The Origin and Development of Vascular Cambium in Girdled Stems of *Eucommia ulmoides* Oliv.

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We conducted anatomical studies of girdled stems of *Eucommia ulmoides* at various developmental stages to elucidate the origin and development of callus and the vascular cambium. In the transverse view, ray initial cells in the cambial zone began to divide both periclinally and anticlinally 2 d after girdling. Fusiform initial cells started to enlarge at 3 d, then gradually proliferated via periclinal divisions. Thus, the callus was derived from the ray initial cells of the cambial zone as well as from fusiform initial cells. In the tangential view, callus cells derived from ray initial cells were short while those from fusiform initial cells were long, thereby producing a heterogeneous structure. However, the fusiform initial cells underwent transverse divisions 10 d after girdling, which resulted in shorter cells and a homogeneous callus structure. Afterward, some short cells divided transversely while others elongated, so that a heterogeneous form was regained. Finally, the vascular meristem that was girdled early in its development redifferentiated from short and long cells in the callus. The long cells developed into fusiform initials, with the short ones becoming ray initials.

Keywords: callus, *Eucommia*, fusiform initial, ray initial, vascular cambium

When a tree stem is girdled, a callus forms. Afterward, the vascular cambium begins to differentiate. Warren Wilson and Grange (1984) have identified three phases of regeneration after wounding: 1) the initial phase (lag phase), when no cell division or enlargement is occurring; 2) the division phase, with cell division and enlargement; and 3) the differentiation phase, when tissues or cambia are differentiated. Artificial debarking causes callus formation and differentiation of the vascular cambium and secondary vascular tissues (Dobbins and Fisher, 1986; Fisher and Ewers, 1989). In addition, external pressure can affect differentiation of the vascular cambium (Brown and Sax, 1962; Brown, 1964).

Although the role of immature xylem is negligible (Sharplees and Gunnerly, 1933), calli develop from immature cells of vascular tissue that already existed on the surface of the exposed vascular cambium. Calli may arise from any of the undifferentiated centripetal products of the vascular cambium; the type of tissue contributing to callus initiation depends on species and the histology of the cambial zone (Noel, 1970). However, theories about the origin of callus formation are contradictory. For example, in a study of *Pinus* stems, Brown and Sax (1962) observed that the new cambium began to differentiate through the callus parenchyma in the fourth week after debarking. Likewise, new vascular cambium was formed within 45 d of girdling in *Fulbernardia*, 76 d in *Trema*. In fully girdled stems of *Arabidaea chica*, new, continuous vascular cambium also differentiated within the massive callus (Dobbins and Fisher, 1986). In contrast, Li and Cui (1988) have studied transverse sections from girdled stems of *Eucommia*. Within the first week, ray cells of the immature xylem swelled, proliferated, and spread laterally under the surface layer. They gradually joined together with neighboring ray cells and were found with other cells derived from the immature xylem. Soon afterward, a cork layer arose near the surface and a newly formed cambium appeared deep within the callus.

These conflicting reports demonstrate that the development of calli in girdled stems has likely been misstated, and that the origin of these vascular cambium initials within the callus has not been studied thoroughly. Therefore, our objective was to determine the origin of callus and vascular cambial initials in girdled *Eucommia ulmoides* stems.

**MATERIALS AND METHODS**

We used a chisel and a grafting knife to remove
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**RESULTS**

**Structure of the Vascular Cambium and Its Derivative Tissues in Intact Stems**

In the transverse view, xylem was situated inside the vascular cambium, with phloem outside the meristem. The xylem was composed of axial parenchyma, vessels, fibers, and ray cells; the phloem comprised sieve tube members with companion cells, phloem parenchyma, successively parallel fibers, and ray cells (Figs. 3 and 4). The cambial zone of the girdled stem was partially eliminated (Fig. 4) but the remaining portion contained one to three cells in a radial file. In the tangential view, fusiform initials averaged 507 μm long. Ray initials were one to seven cells wide and 20 cells (182 μm) long (Fig. 16).

**Callus Formation on Girdled Trunks**

In the transverse view, the remnant vascular cambial zone was approximately 30 μm thick on the second day after girdling. Ray initial cells in the cambial zone enlarged and protruded earlier than did the fusiform initial cells, which had begun to enlarge without division. Callus was forming on all the preexisting surfaces outside of the vascular cambial zone. This callus surface had a protective layer, and was white on the entire exposed trunk (Fig. 5).

In the tangential view, the callus consisted of ray initial cells that had enlarged and proliferated within the cambial zone. However, fusiform initial cells had not begun to divide by 2 d after girdling, although most of those with prominent nuclei were ready (Fig. 17). Nevertheless, at 3 d post-girdling, enlargement and divisions had resulted in isodiametric ray initial cells, with cells extending into peripheral areas. Fusiform initial cells were shortened through active anticlinal and periclinal divisions, being transformed into globular or isodiametric cells. Their end walls were transverse (Fig. 18). In the radial view, the preexisting ray initial cells in the cambial zone proliferated by periclinal division. However, fusiform initial cells were shortened by periclinal and anticlinal divisions (Fig. 29).

At 4 d post-girdling, the callus was 340 μm thick in the transverse view. The number of cells originating from preexisting ray initial cells in the cambial zone increased through division and enlargement. Fusiform initial cells in the cambial zone increased notice-

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**Figure 1.** External morphology of *E. ulmoides* stem immediately after girdling. 2. External morphology with bark formation, 31 d after girdling. 3. Transverse sections showing secondary xylem (X), cambial zone (CZ), and secondary phloem (P) of intact *Eucommia* stem. Arrow indicates phloem parenchyma and companion cell. R, ray cells; 110X. 4. Transverse sections of exposed xylem surface on the girdled *Eucommia* stem. Calli were not observed here; 110X.