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# Wood formation in Angiosperms

## *La formation du bois chez les Angiospermes*

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ABSTRACT

Wood formation is a complex biological process, involving five major developmental steps, including (1) cell division from a secondary meristem called the vascular cambium, (2) cell expansion (cell elongation and radial enlargement), (3) secondary cell wall deposition, (4) programmed cell death, and (5) heartwood formation. Thanks to the development of genomic studies in woody species, as well as genetic engineering, recent progress has been made in the understanding of the molecular mechanisms underlying wood formation. In this review, we will focus on two different aspects, the lignification process and the control of microfibril angle in the cell wall of wood fibres, as they are both key features of wood material properties.



RÉSUMÉ

La formation du bois est un processus de développement complexe, impliquant cinq étapes majeures : (1) la division des cellules à partir d'un méristème secondaire, appelé le cambium ; (2) l'élongation des cellules ; (3) le dépôt d'une paroi secondaire épaisse ; (4) la mort programmée des cellules ; et (5) leur imprégnation par des composés phénoliques conduisant à la formation du bois de cœur. Grâce au développement des techniques de génomique et aux travaux menés sur la caractérisation d'arbres transgéniques, certains mécanismes moléculaires impliqués dans la formation du bois commencent à être mieux connus. Dans cette revue, deux aspects importants pour la qualité du bois seront approfondis : la lignification et le contrôle de l'angle des microfibrilles de cellulose dans la paroi des fibres de bois.



## 1. Introduction

Wood is a renewable natural resource, providing timber (e.g. for house building, furniture, packaging), fibres (for pulp, paper, plywood) and energy (firewood). Recently, considering the widespread depletion of fossil energy resources, wood has become a potential source of lignocellulose-based biofuels. A product of high economical value, wood represented a major advance in plant evolution during the Cretaceous and allows trees to reach considerable heights and lifespans. The major functions of wood are to:

(1) conduct water from roots to the crown;
(2) support an ever-increasing mass of the growing tree, whilst adjusting to various environmental cues (wind, snow, slope, light);

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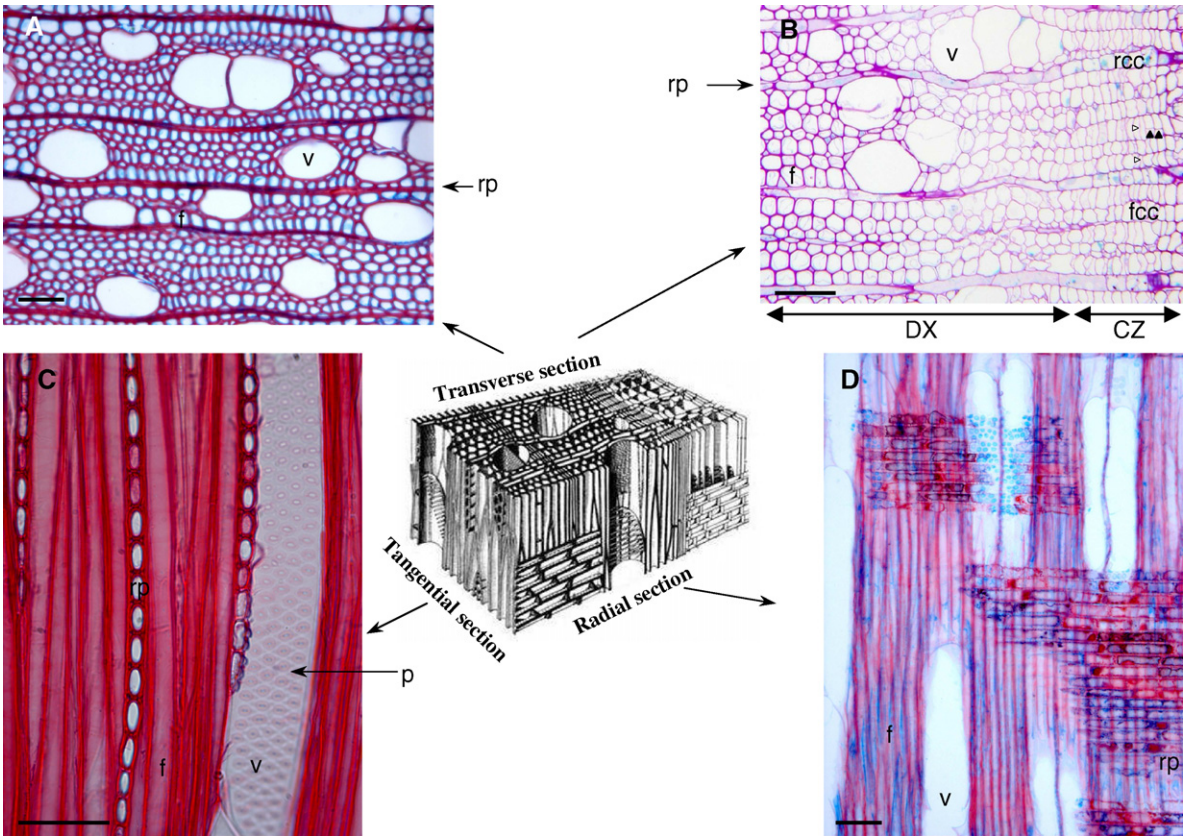


