

# Wood Grain Pattern Formation: A Brief Review

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## ABSTRACT

In trees, new wood develops from a layer of stem cells called the vascular cambium. A subpopulation of cambial cells—the fusiform initials—are elongated and capable of coordinated reorientation in response to internal and external stimuli. Changes in the orientation of fusiform initials in turn leads to changes in the grain pattern of developing wood. This article reviews the phenomenon of cambial orientation, with an emphasis on a recent computer model that takes the plant hormone auxin as the

orienting signal. New model results are presented that demonstrate the surprisingly complex grain patterns that can emerge from simple initial conditions, in qualitative agreement with similar patterns found in wood. Lastly, an alternative theory of wood grain pattern that takes mechanical stress as the orienting signal is critically evaluated.

**Key words:** Auxin; Cambium; Fusiform initial; Pattern formation; *Populus*; wood grain

## INTRODUCTION

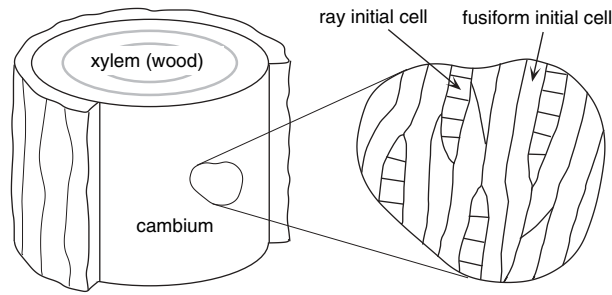
Because the topic of wood grain pattern formation will be new to many readers, we begin with a review of the relevant biology (for more thorough reviews, see Iqbal [1990], Larson [1994], and Savidge and others [2000]). “Wood” is the common word for the xylem that constitutes most of a tree stem or branch (see Figure 1). Wood is formed by the vascular cambium, a thin layer of meristematic tissue that lies under the bark. During the growing season the cells of the cambium undergo a process of repeated cell division and radial expansion. Cells retaining the cambial identity move gradually outward, while the daughter cells left behind differ-

entiate into mature xylem. The end-products of xylem differentiation are called *xylem elements* rather than cells, because maturation frequently terminates with enucleation or cell death. Seasonal variations in the activity of the cambium produce the familiar annual growth rings visible in stem cross sections.

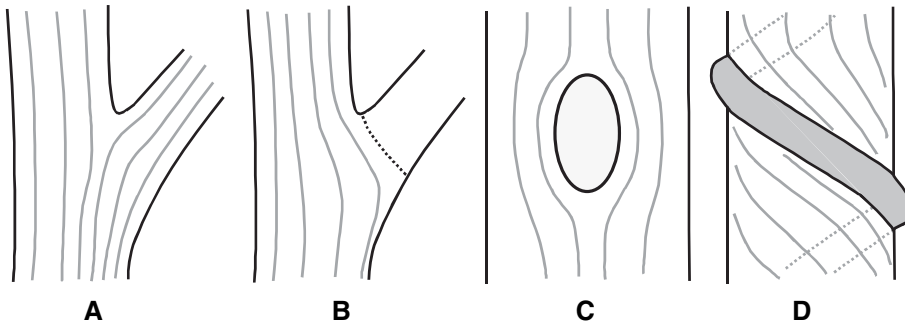
The vascular cambium is composed of two cell types: fusiform initials and ray initials (Figure 1) (Larson 1994). The cuboidal ray initials differentiate into radial strands of tissue in the xylem called *rays*. The elongated fusiform initials (aspect ratio > 10:1) differentiate into all other classes of xylem elements. It is likely that the layer of initials is only one or two cells thick in the radial direction, with adjacent layers of cells having a distinct genetic identity (Schrader and others 2004). The term *cambial zone* is sometimes used to describe the layer of initials and adjacent layers of dividing cells, and we adopt that convention here.

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**Figure 1.** Sketch of the tree stem anatomy discussed in the paper (not to scale). The bark has been removed from a portion of the stem to show the vascular cambium. The two cell types in the cambium can be distinguished based on their very different shapes as seen in tangential section. Ray initials are relatively small and square, and typically occur in lenticular aggregates. Fusiform initials may be hundreds of microns long. The orientation of the fusiform initials determines the grain pattern in newly formed wood.



**Figure 2.** Schematic illustration of grain reorientation in response to the death of a lateral branch [(a) and (b)], an elliptical wound (c), and constriction by a vine (d).

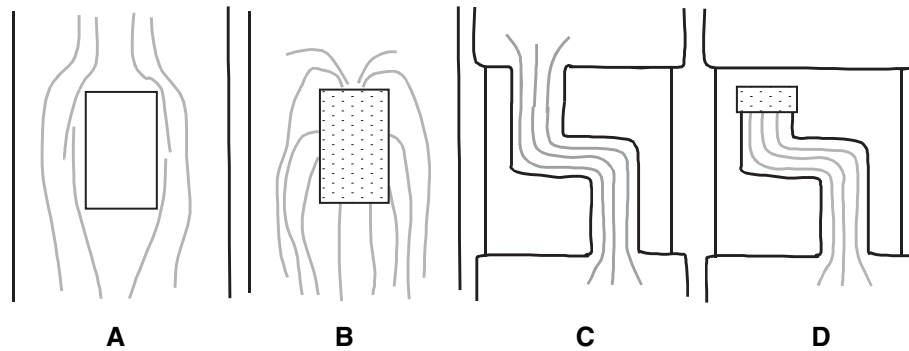
Wood grain is the direction of material anisotropy in wood. It is the chief direction of water movement through intact xylem (Rudinsky and Vite 1959; Kozłowski and Winget 1963; Zimmermann and Brown 1971; Shigo 1985; Schulte and Brooks 2003), and the preferred direction of crack propagation during mechanical failure (Mattheck and Kubler 1995). Grain is often visible on the surface of debarked branches and sawn lumber as the direction of slight striations and cracks (see Figure 5). The anisotropy is due to the fact that xylem elements are highly elongated and aligned parallel to one another. The orientation of the xylem elements reiterates the orientation of the fusiform initials that give rise to them, so a theory of wood grain pattern is properly a theory of cell orientation in the cambium. We will also use the word *grain* to describe the arrangement of fusiform cells in the cambium.

