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The Growing Tree.
pp 18-26
pp 94-117

3

General Aspects of the Growth Process

IT IS worth repeating that growth at the biochemical and cellular level in trees is the same as in other plants. Trees have cells that have chromosomes to carry genetic information, mitochondria to get energy from respiration, chloroplasts to photosynthesize and the rest of the array of cellular organelles that have been revealed by the electron microscope. The path of cellular differentiation is regulated by DNA through the type of enzymes that are produced in a cell. The hormonal growth regulators presumably somehow interact with this developmental system just as in other plants. The details have not been worked out for tree species. In fact trees are not very well suited for studies in genetics, biochemistry and molecular biology. Scientists interested in solving these types of problems want experimental organisms of known genetic constitution that can be grown rapidly for many generations under closely controlled conditions. Trees, at least large trees, meet none of these requirements. Thus, we have accepted essentially on faith that the pathways and cellular control mechanisms worked out for other plants, sometimes even for microorganisms, also apply in trees.[1] In the few cases where these cellular processes have been checked in trees, they appear to be basically the same.

Trees produce most of their bulk—stem, branches, roots—from meristems just as in other land plants. The concept and operation of meristems will be discussed in detail below. Apical meristems at the tip of each root and shoot produce the new cells that result in elongation. Trees have more apical meristems than other plants because they have more roots and shoots. Although the meristems operate in the same way as in other plants, each apical meristem may modify the growth of the others, and simply because there are so many apical meristems in trees, the problem of apical meristem interaction is particularly complex in trees and important to their growth. The "lateral" meristem that produces the wood in trees, the cambium, is tremendously bigger in area than in other plants because trees are so big. What better place to study cambial activity than in the plants where there is most cambium? Trees being the tallest plants have special problems about the distribution of cambial activity to support themselves. At this sort of level the growth of trees begins to have a special, peculiar interest to scientists.

Tree growth is basically additive and cumulative. It is somewhat analogous to the growth of a savings account. The bulk of the tree can be understood as the principle, and growth may be in the form of annual increments that add on like annual deposits to each branch or root, or growth may be through producing new branches and roots, in this case the addition is like interest because the number added is a percentage of the number already there. Unlike bank interest this percentage is usually 200 to 1000 per annum or more, so trees grow a good deal faster than savings accounts. Death and loss of branches and roots and shoots can be compared to withdrawals from the principle.

Growth by meristems is simply additive. To carry the analogy even further it is like a Christmas Club savings account where there is no interest. Meristems are groups of undifferentiated cells that retain the ability to divide almost indefinitely. After each division, one daughter cell stays to perpetuate the meristem and the other passes through successive phases of differentiation before it finally is added to the fixed, dead mass of the tree.[2] Meristems may produce new cells at faster or slower rates, or for a longer or shorter time period each year, depending on environmental conditions, but these rates of increase are seldom more than 100% between years.

A model of this process would look like this:

Meristem division → cell → enlargement →
differentiation → cell death

One hundred percent differences in activity of a single meristem may seem pretty impressive. The really big increments in the growth of a tree, however, come about because of the increase in numbers of meristems growing (for apical meristems) or the increase in the area of the meristem (for the cambium). The number of apical meristems can increase exponentially, because every year each apical meristem may produce several new apical meristems that develop into the branch roots and shoots. The next year every new meristem can produce its new meristems and the number of branches and roots can increase at a phenomenal rate. Every year each apical meristem produces more cells to elongate each branch or root. The annual activity at any one point on the cambium may vary from year to year, just as the activity of apical meristems varies, and the annual amount is recorded by the annual ring width. Ring widths certainly vary a good deal, but as the tree grows the total amount of cambial activity over the tree is much more a function of the increase in the area of the cambium. The area of the cambium is increased in two ways. One way is the extension of the cambium into new roots and shoots as some of the cells produced by the apical meristems resume division and function as cambial cells. The other way is the mechanism, to be discussed later in more detail, for increasing the circumference of the cambium as the circumference of the tree increases due to cambial activity.

The history of annual meristematic activity is preserved in the tree. The width of the growth rings shows how much cambial activity there was in a given year. If the growth ring widths are analyzed up and down the tree it is possible to calculate the total volume of wood produced each year and to correlate cambial activity with weather conditions during a year or with some treatment, like fertilizing or thinning a forest stand.[3] In most cases thinning a forest stand, by removing some of the trees to let the remaining ones get more light, results in a marked increase in the width of the growth ring produced the following year. The annual length increments from apical meristem activity are marked in several ways. Each year when the buds open and the shoot grows out, the bud scales that serve as the protective covering of the bud soon fall off. The scars left on the stem where the scales come off are usually visible for several years and they can be used to mark annual length increments. In many trees, and pines are perhaps the clearest example, the annual length increments on older stems are marked by groups, or whorls, of large branches. In pines these branches develop the same year as the main stem just above them and in hardwoods they develop a year later. In either case it is possible to estimate the age of the tree by counting the number of groups, or whorls, of large branches. This technique is unreliable when the lower branches have fallen off and there are no scars left to indicate where they were or when the trees, like southern pines, produce more than one whorl of branches each year. It is also possible to work out increases in the length of the stem from the annual rings in the wood because the length of the stem that makes up each year's increment will have one less annual ring than the previous year's. The annual increments of roots are far harder to determine. There is usually no external marker like bud scale scars or whorls of branches. In many cases growth ring analysis can be

