Ontogeny of the Fascicular Cambium in the Hypocotyl of *Ricinus*

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피마자의 하배축에 있어서 유관속내 형성층의 초기발생

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ABSTRACT

Developmental anatomy was conducted in order to elucidate the differentiating pattern of fascicular cambial initials in the hypocotyl of Ricinus communis.

The homogeneous procambium with relatively short cells in early stage is transformed into a heterogeneous structure with long and short cells in late stage in tangential view. Fusiform and ray initials are gradually originated from the long and short cells of the procambium in hypocotyl in later stage respectively. Fusiform initials are not shorter than procambial cells because of the successive elongation of vascular meristematic cells. Therefore, the distinction between procambium and fascicular cambium is not made from comparison with their cell length. The characteristics of the fascicular cambium are gradually acquired at or just after completion of hypocotyl elongation.

INTRODUCTION

It has been clear that the pattern of fascicular cambial ontogeny reveals great diversity among many plants(Soh, 1989). However, information on the ontogeny of interfascicular cambium is rare. Swamy and Krishnamurthy(1980) stated that the interfascicular tissue is first converted into parenchyma and then the interfascicular cambium is originated from the parenchyma. And many authors have the same opinion on the origin of the interfascicular cambium(Gemmell, 1969; Esau, 1977; Cutter, 1978; Fahn, 1982). In this context, judging from the direct ontogenetic continuity of fascicular cambium from procambium, the pattern of the interfascicular cambial ontogeny should be different from that of the fascicular cambial ontogeny.

On the other hand, it is reported by the present authors that the interfascicular cambium in the hypocotyl of *Ricinus communis* is originated from a predetermined interfascicular tissue at an early stage of development, but not from differentiated interfascicular parenchyma (Soh *et al.*, 1989). The hypocotyl of *Ricinus communis* seedling is frequently used to examine the growth

and differentiation (Siebers, 1971 a,b, 1972; Fahn et al., 1972). Although there is a report on the relation between the procambium and the fascicular cambium in the seedling by Fahn et al.(1972), there are still many things which should be clarified on the origin of the fascicular cambial initials. Therefore, we try to compare the ontogeny of the fascicular cambium with that of the interfascicular cambium in the hypocotyl of the same plants as those in the previous paper (Soh et al., 1989).

MATERIALS AND METHODS

Seeds with uniform shape and weight(about 0.23g) of Ricinus communis L. were soaked in tap water at room temperature for two hrs and kept on wet filter paper or gauze in Petri dishes for 24 hrs. Germinating seeds with 1 mm-long roots were then selected and four seeds per pot(20 \times 25cm) were planted in fine sand. The pots were maintained in a growth room at a constant relative humidity(60-75) and temperature(25 \pm 1°C). Those were kept in a periodic condition of 16 hrs light(3,500 Lux measure at the shoot tip) and 8 hrs dark. The germinating seeds after 24 hrs(kept in Petri dish as 1-day-old seedling) and the seedling at various stage of growth were harvested for anatomical studies. Segments excised from entire length of hypocotyl or hypocotylary region between 5 mm and 9 mm below cotyledonary node along the order of chronological age, were fixed in FAA and embedded in paraffin. The embedded specimens were sectioned in transverse and longitudinal planes at 10 μ m thickness, and the sections were stained with hematoxylin, safranin and fast green(Soh et al., 1989).

Table 1. Measurement of hypocotyl length during growth of Ricinus communis seedling

Stages Organs (days) (mm)	Hypocotyl	Epicotyl	Characteristics
Beginning of elongation(1)	4		
During active elongation(6)	80		Hooked hypocotyl Folded cotylcdons
End of elongation(11)	145	2	Erect hypocotyl Unfolded cotyledons
After end of elongation(18)	155	8	Unfolded 1st leaf

RESULTS

Four of the eight procambial(or vascular) bundles in the hypocotyl constitute the cotyledonary trace. Of these four, the two bundles of center have been observed at all stages of development(Soh et al., 1989). The developmental stages of hypocotyl in the present study were divided for convinience into four stages: (1) the beginning stage of elongation, (2) the stage during active elongation, (3) the end stage of elongation and (4) the stage after the end of elongation(Soh et al., 1989). The development of vascular meristem and tissue on each stage is

Table 2. Cell length and width of fascicular meristem during the growth of *Ricinus communis* hypocotyl measured with 50 cells each

