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ANATOMY AND PHYSIOLOGY RELATED TO CHEMICAL MOVEMENT IN TREES[1]

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Abstract. Vascular anatomy of woody plants is described and the physiology of translocation in xylem and phloem tissues is discussed. The interaction of anatomy and physiology are related to the uptake and movement of chemicals applied to the foliage and soil or injected into the stem.

Chemicals can be introduced into trees via the leaves, roots, or stems. Foliar application avoids the need to wound trees and to create ports of entry for decay and disease organisms. However, many foliarly applied substances are slowly adsorbed through the protective layers on leaf surfaces, and then poorly translocated away from the leaves to the rest of the tree. Uptake via roots generally involves incorporation or injection of chemical substances into the soil with subsequent absorption by the root system. Placement near roots or root growth into the zone of placement are essential for good uptake. The injection of chemicals directly into the trunk of trees relies on distribution in the transpirational stream. Regardless of the method of introduction, the xylem and phloem are the vascular tissues through which substances are translocated. Here, complex interactions of anatomy and physiology allow for the distribution of introduced chemicals.

The xylem and phloem systems in trees consist of two important components, the symplast and the apoplast. The symplast consists of all the interconnecting living cells of a tree and is united into a continuum by means of protoplasmic connections. The vascular rays and functional phloem are part of the symplast. The apoplast is the non-living cell wall matrix and intercellular spaces that surrounds and contains the symplast. The apoplastic continuum is connected by the death of xylem elements to form the pathway for water movement in transpiration.

Vascular System Anatomy

Most of the xylem and phloem in trees is secondary tissue produced by the vascular cambium. The development of the annual increments of these tissues is coordinated with primary growth in the apical meristems of shoots and roots to produce an interconnected conduction system extending from the zone of differentiation (root hair zone) in roots to mature and developing leaves. Cambial activity results in much greater proportions of xylem than phloem cells in the trunks of trees. Much of the xylem tissue has rigid, lignified cell walls which persist and accumulate even after they are no longer functional in translocation. The phloem tissues are much more succulent, and normally do not persist. They are crushed and distorted between the cambium and bark as a result of circumferential growth. The xylem is primarily responsible for upward movement of water and inorganic solutes. In contrast, the phloem is the avenue for bidirectional movement of organic substances. Xylem elements are dead when functional and movement is apoplastic, whereas phloem translocation occurs in living cells and is symplastic (Chaney, 1979).

Xylem anatomy and transport pathways. The vessel members, tracheids, fibers, and paren-

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chyma cells of the xylem develop in proportions and arrangements that are unique to each species of tree. However, three principal xylem anatomies occur: nonporous, diffuse porous, and ring porous. In nonporous xylem of Gymnosperms such as the pines, spruces, and firs, only one cell type, the tracheid, is found. These cells are typically spindle-shaped and have pitted lignified walls. They occur in radial files of longitudinal stacks of cells interconnected by pits in the sidewalls (Figure 1). Pits in tracheids are normally limited to the radial walls. This location restricts movement across an annual growth ring but facilitates movement tangentially around the stem. Individual tracheids reach 5 mm in length and 10 to 20 microns in diameter.

The xylem of Angiosperms such as hardwood trees contains both tracheids and vessels. Wood is described as diffuse porous if the vessels are uniformly scattered among the tracheids and other cells of each annual growth ring (Figure 2). In ring porous species, large diameter vessels dominate the earlywood of each annual growth ring and are smaller in size or absent from the latewood (Figure 3). The vessels are 10 to 200 microns in diameter with pitted sidewalls and highly perforated or open end walls. They are stacked end to end and may extend uninterrupted for several feet through the stem. Vessel lengths are normally greater in ring porous trees than diffuse porous ones (Table 1), and have been reported to transverse the entire distance from roots to twigs of mature ring porous trees (Greenidge, 1952).

