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Development of Cambium and Length of Vessel Elements and Fibers in Dwarf *Alnus hirsuta* (Spach) Rupr

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In a comparison of cambial cells and their derivatives between naturally occurring dwarf and normal trees, vessel elements and fibers in the annual rings of dwarf trees were found to be shorter, narrower and fewer than those of normal trees. The frequency of anticlinal divisions and loss of cambial initials were low during the differentiation of xylem cells from cambial initials in dwarf trees. The length and intrusive growth of fusiform initials were slightly less than those of normal trees. Thus, it was concluded that the shortening of vessel elements and fibers in dwarf trees was due to the fact that cambial initials were themselves shortened and underwent inactive intrusive growth during differentiation of the xylem mother cells.

Keywords: normal and dwarf *Alnus hirsuta*, cambial initial, intrusive growth, length of vessel elements and fibers

The characteristics of the secondary xylem are affected by environmental factors such as soil, water, altitude and latitude, and wind tolerance (Ford *et al.*, 1978; Forsaith, 1920; Fahn, 1964; Carlquist, 1975; Taylor, 1974; Oever *et al.*, 1981; Bissing, 1982; Lawton, 1984). Since water deficits primarily affect the wood quality of trees (Chalk, 1951; Zahner, 1968), research has focused mainly on variations in the secondary xylem of tree stems (Baas *et al.*, 1983, 1984; Kort & Baas, 1986; Kort, 1990). However, there have been no intensive studies related to the development of cambium and the length of vessel elements and fibers in dwarf trees occurring under a harsh environment such as arid conditions.

During radial growth of trees, the xylem and phloem are formed mainly by periclinal divisions of cambial initials. In addition, anticlinal division of fusiform initials increases the circumference of the trunk. Such cambial behavior in relation to tracheid length and radial growth depends on the amount of photosynthates and growth regulators (Larson, 1963). Comparing the radial increment of the individuals, the result showed how cambial activity is affected by environmental conditions. However, little information is now avaiable on the cambial activity and the radial growth in trees growing in an arid environment.

In this study, the differentiation pattern of cambial cells was reconstructed from serial tangential sections to clarify differences in the secondary xylem between normal and dwarf trees. In particular, the study focused on the differences in radial growth by anticlinal divisions or losses of cambial fusiform initials.

MATERIALS AND METHODS

Stems of *Alnus hirsuta* were collected from Mt. Manduck of Chonlabukdo, Korea (Table 1). A normal and a dwarf tree were selected and material collected from the trunks at a height of 1.2 m. The dwarf tree selected was from individuals which had rooted on rocks where their nutriant source had to be derived from various proportions of detritus, scant soil and organic litter.

For anatomical observation, the stem was sawed 10 mm in thickness and then fixed in 50% alcohol. Transverse, radial and tangential sections of secondary xylem, from the pith to the peripheral region, were made on a sliding microtome and stained with 1% basic fuchsin (Sass, 1971). Wood samples of each annual ring were macerated according to Jeffrey's method (Sass, 1971) to measure the length of vessel elements and fibers.

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Table 1. Wood characteristics of each *Alnus hirsuta* (Spach) Rupr

Species	Diameter of wood (cm)		Number of annual rings		Average width of annual rings (mm)		Locality
	NT	DT	NT	DT	NT	DT	
Alnus hirsuta	10.6	5.8	8	10	6.6	2.9	Mt. Manduck

NT, normal tree; DT, dwarf tree.

To examine the vascular cambium, bark (7×5×5 mm) with adhering secondary xylem was removed from sample trees, then fixed in Navashin's fluid (III) in the field, dehydrated with tertiary butyl alcohol and infiltrated with paraffin at 55°C (Jensen, 1962). Cross sections and serial tangential sections (10 μm in thickness) were prepared using a rotary microtome and stained with hematoxylin, safranin and light green SF.

The radial diameter and cells per annual ring, variation in length of vessel elements and fibers from pith to periphery, and the length of the cambial initials were measured 50 times from sections and macerations. Using a drawing attachment (Olympus, U-DA), drawings of serial tangential sections from the same region were made. We observed the pattern and the frequency of anticlinal divisions on fusiform initials, and the intrusive growth after the divisions. Since the intrusive growth of fusiform initials can not be observed in cambial layers directly, the growth rate had to be determined by examining the differentiated vessel elements and fibers from the mother cell in the transitional state immediately after the division of fusiform initials.

RESULTS

The number and the radial diameter of fibers examined in a series of radial rows from the pith to the peripheral region were higher and wider in normal trees than in dwarf trees (Fig. 1). The length of vessel elements and fibers from the pith to the peripheral region was greater in normal trees than in dwarf trees (Fig. 2) and the lengths they grew increased with distance from the pith. Also, fusiform initials in normal trees (957.2 μm) showed greater length than in dwarfs (880.4 μm). However, the frequency of anticlinal divisions was inversely correlated to the length of the vessel elements and fibers. Thus, the divisions occurred more frequently in the vicinity of pith than at the site of a recent ring. In an individual, 3.3-15.7 successive anticlinal divisions occurred per year in the vicinity of the pith while 0.6-0.8 divisions took place in the last formed ring of older stems.