Because xylem is deposited gradually at the circumference of the branch, and because the orientation of the elements reflects the orientation of the fusiform initials, the mature xylem contains a nearly complete record of the orientation of cambial cells. A series of tangential sections through the wood thus reveals how cambial orientation changes with time (reviewed by Harris [1989] and Larson [1994]). Studies of this kind show that the orien-

tation of fusiform initials can change rapidly in response to stimuli. Some of the large-scale grain-reorientation processes that may be familiar to readers are the following: (1) When a lateral branch dies, the grain of the surviving stem will reorient to avoid the dead branch. (Figure 2a and 2b) (Phillips and others 1981; Kramer and Borkowski 2004). (2) When a tree stem suffers a localized injury, the grain of newly formed wood tends to circumvent the wound (Figure 2c) (Mattheck and Kubler 1995). (3) When a tree stem or branch is constricted by a climbing vine, the grain of the underlying branch will rotate to run parallel to the path of the vine (Figure 2d) (Harris 1969; Mattheck and Kubler 1995). Considering the role of grain direction in water transport and the mechanical strength of the stem, the coordinated reorientation of fusiform initials in response to injuries and branch death is critical to the survival of the tree. During these responses, the orientation of fusiform initials in the cambium can change by  $90^\circ$  in just a few weeks.

## THE ROLE OF AUXIN

The vascular cambium is specialized to accumulate and transport the plant hormone auxin (indole-



**Figure 3.** Schematic illustration of two experiments that indicate auxin plays a role in wood grain pattern formation. Panels (a) and (b) follow Fayle and Farrar's (1965) study of woody root cuttings in several hardwood species. A surface cut (white rectangle, panel a) that removes the cambium induces new vessels (gray) that circumvent the wound. Application of a lanolin paste containing 0.1% auxin to the cut (dotted rectangle, panel b) changes the orientation of new vessels so that many lead to the auxin source. Panels (c) and (b) follow Kirschner and coworkers' (1971) study of black locust (*Robinia pseudoacacia*) stems. They remove the bark from a portion of the stem, leaving only a zigzag bridge of cambium and bark intact. After several weeks, new vessels differentiate that follow the path of the bridge (c). Application of lanolin containing 1% auxin to the top of a severed bridge mimics the inductive role of the stem (d).

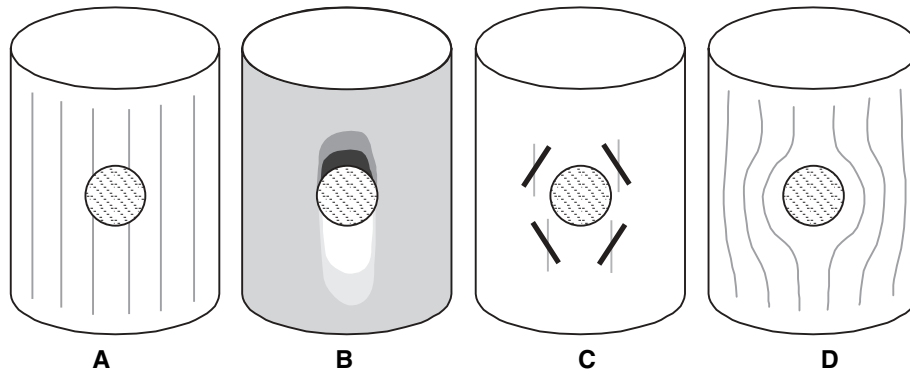
acetic acid; IAA). Studies using radiolabel or GC-MS techniques have repeatedly found that the radial distribution of IAA is limited to the cambial zone and adjacent layers of differentiating cells, with a maximum at or near the layer of initials (Nix and Wodzicki 1974; Lachaud and Bonnemain 1982, 1984; Uggla and others 1996; Tuominen and others 1997; Uggla and others 1998). In addition, members of the AUX/LAX and PIN gene families—encoding auxin influx and efflux facilitator proteins, respectively—show high levels of expression in cambial zone cells (Schrader and others 2003). Because of the proximity of the cambium to the conducting phloem (often just a few cells apart), it is difficult to rule out the presence of IAA in the phloem transport stream. However, auxin transport inhibitors that have no effect on phloem translocation still block nearly all auxin movement (Johnson and Morris 1989; Sundberg and others 1994). This finding supports the view that the main route of auxin transport is through the cambial zone cells. Furthermore, the IAA in tree stems moves basipetally (from the leaves to the roots) with a speed between 0.5 and 1.5 cm/h (Gregory and Hancock 1955; Hollis and Tepper 1971; Zamski and Wareing 1974; Little 1981; Odani 1985; Lachaud 1989), much slower than phloem-mediated transport and consistent with the chemiosmotic model of polar auxin transport (Mitchison 1980; Goldsmith and others 1981).