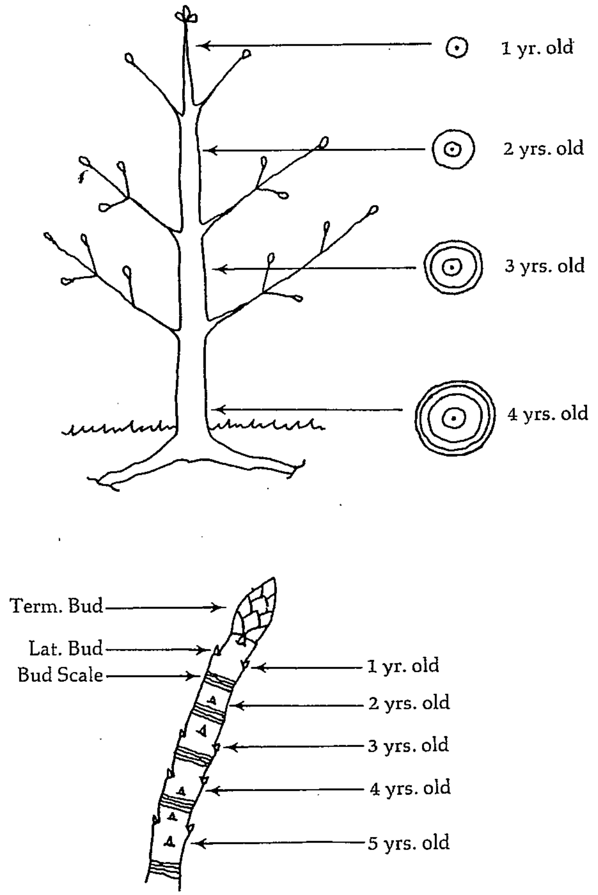

Figure 3

ANNUAL STEM INCREMENTS

Above, each annual length increment is marked both by whorls of branches and by a change in the number of rings in the wood. Annual diameter increments are marked by the rings. Below, annual length increments on twigs and small branches are marked by bud scale scars.

used to determine length increments. Unfortunately many growth rings in roots are discontinuous; they are crescents in cross section rather than rings, so it is usually not possible to determine the age of a root by counting the growth rings.

All the cumulative-additive processes must be superimposed on the life cycle of the tree. A tree, just as any other plant, must reproduce to keep the species going. Trees can reproduce either by flowering and producing seed, called sexual reproduction, or by asexual, vegetative reproduction, as when the broken willow branches from a tree take root along a river bank or as in the many propagating methods used by nurserymen. Sexual reproduction produces individuals of different genetic constitution because of genetic recombination during fertilization; vegetative reproduction duplicates in each individual the genetic makeup of the original plant, thus forming groups of individuals of identical genetic makeup. These groups are called clones and are common in trees that reproduce from buds from the roots, as in aspen, or from layering (rooting) of branches, as in black spruce. From the long-term evolutionary point of view sexual reproduction is more conducive to survival because it produces a varied population of individuals and this population is better able to cope with changing environments than a population of identical individuals. From a short-term point of view, either method may be effective in increasing the number of individuals of a species.

Much of the life cycle of a tree is similar to that of other seed plants. Seeds are formed and fall to the ground. The seeds may germinate immediately, as in the case of the red maple, but in many cases the seeds will not germinate until certain environmental conditions have been met. The most common condition required to overcome seed dormancy in temperate tree seed is a period of cold, moist conditions that is usually provided during a winter so the seeds germinate in the spring when the ground warms up. There are many other requirements—some seeds require light, some require dark, some require abrasion, or leaching. The problems of overcoming seed dormancy are fascinating and manifold. There are books that provide the empirical techniques necessary to make tree seed germinate and there have been a number of studies on the changes that occur in tree seed as dormancy is overcome by various treatments,[4] but basically these problems are problems of all plants, and are not limited to trees.

The germinated seed grows rapidly on stored material and develops into a relatively fragile seedling. The seedling stage is probably the most hazardous stage in the life cycle of a tree. Tremendous numbers of tree seedlings die from drying out, high temperatures, and animal browsing, among other factors. A forester or nurseryman is very concerned with methods to protect trees at this tender seedling stage. But again, all seedlings are tender and easily killed. Trees do not have it any better or worse than other plants.

It is not until a tree enters the phase of vegetative growth that it actually begins to be different from other plants, because it is here that the effort of trying to get above all other plants occurs. Most of this book will be devoted to discussing problems of vegetative growth in trees, the sort of problems that have been mentioned in the first chapter. One phenomenon that is marked in trees, but occurs in other perennial plants, is that there are two phases of vegetative growth. Most trees pass through a juvenile phase and then enter the adult phase.[5] During the juvenile phase they do not flower and usually reproduce more easily asexually. The leaves may look different from the adult phase. A fascinating example of changing leaf shape is *Eucalyptus perriniana* where the juvenile leaves are circular and born pagoda-like with the stem passing through the center of the blade, while the adult leaves are "normal" eucalypt shape,

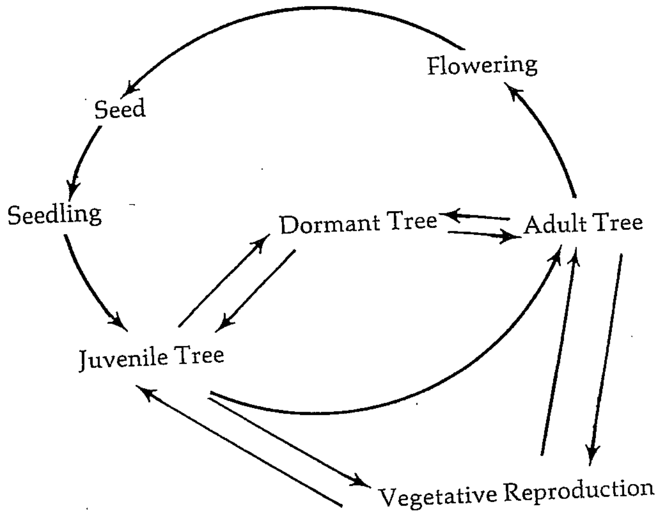

Figure 4
TREE LIFE CYCLE
This diagram is a modification of Dr. J. A. Lockhart's plant life "bi-cycle."

narrow, pointed at the tip and with a petiole. Leaves may be retained longer in the fall, as in the beeches. This juvenile phase is of variable duration, only a year or two in some trees and up to twenty or more years in others. In the adult phase the tree produces flowers that are pollinated and produce seeds and the cycle can start over again. Flowers may be produced abundantly every year, or only intermittently.

