristem occurs gradually as follows: subapical residual meristem → interprocambial residual meristem → interfascicular residual meristem → interfascicular cambium. Apparently, the residual meristem does not convert

into parenchyma but, rather, straightforwardly becomes interfascicular cambium. Therefore, the description in many books that interfascicular cambium differentiates from interfascicular parenchyma is due to the lack of observational evidence about the origin of interfascicular cambial initials.

It is clear that there is structural distinction between interprocambial and interfascicular residual meristem and adjacent parenchyma in both the transverse and tangential view. However, from the results of transverse examination for the differentiation of interfascicular cambium, we could not clearly elucidate the origin of cambial initials. Only from the results of tangential examination it could be verified. In tangential view, the homogeneous structure of interfascicular residual meristem at an early stage changes gradually into a heterogeneous one at a later stage, with long and short cells from which fusiform and ray initials originate respectively.

Future cambial tissue in the fascicular and in the interfascicular region are not the same in transverse section. However, this is not surprising when we consider that the arrangement, size, vacuolation, mitotic activity of cells in various regions of apical meristem are also not the same. The difference between procambium in fascicular region and interfascicular residual meristem is the production of metaphloem and metaxylem just before the initiation of cambium by repeated periclinal divisions or not. It should be clarified in an experiment that secondary vascular elements are produced immediately from the first periclinal division of interfascicular residual meristem cells.

The ontogenetic pattern of the interfascicular cambium in tangential view is almost the same as that of fascicular cambium. The patterns in *Ricinus communis* hypocotyl and *Ginkgo biloba* internode by tangential and transverse observation were also similar. Therefore, the interfascicular cambium has a direct ontogenetic continuity with the residual meristem, and does not have its secondary origin from differentiated parenchyma. It may depend on positional control that certain regions of residual meristem differentiate into fascicular cambium through procambium and other regions into interfascicular cambium in continuity with residual meristem. In order to understand the origin of interfascicular cambium, it is necessary that the process of cambial development is examined physiologically and biochemically.

Although many authors believe that the differentiation of interfascicular cambium depends on some stimulus from the vascular bundles, this meristem is acropetally

differentiated through a course predetermined at an early stage of residual meristem. It is suggested that the differentiation of interfascicular cambium is not determined by adjacent vascular tissue but, under appropriate physiological conditions produced by the adjacent tissue, can be only stimulated. Because only limited research on the ontogeny of interfascicular cambium has been done so far, we do not have much information to discuss in detail with various types of the ontogeny and various factors involved in the ontogeny. Therefore, further developmental and structural study is necessary to understand the origin and development of interfascicular cambium.

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## 적 요

잔존분열조직으로부터 유관속간형성층의 기원은 접선 및 횡단면 관찰로 밝힐 수 있다. 전형성층간 및 유관속간 잔존분열조직과 인접 유조직 사이의 구조적인 특징이 분명하게 나타난다. 따라서 잔존분열조직은 유조직으로 전환되지 않고 유관속간형성층의 발생으로 이어진다. 접선면 관찰에서 초기의 유관속간 잔존분열조직의 균일구조는 후기에 점진적으로 비균일구조로 변하는데, 이경우에 방추형시원세포의 기원이 될 근세포와 방사조직시원세포의 기원이 될 짧은 세포를 갖추게 된다. 그러나 유관속간잔존분열조직에 인접한 유조직의 균일구조는 비균일구조로 변화되지 않고 발생과정의 전시기에 걸쳐서 균일구조를 유지하게 된다. 그러므로 유관속간형성층은 잔존분열조직과 직접적인 연속성을 갖게되며, 분화된 유조직으로부터 2차적인 기원을 갖는것이 아니다. 더욱이 유관속간형성층의 분화유형은 유관속내형성층의 분화유형과 거의 같다.

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