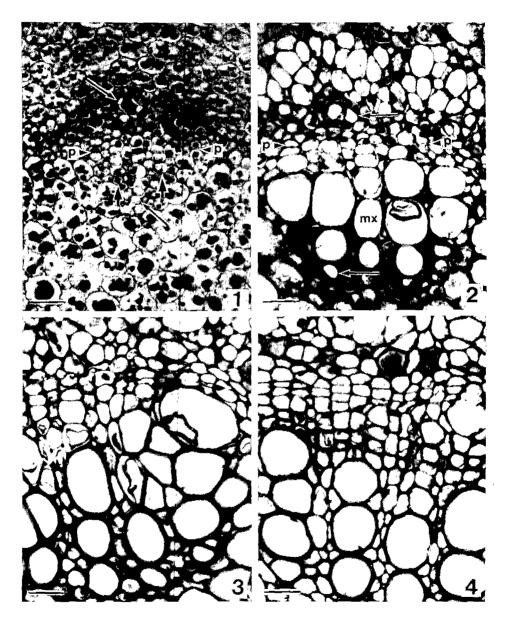
Stages \ Dimension	Length		3V7: 1.1
(days) (<u>\(\mu\) m</u>)	Long cell	Short cell	Width
Beginning of clongation(1)	39.5 ± 9.4		7.0 ± 1.0
During active elongation(6)	90.0 ± 10.6	42.8 ± 8.2	10.3 ± 1.8
End of elongation(11)	191.0 ± 35.9	47.3 ± 9.8	14.3 ± 2.7
After end of elongation(18)	283.3±54.9	49.7±9.7	12.5±4.0

coincident with the chronological age of hypocotyl in most cases. Therefore, the vascular meristem and tissue in early stage are vertically contiguous with the differentiated cambium and vascular tissue in the same bundle of the hypocotyl examined.

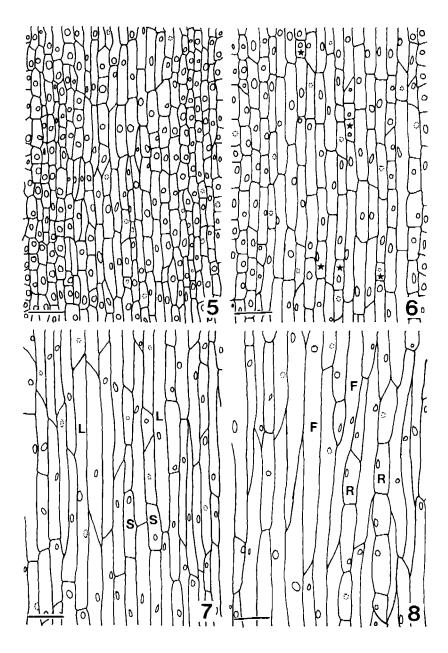
In the transverse section of hypocotyl at the beginning of elongation the protophloem element appears in the outer edge of the procambial bundle and protoxylem vessel is differntiating in the inner edge of the bundle. The procambial cells are stained more densely than the cells of the residual meristem and are divided in periclinal planes(Figure 1). The procambium shows radial seriations of cells. Each radial row has two to four cells. In the tangential section, the procambium has a homogeneous structure composed of relatively short cells with transverse end walls(Figure 5). The cells average to be 40 μ m in length(Table 2).

In the transverse section of hypocotyl during active elongation, the primary phioem elements appear as groups of small cells in the outer edge of the vascular bundle (Figure 2). The metaxylem vessels are differentiated in the inner edge of the vascular bundle. The procambium remains between the phloem and xylem as a zone of radially scriated cell rows with two to four cells in each row. The periclinal cell division in the procambium occurs more prominently at this stage than the previous stage. In tangential section, some procambial cells divide transversely but others begin to elongate. Therefore, the procambium is organized into two systems of cells: small cells (43μ m in length) and clongated cells (90μ m) which are discernible in the procambium (Figure 6, Table 2). All the cells have transverse end walls.

In the transverse section of hypocotyl at the end of elongation, the procambium shows radial seriations of cells caused by repeated periclinal divisions(Figure 3). Each row of the seriations consists of three to four cells. In tangential section, the procambium shows a heterogeneous structure: the presence of long cells(191 μ m long) and short cells(47 μ m) (Figure 7, Table 2), The long cells are actively elongating and have tapering ends or transverse end walls. The short cells have transverse end walls and form axial strands of cells. In the transverse section of hypocotyl after completion of elongation, the radial rows in the vascular meristem have three to five cells each. From these cells phloem and xylem elements are differentiating(Fig. 4). In tangential section, the vascular meristem is clearly heterogeneous(Figure 8). The elongating long cells are 283 μ m in length and possess tapering ends, whereas short cells are 50 μ m and still have transverse end walls(Table 2). The exial strands of short cells are one cell in width and



Figs. 1-4 Transverse sections of the developing hypocotyl of Ricinus communis. Bars = 49 µm. Figure 1: The procambium band(arrow head with p) showing radially seriated cell rows(short arrows) between protophlocm element(upper long arrow) and differentiating protoxylem vessel(lower long arrow) within a procambial(or vascular) bundle at the beginning stage of hypocotyl elongation. Figure 2: The procambium(arrows head with p) between phlocm and xylem in the vascular bundle during the active elongation of hypocotyl. mx: metaxylem, arrow: sieve tube(upper) and protoxylem vessel(lower). Figure 3: The procambium with radial rows of three to four cells at the end stage of hypocotyl elongation. Figure 4: The vascular cambium showing radial seriations with three to five cells in each row.