In most herbaceous species the life of a plant is terminated quite predictably. The plant flowers, senesces and dies. In these cases senescence and death involve fairly drastic changes that are initiated after flowering. Trees on the other hand do not enter senescence after flowering. Most trees are probably killed rather than dying from an internally triggered process of senescence. For example, the fast growing short-lived trees like gray birch and pin cherry that grow in open areas usually die when they are overtopped by taller longer-lived trees that shade the others out of existence. Certainly these trees can grow to respectable sizes and ages if they are not permitted to be overtopped. Striped maple is basically both short-lived and short in height; normally it is overtopped by other trees. Yet I have seen individuals so large that I could hardly recognize them. The question remains whether these trees are in any way "programmed" to die after a certain period or whether they are actively killed because they lack the capacity to become the tallest trees in a mature forest. Certainly the longer a tree lives the more likely it is to be killed by the environment—by the wind storms, lightning, floods, ice, fire, and the multitude of diseases that always seem to be in the process of eradicating some tree species or other. Even if the tree is not killed it may be sufficiently reduced in some attribute such as height, leaf area, root area, so that it cannot compete with other plants and is ultimately killed by competitive shading or drought conditions induced by more vigorous trees.[6]

Some trees manage to survive all these environmental vicissitudes; the best example is the bristlecone pine.[7] These trees may live to be more than 4,000 years old, so old that they even suffer from erosion from blowing soil and erosion is ordinarily a geological phenomenon. These bristlecone pines are impressive, because of their age, dramatic because of their wild twisted forms, but hardly forest giants. On the basis of our definition in the first chapter they might not be called trees at all. They are short, battered plants often with only a single strip of live cambium connecting the leaves and the roots. They also live under conditions which, although extremely arduous, high in the dry mountains, are virtually devoid of plant competition. They are the tallest plants where they live and can make good use of the few leaves they produce. The importance of these ancient trees to the present discussion is that they show no signs of programmed death. Those that survive for 4,000 years must be resistant to disease and capable of patching themselves up by producing vigorous new shoots even after the multitude of injuries that they appear to have suffered. Given freedom from outside threats, these trees appear to be immortal. We may ask whether other trees are not equally immortal, and simply less resistant or less adaptable after injuries, or else less fortunate in lacking competing trees.

In sum, all the growth of trees is by the production and growth of cells through the general process of meristematic activity, though the general process is subject to many modifications. If we are trying to distinguish among growing cells in a tree we need a number of different descriptions of the location of the cell. These are the questions we could ask: Which meristem are the cells associated with? Which phase of growth is the cell in? Which course of differentiation has the cell taken? And further we must ask: What time of year is it? What year? Where is the tree in its life cycle?

4

Form of the Branch & Root System

H. M. WARD summed up the material to be presented in this chapter when he wrote in 1909, "what a complex matter in its summation, but what a simple one in its graduated steps, the shaping of a tree is."[1] The whole branching system of a tree stem is called the "crown," and Ward was referring to the development of the crown of the tree. Crown form is a major part of the aesthetic appeal of a tree. Different crown forms can be used as a creative medium by landscape architects. It is the crown that produces most of the dramatic impact of a tree growing alone in a field or park. Deciduous species in winter reveal the intricate and complex patterns of the branches that bear the leaves. On a large tree there seem to be an astronomical number of branches, so many that it seems impossible to analyze the crown in terms of its parts instead of as a whole unit. Yet, this tremendously complicated structure has developed by the same sort of additive-cumulative growth processes that we have been discussing.

Before passing on to details of crown development it may be useful to survey some of the crown forms that commonly occur in trees. Young trees of most species have a central stem and a pyramidal crown. This pyramidal crown form is found both in young trees that eventually lose their pyramidal form, for instance oaks, as well as in those species such as pines, firs and spruces where the pyramidal form is often retained. The loss of the pyramidal form is usually caused by forking of the main stem and increased growth of some of the major branches so

A final complicating factor in root orientation is the phenomenon of exotropy. Briefly this means that a root which hits an obstacle and bends to grow around it tends to bend back to the original direction when it has gotten by the obstacle. This type of growth can occur in horizontal roots that grow around horizontal obstacles, so geotropism is not involved.[5] Exotropy may complicate the geotropic response when roots grow up or down around obstacles. Thus, exotropy tends to keep the root going in a straight line and geotropism tends to maintain the root in a specific orientation to gravity. Exotropy works even in a root with no geotropic response. The two phenomena presumably are working all the time as the root tip threads its way through the soil moving around large and small obstacles.

8

The Process of Cambial Activity

How the Tree Thickens

IN THE preceding chapters we have covered lightly the proliferation of the root and shoot system. As mentioned in the introduction, this proliferation requires both strengthening of the stem and an increase in transport capacity between the leaves and the roots. This strengthening occurs in trees by cambial activity. The cambial zone, a thin layer of cells between the bark and the wood of the shoot and root system, contains the meristematic cells, the cambium. From these cells are derived new wood cells, called xylem, that strengthen the central core of the tree and also conduct water and dissolved substances from the roots to the rest of the tree. Derivatives of the cambium also produce new tissue on the inner layer of the bark, the phloem, whose specialized cells conduct sugars and other elaborated materials within the tree. This simple system, xylem to the inside, phloem to the outside, permits trees to attain great size by solving most of the problems that arose from the development of large shoot and root systems as trees evolved.

Tree fanciers who live in temperate zones may not appreciate that cambial activity does not always follow this simple system.[1] Some trees produce a succession of cambia, for instance the mangrove *Avicennia* that lives around the world in tropical and subtropical seashore areas. In this tree the "annual rings" that are so obvious in cross sections of the wood are not formed

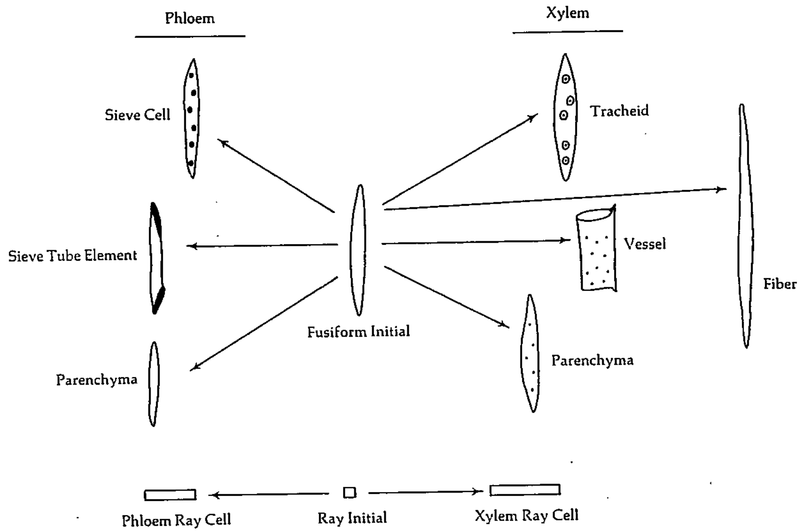

Figure 18

DIFFERENTIATION OF CELL TYPES FROM CAMBIAL INITIALS

Sieve cells and sieve tube members are specialized for phloem transport; vessels are specialized for water transport and fibers for strength; tracheids combine specialization for both strength and water transport; parenchyma often serve in storage.

because the wood cells produced every fall are different from those produced in spring. In *Avicennia* the rings are formed because a new cambium has developed and a ring is left quite comparable to those seen in cross sections of garden beets. Just as in beets, these rings are not necessarily annual; there may be 3 or 4 per year in southern Florida. There are many other types of cambial activity, but they will not be considered here. Perhaps the most sensible thing is to proceed with a detailed examination of the simple system of temperate trees, keeping in mind that this system is "normal" only in the temperate zone.