There have been many suggestions for the role of auxin in the cambium (Sundberg and others 2000; Aloni 2001). Aloni and Zimmermann (1983) suggested that the auxin concentration in the cambium

establishes the size and number of vessels (hollow xylem elements specialized for water conduction) in hardwood trees. Sundberg and coworkers suggested that the radial auxin gradient provides positional information to differentiating cambial cells (that is, a lower IAA concentration would indicate a larger radial distance from the initial layer) (Uggla and others 1996; Sundberg and others 2000). Although IAA may play a role in these phenomena, here we are interested in the evidence that IAA is involved in wood grain pattern formation, and thus in the orientation of fusiform cells.

The best evidence that IAA plays a role in the control of wood grain pattern comes from experiments in which the bark and cambium are removed from a portion of a woody stem (Figure 3). Fayle and Farrar (1965) worked with woody root cuttings of white elm (*Ulmus americana*), sugar maple (*Acer saccharum*), and American linden (*Tilia americana*). They removed rectangular patches of bark and applied to the wound a lanolin paste containing either 0.1% IAA or no IAA. After several weeks, new vessels developed near the wound. The new vessels formed a dense radial pattern around wounds supplied with IAA, and, conversely, they tended to circumvent the wounds that lacked IAA (Figure 3a and 3b). Many subsequent wounding experiments have found qualitatively similar results (Figure 3c and 3d) (Harris 1969; Kirschner and others 1971; Harris 1973; Savidge and Farrar 1984; Zagorska-Marek and Little 1986).

The conclusion of many authors, based on the above studies, is that the orientation of fusiform initials tends to parallel the presumed direction of



**Figure 4.** Schematic of the model. Panel (a) shows a portion of the cambium with vertical grain (gray lines), and a recent circular injury (disk). (b) Because auxin is transported basipetally (that is, downward), auxin accumulates above the wound and is depleted below (grayscale shows auxin concentration). (c) The fusiform initials (black bars) tend to rotate until their apical ends point towards the zone of locally high auxin concentration and their basal ends point away. (d) Newly formed grain (gray lines) circumvents the injury.

auxin flux through the cambium (Harris 1973; Zagorska-Marek and Little 1986; Sachs 1991). However, as remarked by Sachs (2000), this idea requires some care in its interpretation. Because the long axis of the fusiform cells is the probable direction of active auxin transport (Zagorska-Marek and Little 1986), it would naively seem that the orientation of the initials determines the direction of auxin flux, rather than the converse. To resolve this issue, Sachs suggested that cellular polarity is only redirected when the passive diffusion of auxin occurs at an angle to the existing cellular polarity (Sachs 2000). Although the details of his proposal differ significantly from the model discussed below, the functional distinction between the direction of active transport (the grain direction) and the direction of auxin diffusion is an important clarification.

## THE MODEL

In a series of recent articles we presented a mathematical model of auxin-mediated wood grain pattern formation (Kramer 2002; Kramer and Groves 2003; Kramer and Borkowski 2004). The goals of this work were (1) to find a closed set of partial differential equations describing the time evolution of grain patterns, (2) to solve the model under biologically relevant conditions, and (3) to refine the model by comparison with real wood grain patterns. The main points of the model are summarized in Figure 4.

The cambial zone and adjacent layers of differentiating cells is approximated as a two-dimen-

sional surface of negligible thickness, henceforth called the *cambial surface*. All quantities of interest are treated as continuous fields on this surface. The concentration of auxin (and any other substance of interest) is integrated through the radial thickness of the cambium and so has units of  $\text{ng}/\text{cm}^2$ . The model does not resolve cell-scale details of the tissue, and all quantities are treated as homogeneous on length scales less than 0.5 mm. Thus, the grain orientation field at any point  $(x,y)$  on the cambial surface may be defined by taking an appropriate average over the orientation of the fusiform cell walls in a volume centered on that point, spanning the thickness of the cambial zone and covering a tangential area of roughly  $(0.5 \text{ mm})^2$ . (Forest and others, 2006)

We denote the auxin concentration and grain orientation fields as  $m(x,y,t)$  and  $\mathbf{u}(x,y,t)$ , respectively. To date, the model has only been implemented on a flat simulation domain (but note that a flat domain can be mapped without deformation onto the surface of a cylinder). We thus limit the following discussion to vector calculus in the plane.

Next, we need to specify the flux of auxin within (that is, tangent to) the cambial surface. We denote the flux by  $\mathbf{j}(x,y,t)$ , and note that it has units of  $\text{ng}/\text{h}/\text{cm}$ . Following Zagorska-Marek and Little (1986), and by analogy with recent observations of the auxin efflux facilitator PIN1 in vascular tissues of *Arabidopsis* (Galweiler and others 1998), we assume the grain direction is the direction of active auxin transport. Thus, there is a contribution to the flux in the direction of  $\mathbf{u}$  with magnitude  $mv$ , where  $v$  is the speed of active transport. We take the representative value  $v = 1.0 \text{ cm}/\text{h}$  (Gregory and

Hancock 1955; Hollis and Tepper 1971; Zamski and Wareing 1974; Little 1981; Odani 1985; Lachaud 1989).

