Physiological aspects of wood formation

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Functionally the stem of a tree consists of three tissues — the phloem, the vascular cambium and xylem. The phloem and xylem arise from the vascular cambium. The cambium forms a complete sheath in the tree covering the xylem from the root tips to the tips of the twigs. Each Spring when the cambium becomes active it starts to divide and splits off both new phloem and new xylem mother cells. These cells then pass through a process of differentiation, elongation and maturation before they are recognisable as xylem and phloem cells.

However, differences are apparent between ring porous trees on the one hand and diffuse porous and coniferous trees on the other in relation to the initiation of secondary growth. In conifers and diffuse porous hardwoods, vascular cambium activity begins just below the buds as they become active and then activity spreads gradually down the tree as the leaves open. Removal of buds and twigs from such trees in early Spring prevents cambial initiation. The inference is that auxin produced by the buds moves down the phloem and initiates cambial activity. Thus the spread of cambial initiation down the stem is determined by the movement of auxin.

In ring porous trees, cambial activity starts before the buds become active, beginning all over the tree at approximately the same time. The first large vessels in *Fraxinus* sp. for example, are formed before the leaves grow out. This suggests that there is either a great deal of auxin precursor present in the dormant cambial zone or that the cambial zone can manufacture its own auxin activator. Digby and Waring (1966) have suggested that the actual precursor is probably tryptophan and that this is converted to indole — 3 — acetic acid (IAA) at the time of cambial initiation. In ring porous hardwoods then a ring of large diameter vessels is formed over the whole tree from trunk to twig at almost the same time and before the leaves appear. Decapitation will not prevent cambial initiation. Auxin apparently is still necessary to initiate cambial activity, but in ring porous trees it does not have to come directly from expanding buds and leaves where it is produced.

However, there is an obvious dissimilarity between xylem formed at different times during the growing season. In conifers the earliest formed tracheids have a greater radial diameter and a thinner secondary wall than those formed later in the growing season. Likewise in hardwoods there is a decrease in vessel diameter from the

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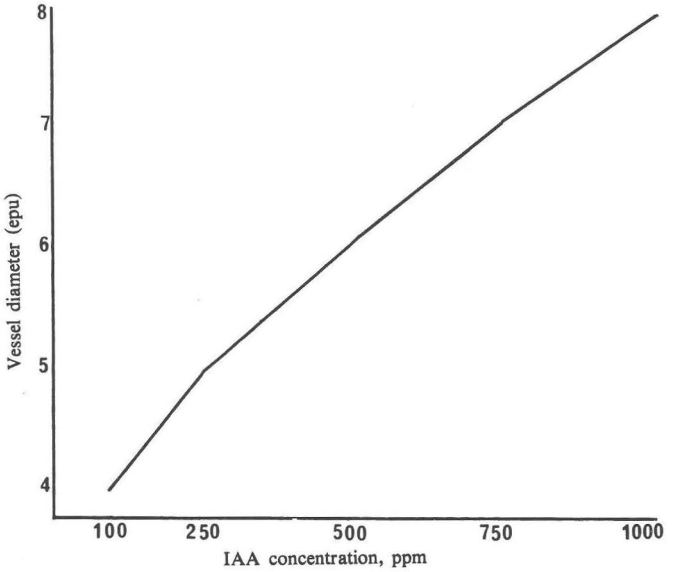
beginning to the end of the yearly xylem increment. The terms earlywood (Springwood) and latewood (Summerwood) are used respectively to distinguish between the initially less dense and the subsequently denser wood, formed in a growing season.

This transition from earlywood to latewood formation is associated with two aspects of xylem cell differentation: (1) decreasing cell size and (2) increasing cell wall thickness. It is now generally accepted that tracheid diameter is controlled by auxins produced in actively growing apical points. The most vigorous shoots with their developing needles appear to be the principal sources of these auxins. Auxins produced in the actively growing shoots are transmitted to the developing tracheids in the stem. Supportive evidence for this theory is found in experiments on the effect of photoperiod on wood formation in young trees of *Pinus resinosa* (red pine). In trees grown under long days (18 hour photoperiod) earlywood is formed and this is correlated with a high auxin content in the rapidly growing shoot (Larson, 1962). Shoot growth and auxin content are both decreased by transfer for two weeks to short days (8 hour photoperiod) and latewood is now formed. Transfer of red pine from the short day regime back to long days causes renewed shoot growth, an increased auxin content and the deposition of a new increment of earlywood. This is a situation in which a false growth ring is produced.