The simplest example of the process of cambial activity is in the conifers, so we will examine cambial activity in conifers in some detail[2] and then discuss the variations that occur in other trees.

Each cambial cell (the cambial initials) produces daughter cells to the inside and outside of the tree, along a radius of a stem cross-section. The initial and its derivatives form a radial file. Thus, all the products of cambial activity—the wood and inner bark—can be subdivided into radial files of cells, each file derived from a common initial cell. Derivatives of the initial cell then pass through the phases of division, enlargement (radial enlargement plus elongation) and differentiation before they finally die. The phase of differentiation in wood cells is primarily occupied with the production of the polysaccharides and lignin that form the secondary wall of each cell. The secondary wall, much like a package containing the living cytoplasm, gives the strength to the wood. After the cytoplasm of the wood cells dies, the cells are left as hollow tubes of cell wall with the insides of the cells interconnected by many pits through the walls that permit water movement from cell to cell. Differentiation in the phloem is somewhat more complex. There are several cell types, cells that are functional in conducting photosynthate and cells that store materials, such as starch,

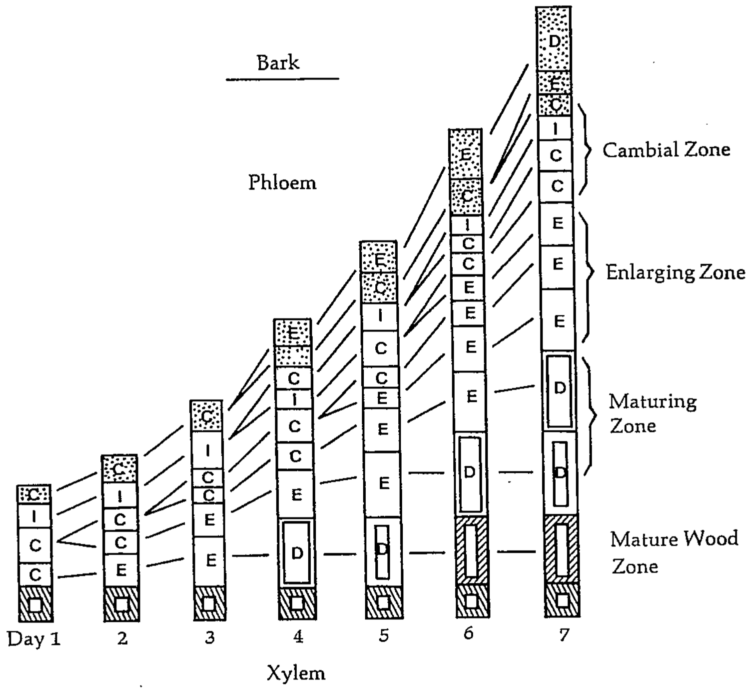

Figure 19

OPERATION OF THE CAMBIUM

In this pictorial model stippled cells are phloem, cells are lettered C *if in the phase of division (cambial cells),* E *if in enlargement,* D *if in differentiation, and unlabelled if mature.*

crystals or brown colored "tannins." The storage cells stay alive for several years and the sieve cells undergo some dramatic changes, such as loss of the nucleus, but, unlike conducting cells in the wood, are still alive when they are functional.

When the initial cell divides, one daughter cell takes over the function of the initial and the other enters the phase of division. These cells in the phase of division are called mother cells. One tricky part of cambial activity is that the initial cell usually produces xylem mother cells, but sometimes produces phloem mother cells. Thus the same initial cell can produce derivatives to the inside (xylem) or to the outside (phloem) so the radial files are continuous from xylem through the cambial zone to the phloem.

There are actually two types of initial cells, one type is long and thin and called a fusiform ("needle-shaped") initial, the other is almost cubical and is called a ray initial. The fusiform initials produce the vertically elongated cells that, in conifers, constitute about 90% of the wood and phloem. The ray initials produce radially elongated cells in radial files that are called rays. Both types of derivatives pass through comparable phases of division, enlargement and differentiation even though the number of divisions, rates of enlargement and course of differentiation are quite different. Despite the differences, as the cells grow and develop the tissues they form seldom have any air holes between cells (an exception to this is compression wood in conifers that will be discussed later in this chapter). Apparently their growth is regulated by stresses within the developing tissue so that complete cell contacts are maintained.

As the xylem derivatives of the initial enlarge radially they push out the initial cell so that it essentially rides along dividing as it goes and as the derivatives pass through the various phases, zones of division, enlargement and differentiation develop along the radial files. The zone where cells are still dividing is called the cambial zone. Over time the cambial zone moves away from the center of the tree leaving the mature cells behind. Once through the phase of division, cells do not change position relative to each other although during enlargement they may be moved relative to the center of the tree, because of the increasing diameter of the wood. The cambial zone is simply, in a sense, a machine for producing new cells and the machine itself is pushed along by its cellular products.

The simplicity of cambial activity in many conifers, such as hemlock and true fir, is that there is essentially only one fusiform cell type in the wood. All the derivatives pass through the same pathway of differentiation so that the wood is quite a homogeneous material of fusiform tracheids elongated vertically and the radially elongated ray cells. Some conifers like Douglas-fir or bald cypress are a little more complicated. They produce occasional parenchyma cells in the wood instead of all tracheids. The parenchyma are the same shape as tracheids, but they do not develop thick secondary walls. Even more complicated is that many conifers, for instance the pines, develop vertically oriented resin ducts in the wood. These resin ducts start in the xylem mother cells. In cross section a small group of cells develops that has denser contents than the other mother cells; they later split apart forming the duct in the center and a lining of parenchymatous epithelial cells. There may be a series of resin ducts formed at the same time around the stem, separated by "normal" tracheids. So in this case certain cells in certain files receive a different signal to become resin canals. Another aspect of resin canals is that they are formed by a number of different cells up and down the tree, but these cells are in vertical strands so that the canal is continuous up and down the tree. There must be some vertical regulation to ensure that the canals are continuous.