There are also diffusive contributions to the flux, characterized by the coefficients  $D_{\parallel}$  and  $D_{\perp}$ , parallel and perpendicular to the grain direction, respectively. It should be clarified that, because of the presence of cell membranes that the anionic form of IAA cannot cross, auxin is not free to diffuse through the tissue (Gutknecht and Walter 1980). Thus, contributions to the diffusion coefficients actually derive in part from the apoplastic pathway (that is, diffusion within cell walls) and in part from the transcellular pathway involving membrane-bound carriers. However, so long as the carriers are not operating near saturation, the result on scales greater than 0.5 mm is equivalent to Fick's law for diffusion (see Appendix A of Kramer [2002] for a derivation in the 1-dimensional case). We estimate  $D_{\parallel} = 0.05 \text{ cm}^2/\text{h}$  and  $D_{\perp} = 0.01 \text{ cm}^2/\text{h}$ , although the later value is only an order of magnitude estimate (Kramer 2002). The complete expression for the flux of auxin is

$$\mathbf{j} = (-D_{\parallel}\nabla_{\parallel}m + v m)\hat{\mathbf{u}} + (-D_{\perp}\nabla_{\perp}m)\hat{\mathbf{w}} \quad (1)$$

where  $\mathbf{w}$  is a vector field perpendicular to  $\mathbf{u}$ , hats denote unit vectors ( $\hat{\mathbf{u}} = \mathbf{u}/u$ ), and the operators  $\nabla_{\parallel} = \mathbf{u} \cdot \nabla$  and  $\nabla_{\perp} = \mathbf{w} \cdot \nabla$  describe the gradient parallel and perpendicular to the grain direction, respectively.

We also use the fact that auxin moves through transporting tissues with relatively little conversion (Lachaud and Bonnemain 1984; Sundberg and Ugglä 1998). As a first approximation, we neglect the effects of auxin biosynthesis, conjugation, and metabolism in the cambium. This is expressed using the continuity equation

$$\partial m / \partial t = \nabla \cdot \mathbf{j} \quad (2)$$

By contrast with auxin transport, the cell and molecular biology of fusiform reorientation is poorly understood. Our equation for the grain as a function of time may be described as "minimal" or "phenomenological." This is to say, it is the simplest equation consistent with the phenomena we are trying to describe. The key observation of Sachs (2000)—that the diffusive flux of auxin is the likely orienting signal—is captured by relating the rotation of the grain vector to the gradient of the auxin concentration as measured across the grain. In terms of the grain angle  $\phi = \tan^{-1}(u_y/u_x)$ , this gives a chemotropic contribution to the evolution equation with the form  $\partial\phi/\partial t \sim -\nabla_{\perp}m$ .

Computer simulations using only the chemotropic term give grain fields that develop sharp

bends and other failures of the continuity condition. We therefore find it necessary to add a Laplacian term to the model,  $\partial\phi/\partial t \sim \nabla^2\phi$ , to maintain a sufficiently smooth grain pattern. Although it is introduced *ad hoc*, the Laplacian term captures the fact that fusiform initials tend to line up parallel to their neighbors. When we originally introduced the Laplacian, we suggested an analogy with the spontaneous alignment of elongated cells and other objects under crowded conditions, possibly mediated by mechanical or paracrine signals (Edelstein-Keshet and Bard Ermentrout 1990; De Gennes 1995; Mogilner and Edelstein-Keshet 1995). More recently it occurred to us that the Laplacian may be explained if individual fusiform cells have a shape homeostasis mechanism (Chen and others 1997). For example, serial tangential sections of xylem in Norway spruce (*Picea excelsa*) show that bent fusiform initials have difficulty maintaining the cambial identity and are preferentially eliminated from the cambium (Wloch 1976).

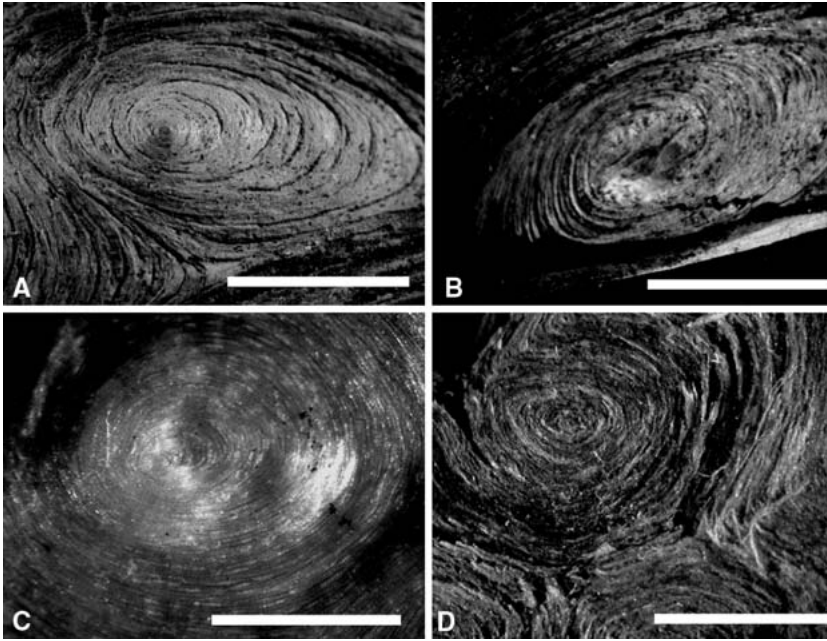
Combining the above terms gives an evolution equation for the grain angle

$$\frac{\partial\phi}{\partial t} = K\nabla^2\phi - \mu\nabla_{\perp}m, \quad (3)$$

where  $K$  and  $\mu$  are model parameters that characterize the strength of the Laplacian and chemotropic terms, respectively (Kramer 2002). Equations (1)–(3), together, provide a complete set of nonlinear partial differential equations describing the relationship between grain angle and auxin concentration in the cambium.