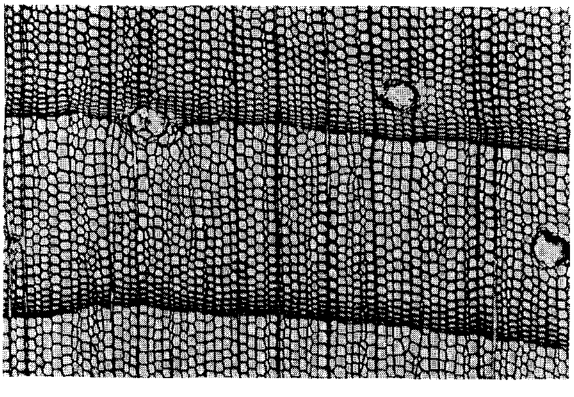

Figure 1. Nonporous xylem of Gymnosperm. Large pores are resin ducts.

Since movement in the xylem is due to physical forces, it follows the path of least resistance. Translocation in ring porous trees represents the simplest pathway. Here water conduction occurs through the large diameter earlywood vessels of only the current growth increment. The vessels of older growth rings are blocked by gases, tyloses, or gums (Chaney and Kozlowski, 1977; Zimmermann and Brown, 1971). In diffuse porous species vessels scattered throughout several annual growth increments of the outer sapwood are active in water conduction. In nonporous trees, it is the earlywood tracheids of several annual rings in the outer sapwood that are used for conduction (Kozlowski, 1964).

The ascent of sap in the xylem may follow a strictly vertical path, and in ring porous species there may be a continuous vascular conduit from a root on one side of a tree to twigs on the same

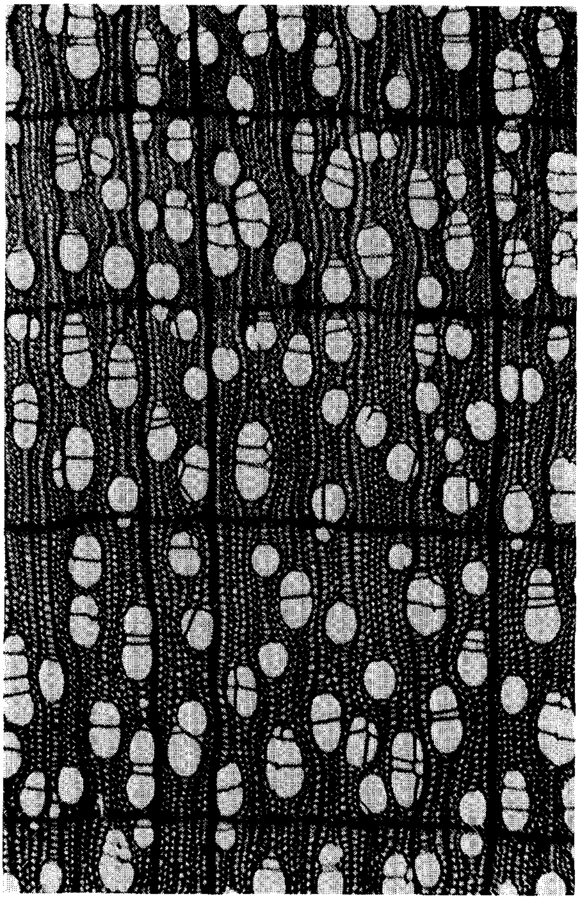

Figure 2. Diffuse porous xylem of Angiosperm.