The complexities of the conifers seem insignificant when compared to the complexities of angiosperm wood, because angiosperm wood normally has at least three types of wood cells. These differences all arise during enlargement and differentiation. There are still only ray initials and one type of fusiform initial in angiosperms and the whole process of cell production by cell division is essentially the same as in conifers. The differences arise during enlargement when some of the derived cells enlarge radially only a little, although they may elongate a great deal, then form thick secondary walls. These cells are the fibers that are specialized to give strength to the wood. Other cells enlarge just a little bit and do not form thick walls, developing into parenchyma cells, apparently specialized for storage. Some cells enlarge a great deal radially, do not elongate, but form thick walls except on the ends where one or more relatively large holes develop as the cell dies. These barrel-like cells are the vessel elements that are specialized for water conduction. Just as in the resin canals, there is some vertically oriented regulation that results in the vessel elements aligning to form long vertical tubes called vessels. Water moves straight through these tubes with minimum resistance.

These different types of wood cells do not develop randomly. There is a consistent pattern of cell types that is the basis of wood anatomy.[3] Each tree species produces wood with such a consistent pattern that it can be identified and distinguished from other species. There are two basic types of wood in the hardwoods (angiosperms). In one type the vessels are all about the same size and are scattered fairly evenly through the wood. This type, called "diffuse porous," is found in maples, birches, beeches, and cherries. In the other type, extremely large vessels, often visible to the naked eye, are formed at the beginning of each growth ring and the vessels formed through the rest of the growth ring are only one-tenth the diameter of the first vessels. This type, called "ring porous," is found in oaks, ashes, elms, and hickories.

The development of these patterns of cell types seems to be based on the distribution of vessels. Analysis of the structure of mature wood suggests that there is not only a vertically oriented regulation that determines the alignment of one vessel element with the next, but also radial and tangential regulations that maintain a consistent pattern in cross section. In different woods there appear to be two types of factors regulating distribution in cross section. One factor determines whether vessels occur singly or in groups. If they do occur in groups this suggests an "epidemic" distribution as though the presence of one vessel stimulated the development of another adjacent vessel. Even in woods where vessels occur in groups the groups are separated and here a type of regulation based on exclusion seems to operate so that a group of vessels excludes the development of other vessels for some distance around it. In the first case the assumption is that the vessel produces something that stimulates further vessel development and in the second case the assumption is that the vessels either produce something that inhibits vessel development or else use up something that is required.

The distribution of vessels then appears to regulate the distribution of other cell types. Parenchyma are usually distributed in some relation to the vessels, often surrounding them. Fibers essentially fill in what is left. Ray cells are basically the same in hardwoods as in conifers, but in hardwoods are aggregated into rays that are much larger and more complex.

The observation that vessels are interwoven into a three-dimensional network further complicates development of the vessel pattern.[4] First of all, the vessels are not just parallel tubes in the wood. They are tubes that interconnect and sometimes end at junctions with other tubes. Second, this whole complicated vessel pattern must be initiated right at the edge of the cambial zone because vessels immediately start to enlarge faster than adjacent cells. Thus, when the pattern is blocked out the radial distances are much compressed compared to those separating mature vessels. Once the vessels start enlarging they get so big that they occupy the space of several radial files and cell production in adjacent files has to stop temporarily.

So far we have just considered the development of individual radial files, but a little consideration of what happens as these files get longer and the tree increases in diameter shows that the cambium must make adjustments to the increase in circumference. The first adjustment is that the cambium must produce new radial files to keep the wood from developing radial splits as the circumference increases. In the 1920's I. W. Bailey's classic work on cambial activity demonstrated that the cambium primarily produces new files rather than having the initials enlarge tangentially.[5] The cambium also has to produce new ray initials to make new rays. M. W. Bannan, in a series of painstaking investigations,[6] has shown that fusiform initials require a certain number of contacts with ray cells, presumably because nourishment moves radially into the cambium from the phloem through the rays. Bannan showed that fusiform initials without enough ray contacts did not survive. Therefore, the cambium must not only produce new files of fusiform cells, but it must also produce new files of ray cells to permit survival of the fusiform cells.

Largely through the work of Bailey and Bannan the process by which the cambium produces new files of fusiform and ray cells is now quite well worked out for conifers, and other investigators seem to be finding that the same general principles apply to the cambium of angiosperms. Basically, the fusiform initial, which predominantly divides in a plane parallel to the

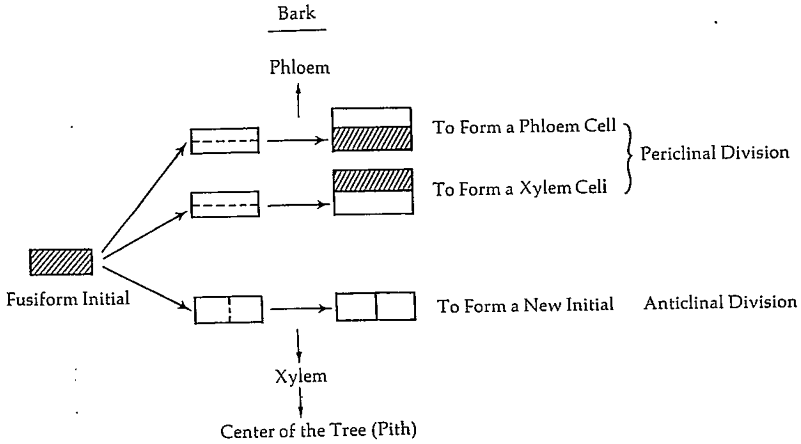

Figure 20
TYPES OF DIVISION OF A FUSIFORM INITIAL

surface of the bark producing a mother cell and an initial cell in the radial file, occasionally divides in a plane perpendicular to the bark producing two initial cells. Ultimately these two initial cells will produce two radial files for a net gain of one radial file. In storied cambia like black locust the perpendicular division divides the cell completely lengthwise so that the two daughter initial cells are the same length. In most cases the new wall is S-shaped and the two daughter initial cells are somewhat longer than half the length of the parent initial but shorter than the full length. These shorter initials gradually elongate back to about the original length of the parent when they redivide perpendicularly. Bannan has estimated that it takes about 3–4 years for the initials to elongate between perpendicular divisions in arborvitae (*Thuja occidentalis*). During its elongation the initial cell continues to undergo parallel divisions. As a result the derivatives gradually get longer as the initial elongates because parallel divisions are almost always the full length of the initial cell.