It is interesting to note that Eq. (3) is related to an empirical description of wood grain in use since the 1980s (Phillips and others 1981; Pellicane 1994). The "flow–grain analogy" is used by wood product engineers to model the influence of knots on the surrounding grain pattern. It assumes that the grain field near a knot is everywhere tangent to the flow field of an inviscid fluid around an obstacle of the same shape (Wilcox 2000). It is not hard to show by direct substitution that the grain angle field given by this method satisfies  $\nabla^2\phi = 0$ . In other words, the  $\mu = 0$ , time-independent limit of our model is equivalent to the flow–grain analogy.

Although Eq. (1)–(3) are adequate for many applications, a discretization of these equations on the square lattice has the drawback that topological defects (for example, the core of a circular grain pattern) are immobilized by pinning to the lattice. Thus, attempts to simulate the formation and evolution of disordered grain patterns (see the next section) require a revision to the model.



**Figure 5.** Whirled grain patterns in (a) white pine (*Pinus strobus*), bar = 8 mm, (b) Eastern hemlock (*Tsuga canadensis*), bar = 10 mm, (c) quaking aspen (*Populus tremuloides*), bar = 1mm and (d) red maple (*Acer rubrum*), bar=4 mm. Digital photographs are contrast enhanced to show grain patterns.

In an earlier work (Kramer and Groves 2003), we overcame defect pinning by working with the grain vector field and dropping the condition that  $u = 1$

$$\frac{\partial \mathbf{u}}{\partial t} = K \nabla^2 \mathbf{u} + \mu \left[ -\frac{1}{2} (3 - u^2) \nabla m + \mathbf{u} \nabla_{\parallel} m \right] + \frac{2K}{L^2} \mathbf{u} (1 - u^2), \quad (4)$$

where  $L$  is a length. Eq. (4) reduces to Eq. (3) when  $u = 1$ . The rightmost term in Eq. (4) is chosen to give a grain field whose magnitude is approximately 1 almost everywhere, but decreases to near 0 within a distance  $L$  of sites where the grain direction is changing rapidly. Thus,  $L$  is a defect core size. Eq. (1), (2), and (4), together, constitute the revised model.

Values for the parameters in Eq. (4) may be determined as follows. Because the grain field is defined to be an average over length scales less than 0.5 mm, we set  $L = 0.25$  mm. In Kramer and Groves (2003) a comparison between simulation results and observed grain patterns in cottonwood (*Populus deltoides*) gave the estimates  $K = 5 \times 10^{-7}$  cm<sup>2</sup>/h and  $\mu = 10^{-4}$  cm/h/ $\bar{m}$ , where  $\bar{m}$  is the average concentration in the cambial region during the growing season, of order 10 ng/cm<sup>2</sup> (Tuominen and others 1997). As expected, the time scale for changes in the grain is several orders of magnitude slower than the auxin dynamics.

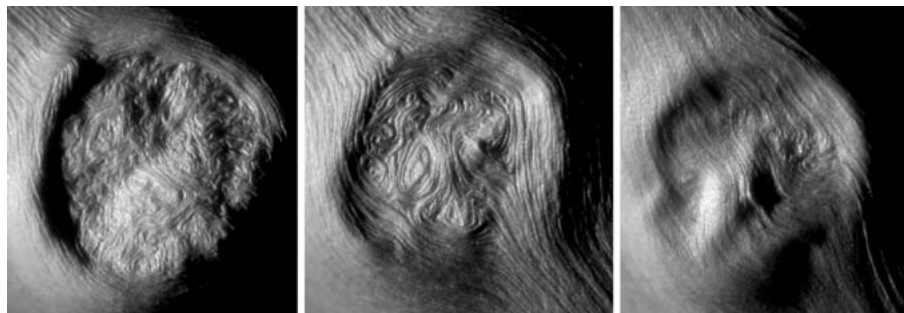
## WHIRLED GRAIN

Simulations of the model described above reproduce the qualitative features of wood grain dynamics as

illustrated in Figures 2 and 3 (Kramer 2002; Kramer and Borkowski 2004). In model branch junctions, the auxin flux out of a lateral branch determines the amount of grain it “captures” from the subjacent stem. Lateral branches with a higher level of auxin export capture more grain. When a branch dies, auxin export stops and the grain reorients to circumvent the dead branch. Similar conclusions apply to injuries with or without an exogenous supply of auxin.

If wood grain were limited to the fairly simple patterns like those shown in Figures 2 and 3, then there might not be enough variety in nature to refine the quantitative aspects of the model, or even to distinguish it from competing models. However, there is a class of grain patterns that do permit these refinements (Kramer 1999; Kramer and Groves 2003). *Whirled grain* is the name given to patterns with a complicated topology like those shown in Figures 5, 6, and 8. For definiteness, we define whirled grain to be any grain pattern that has at least one circular arrangement of initials greater than 0.5 mm in diameter. A lower limit on the size is necessary because the model is only intended to describe the collective behavior of large numbers of initials. Contorted xylem elements that occur in isolation are excluded from consideration (Sachs and Cohen 1982; Kurczynska and Hejnowicz 1991).

Whirled grain is known to occur in more than a dozen tree species, including both hardwoods and softwoods (Figure 5 and Table 1). Its occurrence is always limited to specific locations in the tree, commonly at branch junctions and in places where



**Figure 6.** Wood grain on the debarked surface of a cottonwood (*Populus deltoides*) branch 3 cm in diameter. Three healed branch abscission zones are shown, arranged from youngest (left) to oldest (right). The grain pattern of the new wood is initially disorganized, but gradually returns to a straight condition. These changes in grain pattern take 1–3 years. All three abscission zones are approximately 8 mm in diameter.