side of the tree (Zimmermann and Brown, 1971). However, straight grain is probably the exception in trees rather than the rule (Northcott, 1957) (Figure 4). The effect of this on xylem sap distribution was investigated by Rudinsky and Vite (1959) in conifers unilaterally injected with dye. Five distinct patterns of movement were described: 1) spiral ascent turning right, 2) spiral ascent turning left, 3) interlocked ascent, 4) sectorial winding ascent, and 5) sectorial straight ascent. Kozlowski and Winget (1963) demonstrated similar patterns of movement in Angiosperm trees. The significance of the complicated patterns of water movement to distribution of injected substances is obvious. From a few injection points, uniform distribution in the crown can be achieved. Even in the sectorial straight ascent pattern, some tangential spreading occurs. Knowledge of the xylem anatomy and occurrence of spiral grain of trees to be injected can influence the spacing and depth of the injection. For example, trees such as elm which normally exhibit spiral grain should require fewer injection points than trees such as ash which have straight grain. Chemicals injected into ring porous trees such as oak should be placed shallowly in the current annual xylem ring, whereas a deeper placement into several annual rings in diffuse porous trees such as sweetgum would be equally effective.

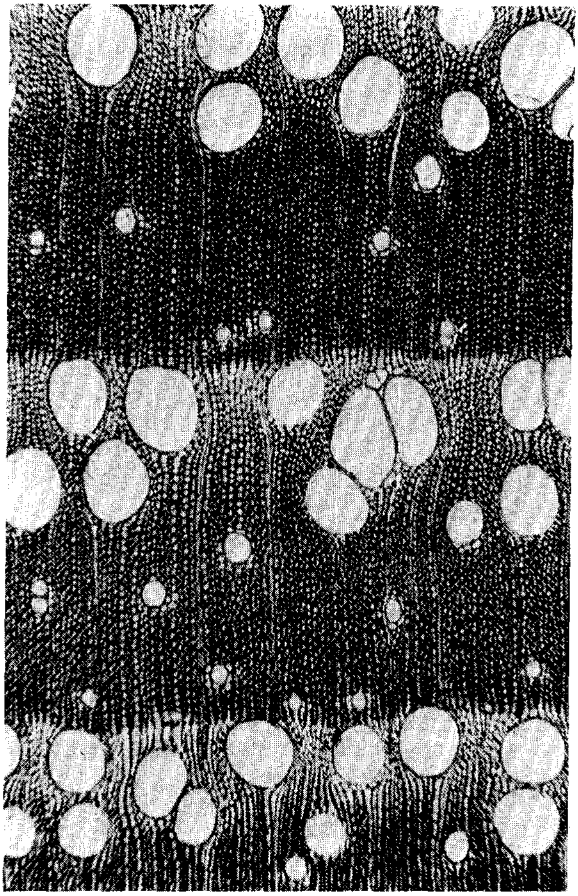

Figure 3. Ring porous xylem of Angiosperm.

Anatomical response to trunk injection. Trunk injection severs xylem cells, breaks the continuity of water columns, introduces air into cells, and initiates a wound healing response. The result is that injected chemicals may enter the transpiration stream slowly and be poorly distributed. The introduction of air to tracheids and vessels may result in differential pressure gradients across pit pairs with the development of aspirated pits which prevent water and solute movement (Zimmermann, 1983). Gums or resins may also be produced in response to the wounding which will plug conduction pathways. The growth of adjacent parenchyma cells through pits in vessel walls to form tyloses may also be stimulated by the wounding. These responses may impede the initial distribution of injected substances and result in compartmentalization of materials adsorbed to cell walls or forced into intercellar spaces and cell wall matrices (Moore, 1978; Shigo et al., 1980). Trees will vary widely in their response to injection, however, since the capacity to form tyloses, to produce gums and resins, and to initiate barrier zone formation also varies.

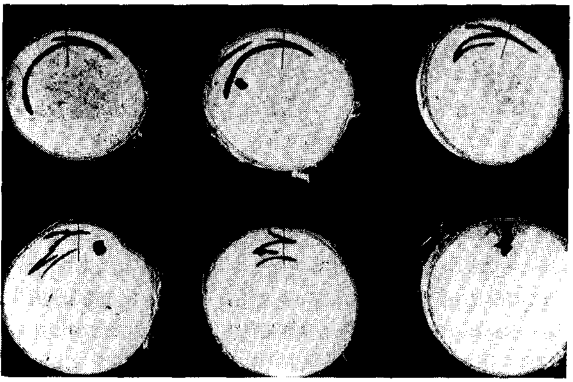

Figure 4. Interlocked water conduction pattern. (From Kozlowski and Winget, 1963).