This type of perpendicular division produces the needed extra radial files. Elongation of the new initial cells maintains, and even increases, the average length of the derivatives. But where do the new ray initials come from? The answer is that they come from unequal perpendicular divisions where the small cell becomes a ray initial and the large cell stays a fusiform initial. There are several types of these unequal divisions; a small cell may be cut out of the side of a fusiform cell, or off the tip, or a medium sized cell may be subdivided by successive divisions into a series of ray initials.[7] Bannan has also found that some fusiform initials that are small and lack ray contacts may even be lost from the cambium.

An interesting aspect of these perpendicular divisions is that there seems to be some sort of feedback type of control over the fate of new initial cells. Apparently each fusiform initial must be in contact with several rays to survive. If, after a perpendicular division, one of the daughter initials is too small to have enough ray contacts then it is highly probable that it will subdivide to develop a new ray. Thus, rays develop in the very areas where there are not enough of them.

Both conifers and angiosperms produce wood that appears to be specialized for bending up leaning stems. This wood is called reaction wood, because it is often assumed to be formed solely as a reaction to the tipping of a stem or any branch that is not vertical. Reaction wood in conifers is called compression wood.[8] It forms on the under side (the compressed side) of tilted stems and branches. The mature wood is actually under compression; it is trying to enlarge, so it tends to right the organ by pushing it up. Compression wood is easily seen in most species because it is a dark red-brown color, rather like the latewood in annual rings. Under the microscope compression wood cells are round in outline with spaces between the cells, instead of the usual closely packed hexagons of "normal" wood. The walls are much thicker than usual. They are highly lignified, and special microscope techniques show that the cellulose microfibrils of the secondary wall are oriented at an unusually large angle to the long axis of the cells. These differences in the cell wall are presumably related to the great longitudinal, expansive force that the cells develop. One recent suggestion for the origin of the force is that during lignification of the cell wall as the lignin is deposited on the cellulose framework the lignin swells between the cellulose microfibrils, forcing them apart and lengthening the cell.[9]

Reaction wood in angiosperms is called tension wood. It forms on the upper side of leaning stems or branches (the tension side). Tension wood is actually in tension, trying to shrink, and tends to pull the stem or branch upright. It does the same job as compression wood but on the opposite side of leaning stems and with the opposite stress. Tension wood is not usually obvious except under the microscope. In sections it can be readily seen because the fibers are almost unlignified and because there are so few vessels. The fibers have an extra layer of secondary wall, and the microfibrils of this layer are almost parallel to the long axis of the cells, just the opposite of compression wood cells. Recent investigations suggest that the tension in the wood develops partially due to swelling between the microfibrils that tends to shorten the fibers (but there is very little lignin to account for this swelling). There are a number of observations using the electron microscope that show that the extra layer of secondary wall swells out during differentiation and presses against the external layers of the wall. This type of pressure from inside could also lead to the development of a tensile stress as the cell shortened.

9

Regulation of Cambial Activity

The Timing, Rate, and Type of Thickening

THE THREE PHASES of cambial activity, division, enlargement and differentiation, each have separate sets of controls. Division restricts the whole process of cambial activity because if no cells are produced then the other phases cannot take place. But given that cells are produced, there are all possible combinations from large cells with thin walls and small cells with thick walls (the normal pattern in annual rings) to large cells with thick walls and small cells with thin walls. Under certain environmental or experimental conditions it seems that each phase may vary in intensity independent of the other phases. All the phases of cambial activity are modified by environmental conditions such as temperature or moisture, but specific regulation seems to be through the leaves, directly or indirectly. In fact, most of the variation in cambial activity is a response to photosynthate or growth regulators (auxin, gibberellin, inhibitor) produced by the leaves.

Each spring cambial divisions must be initiated after the winter rest period. In conifers and diffuse porous trees, cambial activity starts just below the buds as they become active and then activity spreads gradually down the tree. Removal of the buds stops initiation, but the effect of the buds can be partially replaced by auxin. The inference is that auxin produced by the buds moves down the stem and initiates cambial activity so that the spread of initiation down the stem is determined by the movement of the auxin. In ring porous trees, cambial activity starts before the buds become active, beginning over all of the tree at about the same time. The first large vessels are formed before the leaves grow out. Wareing has shown that in ring porous trees there is a great deal of auxin precursor present in the dormant cambial zone and that this precursor appears to be rapidly converted to auxin simultaneously over the whole tree.[1] Auxin apparently is still necessary to initiate cambial activity, but in ring porous trees it does not have to come directly from the expanding buds and leaves where it is produced.

Once divisions are started, cell production by the cambial zone is a function of both the rate of redivision of cells in the dividing phase and the number of cells in that phase. In other words the rate of cell production is the same (2/day, for example) whether there are 10 cells that divide every 5 days or 20 cells that divide every 10 days. A good indication of the rate of division is the percentage of the cells in the phase of division that are actually dividing. The faster the rate of division, the higher the percentage of cells that are dividing. This percentage of dividing cells is called the mitotic index (mitosis being the division of the cell nucleus). The number of cells in the cambial zone, the cells that can divide, is lowest in dormant trees and greatest during the period of weeks, or even months, shortly after activity is initiated in the spring. The mitotic index is greatest when cell number is greatest. During this period of maximum cambial zone cells in conifers, the mitotic index of fast and slow growing trees of a species on one area is about the same. The differences in the rate of cell production between trees are due almost entirely to differences in the number of cells that are dividing.[2] Apparently the rate of division is pretty much genetically determined, but the length of time that cells remain in the phase of division can be regulated by the activity of the crown. The regulation may be through the amount of available photosynthate or the amount of growth

regulators produced by the leaves. Both of these would be greater in dominant trees and less in suppressed trees and so far there are no data to separate the two possible regulatory mechanisms.

As the summer progresses cell production slows and stops. Mitotic activity drops to zero and the number of cells in the cambial zone returns to the minimum number present in the dormant tree. Apparently cell production continues as long as the leaves are still producing auxin. In diffuse porous trees only enlarging leaves produce auxin; mature leaves do not, so that when late leaf production and leaf growth stop around the middle of July, cambial activity also stops because there is no more auxin moving down from the stem. In conifers and ring porous hardwoods the mature leaves continue to produce auxin and cambial activity can continue long after leaf growth has stopped.[3] In pines some cell production may continue even after the first frost of the autumn.