**Table 1.** Species in which Whirled Grain Has Been Reported

| Species                     | Common name       | Reference                     |
|-----------------------------|-------------------|-------------------------------|
| <i>Abies alba</i>           | Silver fir        | Neeff 1914                    |
| <i>Acer rubrum</i>          | Red maple         | See Figure 5                  |
| <i>Eucalyptus sp.</i>       | Eucalyptus        | Andre 2000                    |
| <i>Fagus sylvatica</i>      | European beech    | Neeff 1922                    |
| <i>Fraxinus excelsior</i>   | Common ash        | Hejnowicz and Kurczynska 1987 |
| <i>Melia azedarach</i>      | Chinaberry        | Lev-Yadun and Aloni 1990      |
| <i>Pinus strobus</i>        | White pine        | See Figure 5                  |
| <i>Populus deltoides</i>    | Cottonwood        | Kramer 1999                   |
| <i>Populus tremuloides</i>  | Quaking aspen     | See Figure 5                  |
| <i>Quercus calliprinos</i>  | Kermes oak        | Lev-Yadun 2000                |
| <i>Quercus ithaburensis</i> | Valonia oak       | Lev-Yadun and Aloni 1990      |
| <i>Tilia cordata</i>        | Littleleaf linden | Hejnowicz and Kurczynska 1987 |
| <i>Tsuga canadensis</i>     | Eastern hemlock   | See Figure 5                  |
| <i>Tsuga mertensiana</i>    | Mountain hemlock  | Sutton and Sutton 1981        |

*Whirled grain is defined to be at least one circular grain pattern greater than 0.5 mm in size (isolated circular vessels not counted).*

newly forming tissue is advancing across an open wound or over the stump of a dead lateral branch. In some species the occurrence of whirled grain is a predictable outcome of development, whereas in others it is infrequent and sporadic.

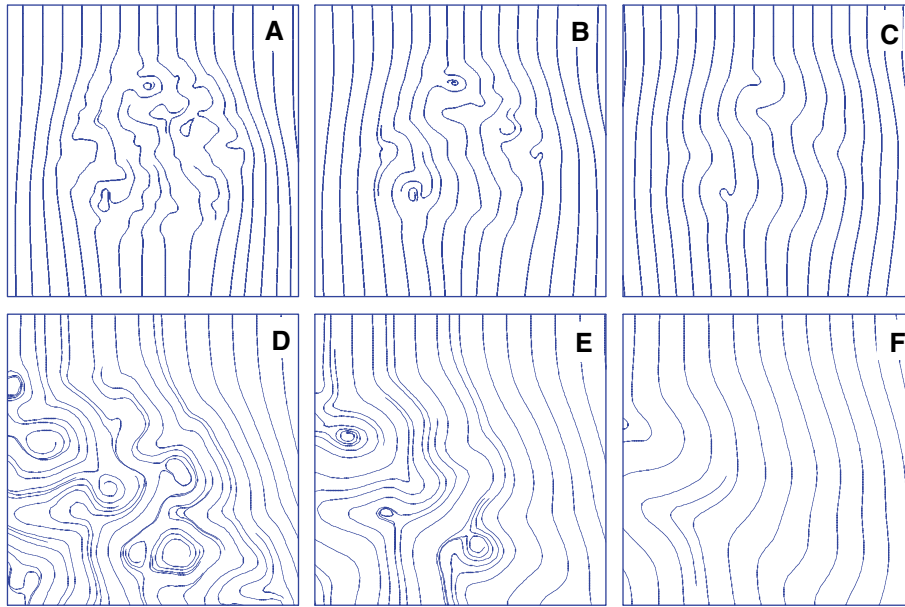
Whirled grain patterns have been used by several authors to dissect developmental cues in the cambium (Hejnowicz and Kurczynska 1987; Lev-Yadun and Aloni 1990; Andre 2000). The earliest example we know of is Fritz Neeff, who in the early 1900s published two remarkable monographs on dynamic changes in grain pattern (Neeff 1914, 1922). In his 1922 paper, Neeff observed that whirled grain patterns are consistent with a polar orienting signal in the cambium. Many of the illustrations in that article include arrows superimposed on sketches of wood grain, implying that wood grain has vector symmetry. Neeff also included many sketches of the

time-evolution of whirled grain, clearly showing the creation and elimination of circular patterns.

Whirled grain has been a valuable test case during the development of our model. We used whirled grain patterns to argue that wood grain may be treated as a continuous vector field, and that the continuity condition only breaks down at isolated points and lines—called topological defects (Kramer 1999). We subsequently showed that each kind of topological defect observed in cottonwood also occurs in model simulations, including circle patterns, patterns where three or four grain lines meet (Y- and X-patterns), and line discontinuities (Kramer and Groves 2003). We also used a digital analysis of whirled grain images to estimate the ratio  $K/\mu$  in cottonwood (Kramer and Groves 2003).