Mechanism for transport and environmental influences. Water moves in the xylem by two mechanisms. In early spring before leaves appear and when soil moisture is readily available, water may be pushed up the xylem by root pressure. This phenomenon, common in herbaceous plants, occurs in only a few tree species (Kramer and Kozlowski, 1979). More commonly in trees, water is pulled up the xylem as a result of transpiration from the leaf surfaces. Water and dissolved solutes are pulled along gradients of decreasing pressures through the vessels and tracheids in a continuum held together by the cohesive forces between water molecules.

Absorption of water by roots lags behind transpirational loss from leaves during the day (Kramer, 1969). The severity of the lag influences the negative pressure in the xylem and is related to the availability of soil moisture and the vapor pressure gradient from the evaporating leaf surfaces to the atmosphere. Transpiration increases when the vapor pressure gradient increases. Table 2 illustrates the decline in vapor pressure gradient at a constant temperature as the relative humidity of the air increases. The absorption lag and negative pressure in xylem normally will be greater during a hot day with low humidity than during a cool day with high relative humidity. Uptake of trunk injected substances will be most rapid when environmental conditions produce low negative pressures in the xylem. Hence midday is better than early morning or late evening for ease of injection, high temperatures better than low ones, and low relative humidity better than high humidity. Internal xylem pressure can respond very rapidly to changes in environmental conditions. Even intermittent clouds can produce perceptible changes in the ease of trunk injection.

Phloem anatomy and transport. Two distinct kinds of phloem cells are involved in translocation. In Gymnosperms the phloem consists of sieve cells. These vertically elongated cells are characterized by sieve areas scattered along the cell wall. In Angiosperm phloem, sieve tube members also have sieve areas on the sidewalls, but these are characterized by a concentration of large pore sieve areas on the end-walls in a sieve plate. The sieve tube members form vertical stacks called sieve tubes that are interrupted only by the highly perforated sieve plates.

The mature functional phloem is a living cell with a network of cytoplasmic connections extending through the pits in the sieve areas and sieve plates. A carbohydrate called callose and a proteinaceous material called slime occur in the cytoplasm. Large quantities of these substances quickly accumulate around sieve areas and sieve plates when a cell is injured as a protective mechanism to prevent leakage of cell contents (Crafts, 1961).

The most widely accepted theory for translocation of substances in the phloem is the Munch pressure flow hypothesis. Different sugar concentrations in sieve elements and surrounding parenchyma cells at sources and sinks cause osmosis to occur. Water flows in at the source, building up pressure. Upon storage or utilization of sugar in the sink, the osmotic concentration of the phloem is reduced and water flows out. Because water is

Table 1. Length of vessels in trunks of various hardwood trees.

Species	*Average length*	
	Min	*Max*
	ft	
Diffuse porous		
Acer saccharum	2.7	3.1
Betula lutea	2.8	4.7
Fagus grandifolia	16.0	18.2
Populus tremuloides	3.3	4.3
Alnus rugosa	2.8	4.0
Ring porous		
Quercus rubra	28.0	50.0
Fraxinus americana	25.3	60.0
Ulmus americana	17.0	27.9

Table 2. Effect of increasing relative humidity on vapor pressure gradient from leaf to air at a constant temperature of 30°C.

Leaf and air temperature (°C)	30	30	30
Relative humidity of air (%)	20	50	80
Vapor pressure at evaporating leaf surface (kPa)	4.24	4.24	4.24
Vapor pressure in air at indicated temp. (kPa)	0.85	2.12	3.39
Vapor pressure gradient from leaf to air (kPa)	3.39	2.12	0.85

moving in at the source and out at the sink there is a mass flow of water in the sieve tubes. Substances dissolved in the water (e.g., sugars, insecticides, herbicides, growth regulators, etc.) flow along with the water.