An additional factor that seems to affect the rate of cell production is the effect of wind sway. The tree stem sways in the wind and as it bends the cambial zone is subjected to repeated strains (changes in length) and stresses (changes in forces acting). This sway appears to stimulate cell production. Trees that sway in only one direction tend to become oval because they produce more wood in the direction parallel to the sway than perpendicular. Trees that are guyed so that the stem cannot sway have an overall reduction in cell production in the lower stem. Somehow the stresses and strains induced by swaying stimulate cell production. Stresses and strains in themselves probably do not affect the process, but they might affect the redistribution of auxin moving down the stem or sensitize the cells so that they are more responsive to the auxin that is present. The phenomenon itself is well established but the mechanism of the phenomenon is not.[4]

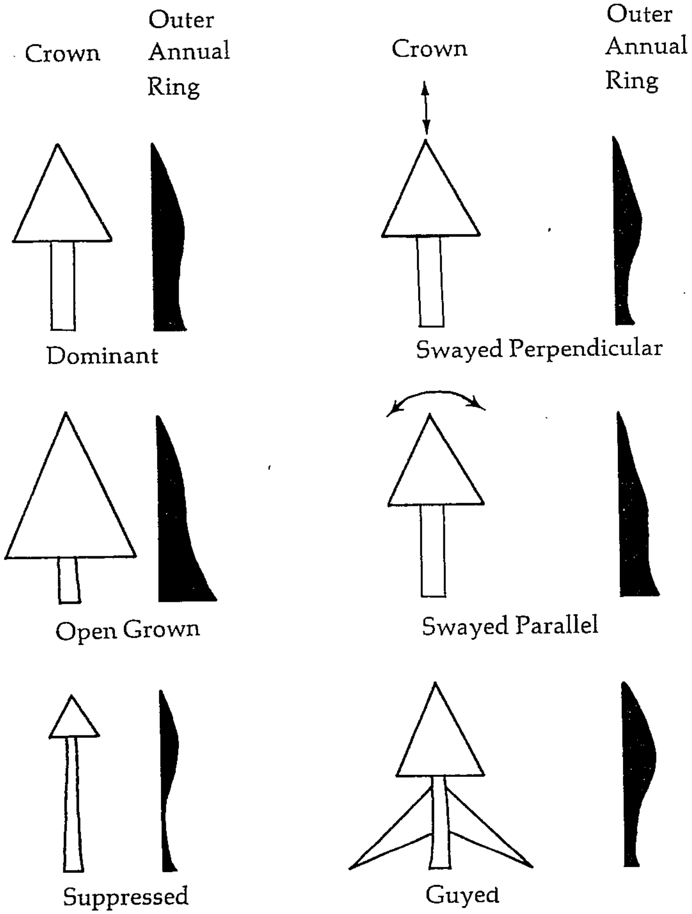

Figure 21

LONGITUDINAL DISTRIBUTION OF CAMBIAL ACTIVITY

The relation of crown size (left) and sway (right) to the distribution of cambial activity in the outermost annual ring.

Final cell diameters go through regular annual cycles. The largest cells are produced during the spring and summer and constitute the early wood of the annual ring. Towards the end of periods of cambial activity, cells enlarge less and the late wood of the annual ring contains relatively small diameter cells. The diameter of the cells seems to be proportional to the auxin concentration and inversely proportional to water stress. The width is greatest during stem and needle elongation. In some species like red pine the diameter begins to decrease slowly after shoot elongation stops but needle elongation is still active and then drops rapidly as needle elongation stops. In other species like white pine there is no drop in diameter marking the end of shoot elongation. Larson has successfully regulated tracheid diameter by regulating the photoperiod, because needle elongation is regulated by photoperiod, and also by the addition of external auxin. In experiments where auxin is added to stems, cell diameter increases as auxin increases, up to a maximum diameter, but if the stem is treated to reduce the amount of internal auxin reaching the cambium (by adding triiodobenzoic acid to block polarized auxin transport), then the diameters decrease.

Somewhat the same results have been found for vessel size in hardwoods. Fiber diameter scarcely changes throughout annual rings, although there is a sudden decrease in the last few cells. Vessels, however, are larger in the early wood and smaller in the late wood. The huge vessels of ring porous trees are somewhat special. They develop very early, before the leaves, presumably under conditions of high auxin, but in any case under completely different conditions from any cells in conifers or diffuse porous trees. Cambial activity can be induced in dormant hardwood stem segments by adding growth regulators and the diameter of the vessels formed is proportional to the concentration of auxin supplied. Vessel diameter

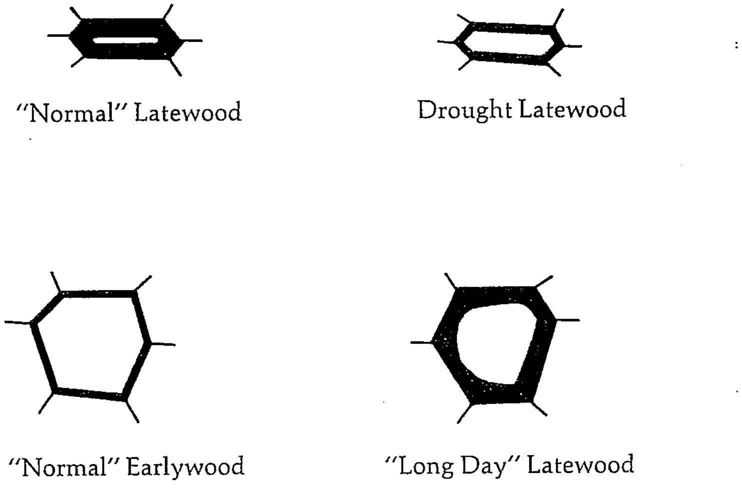

Figure 22
TRACHEIDS
The range of combinations of radial diameters and wall thickness observable in tracheids.

is reduced if the segments are grown under conditions of water stress.

Experiments applying growth regulators mixed in lanolin to the tip end of stem segments shed some light on other problems of cambial activity. One such problem is why some cells become vessels and others not. In stem segments either gibberellin alone, or auxin alone, initiates cambial activity. With gibberellin alone there is no production of vessels, while with auxin alone vessels develop, but only a few cells are produced. Apparently there must be auxin moving down the stem, normally from the leaves, to permit any vessel development. Presumably at the levels of auxin normally occurring in stems the number of cells that become vessels is limited; perhaps they use up all the auxin or perhaps they somehow inhibit other cells, but the auxin is necessary to permit the extraordinary radial enlargement associated with vessel development.[5]

Another basic question in the study of cambial activity is why most daughter cells resulting from divisions of initial cells become xylem mother cells, but some become phloem mother cells. Some experiments suggest that the ratio of xylem to phloem in stem segments can be regulated by varying the ratio of auxin to gibberellin. High auxin produced relatively more xylem and high gibberellin produced relatively more phloem. These data certainly do not solve the problem of the determination of daughter cells after the division of the initial, but they do suggest that the determination is somehow, like most other aspects of cambial activity, regulated by the growth regulators coming from the leaves.