**Fig. 1.** Wood results from the three-dimensional association of different cell types, as represented on the central scheme (adapted from [91]) Transverse (A, B), tangential (C) and radial (D) sections from poplar (*Populus tremula x P. alba*, INRA clone 717-1B4), stained with safranine/Astra blue. CZ: cambial zone; DX: differentiating xylem; f: fibre; fcc: fusiform cambial cell; p: pit; rcc: radial cambial cell; rp: ray parenchyma; v: vessel. Empty arrowhead indicates a newly deposited tangential wall (periclinal division) in the cambial zone. Full arrowhead indicates a newly deposited radial wall (anticlinal division) in the cambial zone. The scale bar corresponds to 50 μm.

(3) contribute to tree growth over more than one year by storing temporary reserves.

In angiosperm trees, different cell types fulfil these three functions. Vessels and fibres are involved, respectively, in water conduction and mechanical support, while parenchyma cells, organized in rays, are involved in the radial transfer of assimilates between phloem and xylem, their temporary storage as starch or lipids, and their remobilization at the new season. Angiosperm wood is therefore heterogeneous. In the homogeneous wood of gymnosperms and some primitive angiosperms, the tracheids ensure both water conduction and tree support. In this review, we will focus on wood formation in angiosperms.

Wood formation is a complex developmental process, involving five major developmental steps, including

(1) cell division from a secondary meristem called the vascular cambium;
(2) cell expansion (cell elongation and radial enlargement);
(3) secondary cell wall deposition;
(4) programmed cell death;
(5) heartwood formation.

It has been extensively reviewed in terms of developmental biology [1–3]. In this review, we will first describe these different developmental steps, and then summarize the recent advances in deciphering molecular mechanisms underlying wood formation, thanks to the development of genomics on woody species. Two major wood features will be emphasized: the lignification process and the control of cellulose microfibril angle in the cell wall.

## 2. Wood formation, a complex developmental process

### 2.1. Wood is produced by the vascular cambium

Wood, also called secondary xylem, is produced seasonally at the periphery of the trunk by the vascular cambium. Derived from the procambium, this meristem is responsible for shoot and root secondary growth [4]. It is of major importance in the perennial life of trees as it regularly produces functional xylem and phloem cells, towards the inner and outer parts of the trunk, respectively. The cambium is made of initials, which divide to produce phloem and xylem mother cells [4]. When it is reactivated in the spring, in many species, the cambium starts to produce first phloem cells, sometimes several weeks before any xylem cells are produced. However, at