Differentiation patterns of fusiform initials were observed in serial tangential sections (Fig. 3) and cross sections of secondary xylem. After the anticlinal divisions, a new wall formed between the two daughter cells was usually longitudinally oblique in the central site (Fig. 3c, e, f). But, a few cells had nearly transverse (Fig. 3c) or laterally longitudinal walls (Fig. 3f). The newly formed initials elongated by intrusive growth between xylem mother cells. Sometimes, the loss of shorter initials occurred in fusiform cells which divided unequally. The "spaces" created from the loss of the shorter initial allowed the intrusive growth of adjacent fusiform initial.

In the differentiation of cambial initials, anticlinal division of fusiform initials occurred continuously dur-

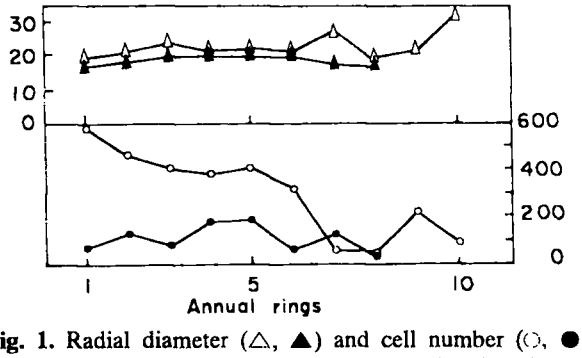

Fig. 1. Radial diameter (△, ▲) and cell number (○, ●) of fibers in annual rings from pith to peripheral region of *Alnus hirsuta*. △—△, ○---○: normal trees, ▲—▲, ● · ●: dwarf trees.

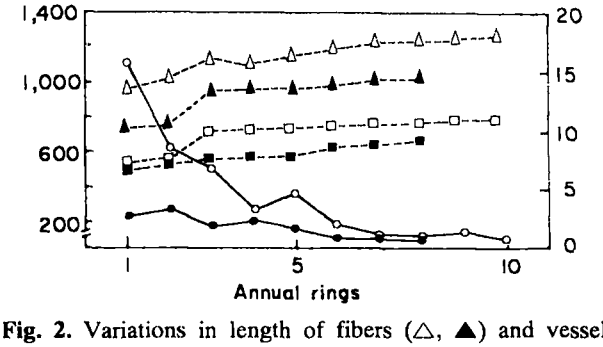

Fig. 2. Variations in length of fibers (△, ▲) and vessel elements (□, ■), and frequency of pseudotransverse division (○, ●) from pith to peripheral region of *Alnus hirsuta*. △—△, □---□, ○---○: normal trees, ▲—▲, ■—■, ● - ●: dwarf trees.

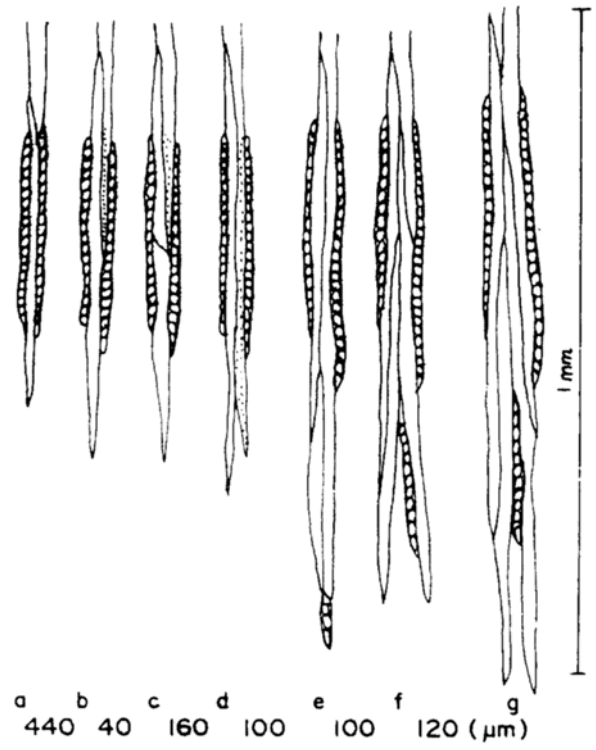

Fig. 3. Drawings from serial tangential sections of secondary xylem showing the developmental changes of fusiform initials in *Alnus hirsuta* normal trees. a, b. elongation through intrusive growth (dotted cell) in the cell on the upper right side and elongation of the left cell; c, d. pseudotransverse division (c) and loss of new wall (d) in the central part of the left cell; e, f. elongation after pseudotransverse division in the lower part of the left cell and the upper part of right cell. The numbers indicate the distance in radial files between each section.