The aspect of differentiation that has been studied most in the development of the xylem is secondary wall formation. Secondary wall thickness also follows a pattern across an annual ring, just as radial diameter does. Usually annual rings of conifers have early wood cells that are large in diameter and thin-walled, and latewood cells that are small in diameter and thick-walled. The characteristic dense, dark latewood is the result of these narrow, thick-walled cells. In white pine, which has relatively little latewood, the thick-walled cells are formed only after needle elongation has stopped so the increase in thickness coincides with the rapid decrease in diameter as cambial activity stops. In red pine, there is usually a good deal of latewood because thick walls begin to develop after shoot elongation stops, but before needle elongation stops, so there is a zone of relatively large diameter, thick-walled cells and then the annual ring is terminated by small diameter, thick-walled cells.

Young red pine, grown under continuous long days at high light intensity, continue to produce large-celled early wood, but the cell walls get thicker and thicker until they produce what is called "long day latewood." On the other hand, under drought conditions pines may produce lots of narrow cells with thin walls. Thus, although thick walls are usually associated with narrow cells, all different combinations may occur.[6]

There are basically two theories about the regulation of cell wall thickness. One is that the thickness is related to the photosynthate left after respiration and growth of other parts of the tree. Thus, normal thick-walled latewood is formed after the drain on photosynthate by needle and shoot elongation has stopped. There is a positive relationship between light intensity and wall thickness, presumably because as light increases photosynthesis increases. There is also a negative relationship between the night temperature, which increases night respiration, and wall thickness. High temperature reduced wall thickness by reducing net photosynthesis. Larson's experiments with radioactive carbon dioxide also suggest that wall thickness is related to net photosynthesis as above.[7]

The other theory is that wall thickness is regulated by the length of time that cells are in the phase of cell wall thickening. Earlywood cells differentiate so fast that cell walls are thin, but latewood cells stay near the phloem for a long time and wall thickening proceeds for a long time. In larch, 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 cytoplasm.[8]

It seems quite likely that both these 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. At least, the two theories do not seem mutually exclusive.

One aspect of the regulation of cambial activity that is important to the tree is the production of reaction wood. When a stem is leaning the course of differentiation of cambial derivatives changes. In jack pine the developing tracheid must be leaning throughout the whole phase of enlargement and differentiation to become a typical compression wood cell. Just tilting a seedling during the enlargement phase did not affect the cell wall thickening phase.

For years there has been an argument about whether compression wood is formed due to the effect of gravity or to the effect of the compressive stress on the under side of the leaning stem (*vice versa* for angiosperms). Jaccard's experiment of bending stems into circles showed that compression wood always formed on the under side of the stem whether the wood was on the inside of the circle (in compression) or on the outside (in tension).

The hypothesis that developed was that in leaning stems auxin was transported laterally and was at a high concentration on the underside. The circle of proof was completed when it was shown that high auxin concentrations on upright conifer stems could induce compression wood and low auxin concentrations (induced by TIBA blockage of auxin transport) on upright angiosperm stems induced tension wood formation. Thus, it seems that the same mechanism of lateral auxin transport and accumulation on the underside of the stem can account for both compression and tension wood formation because the former develops in high concentrations and the latter in low concentrations.

There are, unfortunately, many examples where reaction wood does not form on the "normal" upper side of leaning

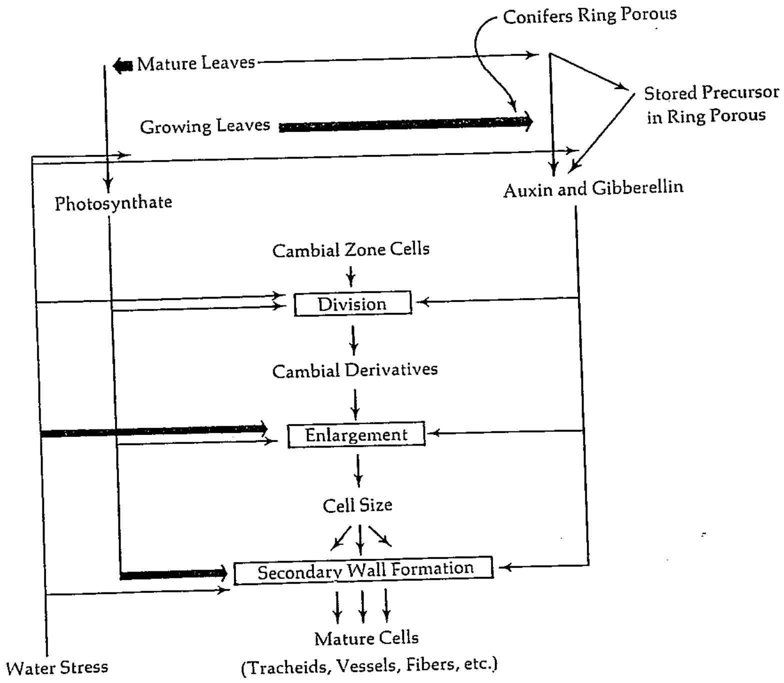

Figure 23

REGULATION OF CAMBIAL ACTIVITY

Shown in a flow chart.

stems or branches. Perhaps the best known is in branch epinasty. If a branch normally forms reaction wood on one side, when it is bent up, lessening the branch angle, it may form reaction wood on the opposite side and this reaction wood tends to return the branch to its original position. There are other experiments where branches are disoriented and they form compression wood on the tops, bottoms, sides or even spiraling along the branch.[9]

It is difficult to see how epinasty could affect lateral transport. It is even more difficult to see how transport is affected in the more sophisticated bending experiments. These experiments seem to suggest that perhaps stress does somehow enter the picture of regulating compression wood formation, perhaps in collusion with gravity. In complex bends about the only consistent stimulus-response relationship seems to be between stress and compression wood. Perhaps stress, or rather strain (changes in length resulting from applied stress), can affect auxin distribution, but the answer is not known yet.