The use of topological defects to constrain mathematical models has had great success in the physics





**Figure 7.** Model results showing the development of whirled grain in a circular abscission zone 10 mm in diameter. Panels (a)–(c) show the grain pattern after 25, 50, and 100 days of active growth. Only enough grain lines are drawn to give a sense for the curvature of the grain pattern. The simulation domain is  $(24 \text{ mm})^2$ , but for clarity only the central  $(15 \text{ mm})^2$  square region is shown. Panels (d)–(f) magnify a portion of panels (a)–(c), respectively,  $(6 \text{ mm})^2$  in size, to illustrate the detailed topology of the grain pattern. Parameter values are as described in text. Initial conditions are straight grain outside the abscission zone and randomly assigned grain directions inside. Initial auxin concentration is uniformly  $10 \text{ ng/cm}^2$ , corresponding to an initial flux of  $10 \text{ ng/cm/h}$  per hour. Boundary conditions are periodic in both  $x$  and  $y$ .

of liquid crystals and other partially ordered inorganic systems (Davis and Brandenberger 1994; De Gennes 1995). In biological pattern formation, topological defects have received less attention. Examples of topological defects in biology are fingerprint whorls (Galton 2005), “pinwheels” in the orientation map of the mammalian visual cortex (Bonhoeffer and Grinvald 1991), and whorls in the patterns of hair and fur (for example, on the crown of the head) (Kidd 1903; Wunderlich and Heerema 1975). In the first two cases, the creation of topological defects and their spatial organization have been used as benchmarks for computer models of development (Lee and others 2003; Kucken and Newell 2005).

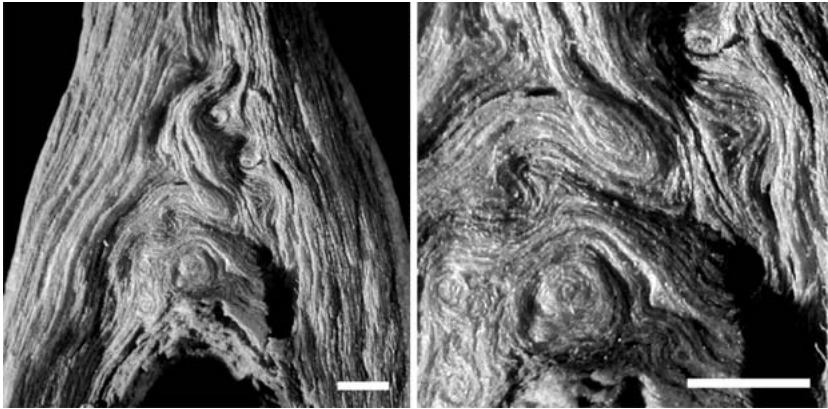
In Kramer and Groves (2003) we modeled a whirled grain pattern by starting with a random grain field and evolving it over time. This is obviously an artificial initial condition, because most of the grain in a real tree is relatively straight. Here we return to the topic of whirled grain generation, with a focus on the physiological events in the tree that give rise to these patterns.

Trees in several genera have evolved a specialized mechanism for casting off dead branches, analogous to the abscission of leaves and fruit (Eames and MacDaniels 1925). We have made a study of this

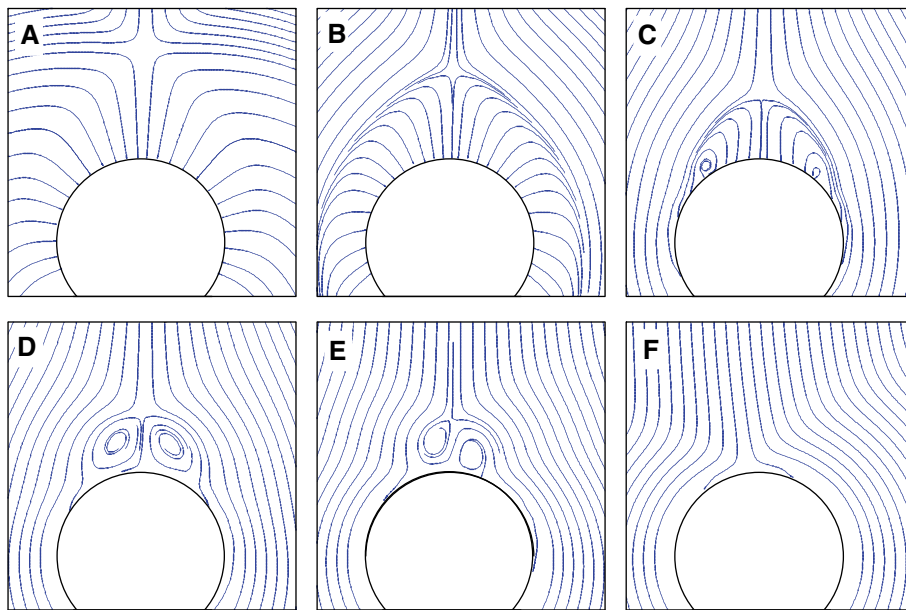
process in *Populus*. Branches with a diameter as large as 5 cm maintain a zone of relatively soft tissue at their base. If the branch loses vitality, the tissue in this zone weakens and the branch detaches. The exposed abscission zone fills with a layer of parenchyma—soft tissue composed of small cells that lack a cambial identity. Within a few weeks of branch abscission, a thin layer of cells within the parenchyma converts to a cambial identity. New fusiform initial cells begin to elongate, but initially they have no preferred direction (Novitskaya 1998). The result is a thin, circular disk of cambial tissue where the grain field is randomized. Only gradually do localized regions of ordered initials develop. Over the next few growing seasons, the grain eventually returns to a defect-free condition. Figure 6 illustrates three abscission zones in cottonwood at different stages of the healing process. Figure 7 shows model results for an analogous situation.