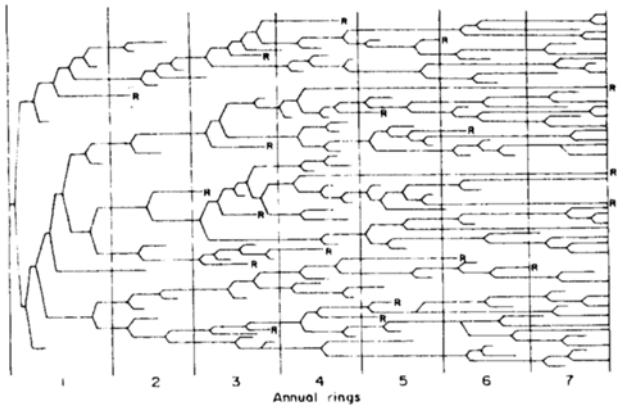

Fig. 4. Diagram showing the developmental changes of cambial initials from the pith (1) to the peripheral region (7) in a normal *Alnus hirsuta*. The forking of a horizontal line indicates an oblique, anticlinal division. Lateral longitudinal divisions are denoted by side branches. Termination of a horizontal line marks the disappearance of fusiform initials from the cambium. The letter R indicates the transformation of fusiform initials into ray initials. The boundaries of annual rings are depicted by vertical lines with the relative width of the annual rings is not considered.

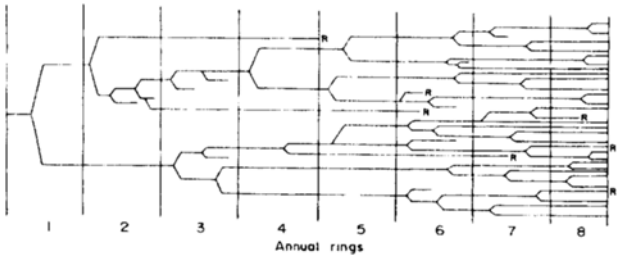

Fig. 5. Diagram showing the developmental changes of cambial initials from pith (1) to the peripheral region (8) in a dwarf *Alnus hirsuta*.

ing an increase of cambial circumference. In normal tree (Fig. 4), only 32 fusiform initials and 2 ray initials survived after 133 anticlinal divisions from one fusiform initial during radial growth of seven years. This behavior of the cambium could be characterized by a high frequency of anticlinal division and an associated high rate of loss of initials (99). On the other hand, in a dwarf tree grown during the same years (Fig. 5), the number of anticlinal divisions was 37, the loss of initials was 14, and only 21 fusiform initials and 3 ray initials formed from a fusiform initial. Thus, intrusive growth is higher in normal trees (29.1%) than in dwarf ones (21.6%).

DISCUSSION

The reduced radial growth of trees growing under arid environments is characterized by short vessel elements and fibers. This result corresponds with many other reports on the growth rates of trees (Baas *et al.*, 1983, 1984; Dinwoodie, 1963; Iqbal & Ghouse, 1982, 1983; Mahmooduzzafar & Iqbal, 1986; Taylor, 1974; Kort, 1990; Lim & Soh, 1991). Shorter axial elements needed to be investigated because they reduce the tensile strength of wood (Zahner, 1968; Kort, 1990).

In the present study, dwarf growth resulted from the length reduction of the vessel elements and fibers due to the reduction of length and intrusive growth of the fusiform initials themselves. The occurrence of short fusiform initials in dwarf trees can be interpreted by the fact that low water potential in the cambial region must restrict full expansion at the tips of initials. Therefore, short fusiform initials in dwarf trees are an important cause of short axial elements.

In nonstoried cambial species such as *Alnus hir-*

suta, the length of newly formed xylem mother cells results in two shorter cells up to half the length of the cambial initial by pseudotransverse anticlinal division, usually near the center (Bannan, 1957). The new xylem mother cells elongate through the intrusive growth to the length of complete fusiform initials, or become greater in length than the initials and invade into the "spaces" created by the loss of adjacent cells in the cambium, or they can penetrate between cells. Therefore, the rate and amount of intrusive growth of new fusiform initials in dwarf trees growing under a water deficit is reduced and would be an important factor governing the short axial elements in this species. An obstacle to these processes such as in a harsh environment like water deficit results in the reduced length of vessel elements and fibers due to retarded intrusive growth. Although low frequencies of pseudotransverse division in the cambium tend to increase cell length as reported by Bannan and Bailey (1956) in conifer cambium and Philipson *et al.* (1971), the resultant increase of cell length in dwarf trees is not as great as might be expected since the loss of initials is reduced. Therefore, this small loss of initials would not allow the space for elongation of the surviving daughter initials. The final length of derivative cells, vessel elements and fibers, also depends on the degree of intrusive growth undergone after being cut off from the cambium (Mahmooduzzafar & Iqbal, 1986).

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