Figs. 5-8 Tangential sections of the vascular meristem in the hypocoryl of Ricinus communis at the same stages as shown in Figures 1-4. Bars = 49 μm. Figure 5: The procambium with homogeneous structure composed of relatively short cells with transverse end walls. Figure 6: The procambium showing initial transformation from homogeneous to heterogeneous structure with relatively long cells and short cells(stars). Figure 7: The procambium having heterogeneous structure composed of long cell(L) with tapering ends or transverse end walls and short cells(S) formed axial strands. Figure 8: The fascicular cambium with fusiform initials(F) and ray initials(R).

three to seven cells in height. This vascular meristem is regarded as the fascicular cambium.

DISCUSSION

The procambium having a homogeneous structure composed of relatively short cells in early stage become a heterogeneous structure with long and short cells in late stage in tangential view (Figures 1-3.) Fusiform and ray initials are gradually derived from the long and short cells of the procambium in later stage in *Ricinus* hypocotyl respectively(Figures 2-4). Because the homogeneous structure in not seen as a storied arrangement of cells, the present results do not correspond with the observations of Fahn et al. (1972). So the pattern of the origin of cambial initials almost resembles the pattern of the interfascicular cambium of the same species, and in more similar to that of the fascicular cambium of *Ginkgo biloba* than that of some other dicotyledons(Soh, 1972, 1989; Soh et al., 1989). The characteristics of fascicular cambium is nearly acquired at the stage of end of hypocotyl elongation, if the discrimination of fascicular cambium from procambium is based on the feature of end walls of vascular meristematic cells in *Ricinus*(Figure 3). The initiation of fascicular cambium occurs somewhat earlier than that of interfascicular cambium(Soh et al., 1989).

The radial seriations of procambial cells occur in earlier stage of hypocotyl development in *Ricinus* (Figure 1). Therefore, the periclinal division of procambial cell occurs in much more earlier stage than that of interfascicular cells(Soh et al., 1989). Cumbie(1967) described the differences between the end walls of the cells of the procambium and the cambium: most of the end walls of the elongated procambial cells are essentially transverse, whereas most of those of fusiform initials are abruptly tapered. On the other hand, most of the end walls of the elongated procambial cells are tapered in later stage like most of those of fusiform initials in some species(Soh, 1972, 1974 a,b; Enright and Cumbie, 1973; Soh et al., 1988; Kang and Soh, 1988). In *Hoheria*, the end walls of the fusiform initials are not markedly pointed until at the initiation of fascicular cambium (Butterfield, 1976).

Characteristics of the fascicular cambium are gradually acquired after the completion of hypocotyl elongation in *Ricinus*(Figures 4, 8). In this respect, the cambial initiation resembles the one of *Glycine max*(Kang and Soh, 1988). The cell elongation of the procambium occurs simultaneously with the elongation of hypocotyl, and also proceeds subsequently after cessation of hypocotyl elongation in *Ricinus* seedling(Table 3). Therefore, this cells elongation seems to result from instrusive growth of cells and is similar to that of *Glycine max*(Kang and Soh, 1988).

Fusiform initials are not shorter than procambial cells because of the successive elongation of vascular meristematic cells in *Ricinus*(Table 2). Such a progressive elongation of cells from procambium to cambium is also observed in some woody plants such as *Ginkgo*, *Aucuba*, *Weigela*, *Syringa* and *Robinia*(Soh, 1972, 1974a,b). In *Coleus*, fusiform initials in the first cambium are !onger than the late procambial cells(Bruchk and Paolillo, 1984). Therefore, we

can not distinguish procambium from fascicular cambium comparing with their cell length, although there is an abrupt decrease in the length of tracheary elements in passing from the last-formed primary xylem to the adjacent first-formed secondary xylem(Bailey and Tupper, 1918; Bailey, 1920, 1944).

적 요

생강충에 있는 피자마의 하배축에 있어서 유관속내 형성층의 기원 유형을 밝히기 위하여 발생해부학적 연구를 시도했다. 접선면 관찰에서 초기의 전형성층은 비교적 짧은 세포로 되어 있으며 균일한 구조를 갖추고 있으나 후기에는 긴세포와 짧은 세포로 된 불균임한 구조로 전환된다. 형성층 방추형원시세포와 방사조직원시세포는 하배축생장 후기의 전형성층의 진세포와 짧은 세포로 부터 점진적으로 기원된다. 유판속 분열조직세포의 계속적인 신장으로 인하여 방추형원시세포는 전형성층세포 보다 짧지 않다. 그러므로 유판속내 형성층과 전형성층간의 구별은 그들 세포 진이의 비교로는 되지 않는다. 유판속내 형성층의 해부학적 특징은 하배축신장의 완료와 동시에 또는 그후에 정진적으로 갖춰진다.

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