Direct evidence for the control of cell size by auxin is seen in experiments in which IAA is applied to decapitated stems of pine growing under short day conditions. Wide tracheids are induced in response to IAA instead of the narrow ones formed previously (Larson, 1962). The normal acropetal progress of latewood formation is then explained by the decreasing availability of auxin, especially to the lower trunk, as shoot growth in the crown declines. Auxin is available at high concentrations and for a longer time at successively higher levels in the trunk and branches. Hence, the sequence of latewood formation, at least in terms of cell size, is acropetal. Such auxin gradients have been demonstrated within tree stems.

A similar case can be made for the regulation of vessel diameter in ring porous hardwoods. When *Robinia pseudoacacia* plants were grown under short days for three weeks, shoot growth, cambial activity, and xylem production all ceased (Digby and Waring, 1966b). When the plants were decapitated and IAA in varying concentrations together witha constant low level of gibberellic acid (GA) applied to the decapitated stem, cambial activity resumed and xylem was formed. In the experimentally induced xylem there was a clear correlation between vessel member diameter and the concentration of applied auxin (Fig. 1).

FIGURE 1
The effect of applied IAA on radial vessel diameter in *Robinia pseudoacacia* Concentration of GA was 100 ppm in all treatments. (After: Digby and Wareing, 1966)



This work also showed that auxin and gibberellin act together in promoting normal xylem development. In addition, there is evidence that developmental processes in the vascular cambium involve the interaction of other factors. For example, in stem segments of willow (*Salix fragilis*), Robards *et. al.* (1969) discovered that the number of cells in the differentiating xylem undergoing extensive growth in width (presumptive xylem members) was increased by separate application of an array of substances including auxins, G.A., 6 — furfurylaminopurine (a cytokinin), sucrose and myco-inosital (Table 1).

TABLE 1
Effect of chemicals on Xylem Differentiation in stem segments of willow. (After: Robards *et al.*, 1969).

Treatment	% of vessel member among Differentiating Xylem cells
1. Control	2.8 ± 0.6
2. I A A	9.6 ± 0.5
3. G.A.	9.2 ± 1.1
4. 6 — furfurylaminopurine	7.2 ± 0.5
5. Sucrose	12.6 ± 0.8
6. Myco — inosital	13.1 ± 1.7
7. 2 + 3 + 4 + 5	31.5 ± 4.7

We may conclude then that the enlargement of differentiating xylem members is regulated by seasonally varying concentrations of endogenous substances flowing from the growing shoot and that the transition from earlywood to latewood production occurs at the time of cessation of extension growth of the shoot.

However, tracheid diameter is only one measure of tracheid morphology and the second measure — cell wall thickness is also involved in latewood formation. Many studies have shown that cell diameter and cell wall thickness are to a large extent independent and regulated by different physiological processes. Whereas cell diameter is primarily determined by the amounts of growth promoting substances reaching a developing cell, wall thickness appears to be determined by the amount of photosynthate reaching a developing cell.

In the developing shoot, leaf or needle elongation follows shoot extension, and as the new foliage begins to elongate,it requires large amounts of photosynthate. New foliage is unable to manufacture sufficient photosynthate for its own building needs, so it imports photosynthate from other parts of the tree. Therefore, a large proportion of the stored and newly manufactured photosynthate in a tree is directed towards the developing foliage and shoot. Gordon and Larson (1968) have shown that during the third to the seventh week after bud break considerable photosynthate is directed upwards into the terminal shoot. At this time thin walled tracheids are formed in the lower stem. Eventually, the current year foliage reaches a development stage when it is self-sufficient in photosynthate and much more building material becomes available within the tree for wall thickening. Thus it has been shown experimentally that increases in cell wall thickness in differentiating cells of the lower stem occur 7-9 weeks after bud break. At this time shoot extension is almost completed for the year and new foliage is almost mature (Richardson, 1964).

Another probable factor in determining the thickness of cell walls is the length of time that cells remain in the cell wall thickening phase. Whitmore and Zahner, (1966) have proposed that earlywood cells differentiate so fast that cell walls remain thin, but latewood cells stay near the phloem for a much longer time and wall thickening proceeds for a longer time. In addition Daley and Leighton, (1968) have shown that short days cause the production of an inhibitor that permits walls to be synthesized for a longer period, perhaps by retarding the breakdown of the protoplasm. It seems quite likely that all of those theories are correct and that they should somehow be combined. For instance, conditions of high net photosynthesis might increase the rate of wall-thickening, whereas an inhibitor could

increase the length of time for thickening. Both would result in a thicker wall.