Whirled grain also tends to form in the region immediately above (more accurately, distal to) a recently dead lateral branch. Figure 8 shows an example of whirled grain in quaking aspen (*Populus tremuloides*) that arose when the subjacent lateral died. The development of whirled grain under these conditions is unpredictable; the main stem from which we excised the sample shown in Figure 8 had





**Figure 8.** Wood grain on the debarked surface of a quaking aspen (*Populus tremuloides*) stem 23 cm in diameter. Whirled grain patterns are visible in the region above a dead lateral branch. Although the pattern changes with time, the presence of whirled grain above the branch can persist for decades. Bar = 2 mm.



**Figure 9.** Model results showing the development of whirled grain in the zone above a lateral branch 6 mm in diameter (circle). At time 0 the lateral stops exporting auxin. Panels (a)–(f) show the grain pattern after 0, 2, 4, 5, 10, and 40 years (approximating one growing season as 100 days of active growth). The total simulation domain is 60 mm tall  $\times$  34 mm wide. For clarity, only the (10 mm)<sup>2</sup> square region immediately above the branch is shown. Parameter values are as described in text. Boundary conditions: There is a homogeneous auxin source along the top edge of the simulation domain with a flux of 10 ng/cm/h and, before time 0, a second auxin source around the circumference of the lateral branch with a flux of 15 ng/cm/h. Auxin that passes out the bottom or side edges of the simulation domain is removed.

several other dead laterals with no whirled grain. Figure 9 shows analogous model results. We see that whirled grain is “nucleated” in zones where the grain direction has a large gradient, then expands to fill the zone above the dead branch. Notably, the occurrence of whirled grain in the model is also sporadic, showing a subtle dependence on the initial conditions (that is, the grain pattern near the live lateral branch). The observation that whirled grain can be nucleated in regions where the grain direction is changing rapidly appears in Neeff (1922) and Lev-Yadun and Aloni (1990). The model provides

the first clear indication that auxin chemotropism is an adequate explanation for this phenomenon.

## THE MECHANICAL MODEL

There is a competing model of wood grain patterning that should be discussed in a review of this sort. Claus Mattheck and coworkers have published extensively on the idea that evolution has steered various aspects of tree growth toward a mechanical optimum (Mattheck 1991; Mattheck and Kubler

1995; Mattheck 1998). Regarding wood grain patterning, they suggest that wood grain tends to rotate until it is parallel with the direction of largest tensile stress in the tree stem. There is some precedent for this idea in the hypothesis that some trees develop spiral grain as a response to wind-imposed torques on the tree crown (Wentworth 1931; Harris 1989; Eklund and Sall 2000), and in the observation that stresses imposed on a growing plant tissue can influence the orientation of newly forming cell walls (Lintilhac and Vesecky 1981, 1984). The theory of Mattheck and coworkers makes little explicit mention of the vascular cambium, but presumably they are suggesting that the fusiform initials interpret mechanical stresses within the cambium as an orientating signal.

The mechanical theory of Mattheck and coworkers has several drawbacks. (1) To our knowledge the theory has not yet been presented as a complete set of differential equations, so it is difficult to evaluate its merits. (2) No attempt is made to account for the fact that the cambium is a soft tissue sandwiched between the much stiffer wood and bark. Instead they approximate the cambium as a flat plate subject to stresses only along its edges (Mattheck and Kubler 1995, pg 533). This is not likely to be a good model for the distribution of stresses in the cambium. (3) It is not clear how the mechanical theory can account for the experiments discussed above (see Fig. 3), in which auxin application causes significant changes in the grain pattern. (4) As we remarked in the previous section, whirled grain patterns exhibit a vector symmetry that is more restrictive than a strictly mechanical theory can account for (Neeff 1922; Kramer 1999). (5) The preponderance of evidence suggests that spiral grain in tree stems is determined by factors other than wind-imposed torques (reviewed in Harris 1989). Thus, although we do not rule out a role for mechanical stress in grain pattern formation, it is unlikely to be the primary orienting signal.

## PROSPECTS

In this article we have briefly reviewed a model of wood grain pattern formation as developed by Kramer and coworkers (Kramer 2002; Kramer and Groves 2003; Kramer and Borkowski 2004). The model combines two dynamic processes, characterized by widely separate time scales: auxin transport through the vascular cambium (time scale minutes to hours) and fusiform initial reorientation (time scale days to weeks). We developed a set of partial differential equations that captures the qualitative

features of this system in the simplest reasonable way. Despite these simplifications, the model manages to reproduce much of the phenomenology of wood grain pattern. This includes straight and helical grain on a cylindrical branch, the dynamics of changing grain patterns at branch junctions, and the generation of specific classes of topological defects in whirled grain. The model is thus a proof-of-principle that auxin chemotropism may be the primary orientating signal in the cambium.

The model is intended to be a starting point for more realistic approaches, including, for example, (1) more accurate hormonal dynamics including auxin biosynthesis and metabolism (Lachaud and Bonnemain 1984; Sundberg and Uggla 1998); (2) gene signaling networks, for example possible feedback between auxin concentration and cell carrier expression (Davies 2004; Vieten and others 2005); (3) subcellular resolution of the cell wall geometry, auxin concentration, and auxin carrier localization (Kramer 2004; Swarup and others 2005); (4) oscillations of cambial orientation in some species, possibly mediated by the chemotropic term, that lead to wavy grain patterns (Harris 1989); and (5) variation in model parameter values with developmental stage, season, location in the tree, and between species (Hollis and Tepper 1971; Little 1981; Lachaud and Bonnemain 1984). These improvements await the results of additional experiments.

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