Irrespective of the mechanisms involved there seems to be no longer any doubt but that the transition from earlywood to latewood-production is associated with:

1. A declining level of growth promoting substances as extension growth in the crown slows down or ceases.
2. The availability to the differentiating xylem cells of products of photosynthesis, associated with the maturation of foliage of the current year.

In any consideration of wood quality then, it is important to remember that it is events taking place within the crown of the tree which determine the course of wood formation. Thus any environmental factor that causes a temporary suppression of terminal growth will result in a reduction of tracheid or vessel diameter in some part of the stem, and any factor that promotes vigorous terminal growth activity will result in increased cell diameter. Thus the crown size and vigour largely controls the type of wood deposited. Since crown size and vigour can be very largely controlled through silvicultural practices such as spacing, thinning and pruning, it can be readily appreciated that the quality of wood produced can be silviculturally controlled.

Manipulation of stand density is perhaps the most powerful method available to the silviculturalist for regulating wood quality. As a general rule, the open grown tree will have a long crown, extending almost to ground level. It will have very actively growing apical meristems and foliage. In addition there will be very little by way of an auxin gradient, since all points in the central stem will be very near the crown. In addition the crown will manufacture very little photosynthate for export to the main stem, consuming almost all of its manufacture. Hence in an open grown tree or in young trees at wide spacing the wood produced will consist of cells with wide diameters and thin walls. These are the characteristics of juvenile wood.

As a stand of trees develops, the crowns gradually recede upwards with age and stand closure. As this development proceeds the quality of the wood changes and latewood begins to be laid down at the base of the stem, though cells with juvenile traits will still predominate in the wood laid down within the live crown. This is why one invariably finds a core of juvenile wood surrounding the pith within any woody stem. In general then it may be said: "that the width of the zone of juvenile wood depends upon the rapidity with which the crown recedes," i.e. upon the rapidity with which the plantation closes canopy. This latter of course depends to a large extent upon initial espacement.

Once a plantation has closed canopy stand density can be regulated by thinning. The purpose of thinning is to provide more growing space for the remaining trees. Thus, following a heavy thinning, upward crown recession slows, the foliage throughout the crown thickens and the efficiency of the crown as a whole increases. The concentrations of growth promoting and growth inhibiting substances increase all over the tree. The availability of photosynthate also increases. Measurable changes in wood quality, such as an increase in the proportion of juvenile wood, a more gradual latewood transition down the stem, and a decrease in the percentage of latewood in the lower stem, follow. The intensity of thinning determines the degree of response.

Pruning of live branches in analogous to artificially creating a stand-grown tree from an open grown one. The purpose of "green pruning" is to produce a longer length of clear wood by removing the lower branches. However, the resulting change in crown size may accentuate gradients of auxin and other growth promoting substances. Hence the proportion of juvenile wood within the crown may decrease, the latewood transition down the stem may become more abrupt and the percentage of latewood in the lower stem may increase.

The primary effect of fertilization is on crown and root development. The effect on wood formation is secondary, and is the result of crown development by increasing the photosynthetic efficiency of the foliage. Thus heavy fertilization of young stands can result in a lowering of the wood quality because it increases crown and branch size and delays natural prunning. Young trees are in the stage of juvenile wood production and fertilization not only enlarges the core of juvenile wood but also delays the transition to mature wood.

Fertilization of pole-stage stands has been shown to have a much smaller effect upon wood quality. In pole stands, the crowns have generally closed and the base of the live crown has receded up the stem. Because of this crown-stem relation, moderate fertilization in pole stands generally results in increased growth of both earlywood and latewood with relatively little change in wood quality. (Table 2).

TABLE 2
Effect of fertilizer upon wood properties in 37 year old Norway Spruce. (After: Seibt, 1973)

Fertilizer	Ring Width (mm)	% Latewood	Density g./cm ^{3}
0	1.64	20.4	0.497
NPK	2.01	23.8	0.492
NKCa	1.95	22.0	0.497
NPCa	2.16	16.0	0.478
PKCa	1.92	22.7	0.500
NPKCa	2.18	20.5	0.490

From this brief *resume*, it is apparent that environment plays a decisive role in wood formation by its effects on tracheid diameter and wall thickness. The effect of environment on these cell properties is indirect. The direct effect is on the vegetative growth of the crown, the production site of substances that regulate tracheid diameter and the photosynthates that contribute to wall development. In short, crown attributes determine both timber yield and quality. Although our information on the physiology of wood formation is still meagre we probably have sufficient knowledge of tree growth to be able to manipulate the type of wood produced to our forestry needs. Perhaps the biggest problem facing the forestry community today is deciding what type of wood will be needed in the future.

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