Materials that can move across membranes and into the cytoplasm of phloem cells can be translocated in this tissue. The ability of a substance to penetrate phloem cell membranes generally depends on it having ionizable groups which can exist in a charged or noncharged form (Hess, 1985). Substances do not readily enter the phloem at injection sites because the positive pressure in the functional phloem flushes the material away until callose and slime formation seal off the injured phloem elements. Organic substances applied to the foliage or those absorbed by the roots are more likely to enter the phloem translocation system.

Root Anatomy and Uptake from Soil

The pathway of water and solutes from the root surface to vascular tissues may involve the symplast, the apoplast, or a combination of the two. In a young root which has not yet developed a vascular cambium, the zone of most rapid uptake lies behind the meristematic zone where root hairs develop. Here water and solutes may be absorbed by epidermal cells or their extending root hairs and, once inside the symplast, move through the cortex and endodermis into the xylem tissue (Figure 5). Another pathway is via the non-living cell walls and intercellular spaces. However, the apoplastic pathway is effectively blocked in young roots by the innermost layer of cortex, the endodermis. Endodermal cells contain suberin in the radial and transverse cell walls, the casparian strip, that is continuous across the cell wall and firmly attached to the cell protoplast (Esau, 1965). Consequently, the apoplastic pathway is effectively blocked and transport across the symplast of endodermal cells is necessary. The endodermis constitutes an important barrier to free uptake of water and substances directly into the xylem.

Because of the internal origin of lateral roots (Figure 5) and development of the vascular cambium, the endodermis is ruptured or entirely shed from older roots. Resistance to movement of molecules across these roots is imposed by the bark, phloem, and cambium. Although these tissues have low permeability, breaks around lateral roots, lenticels, and cell walls provide avenues for solely apoplastic movement to the xylem.

The impression is often given that older suberized roots are unimportant for absorption. However, it seems unlikely that the limited root surface area provided by young unsuberized roots could account for all the water and solutes absorbed (Kramer and Bullock, 1966). In fact, it appears quite certain that in trees, absorption is not restricted to the unsuberized regions of roots, but that a major part of absorption can occur through older roots when water and solutes are available near those roots (Kramer, 1969). Absorption by young roots is important because their growth places them in soil regions that may not have been exploited. Depletion quickly occurs in soil around older roots. Hence, placement of soil applied chemicals need not be restricted to the dripline or where roots are actively growing. Placement near large older roots will also allow for uptake.

Foliar Absorption

The protective leaf cuticle is a complex mixture of pectins, cutin, fatty acids, and waxy alcohols (Kolattukudy, 1970). It combines properties of permeability to water and dissolved solutes with water repellency. Water repellency is imparted by the hydrophobic constituents of the cuticle and by irregularities in the surface due to leaf hairs and deposits of waxes and resins. Wetting agents and surfactants facilitate foliar uptake because they reduce the surface tension and contact angle. Most foliar absorption occurs within a few hours after application. As solutes crystallize out of solution, their rate of absorption drops markedly (Mitchell et al., 1960).

There are numerous pathways of penetration into leaves. The greatest absorption occurs along the walls of hairs, in basal cells of hairs, or in epidermal cells surrounding hairs. Penetration into epidermal cells on both sides of veins and in guard cells also commonly occurs. Random breaks and cracks in the cuticle caused by insects or other environmental factors also produce avenues through the cuticle.

Once the cuticle is penetrated, solutes can move by diffusion through cell walls or can enter the protoplasm and move in the symplast (Kramer, 1969). Movement out of leaves generally occurs in the phloem. Because there can be considerable exchange between phloem and xylem, substances moved away from leaves via the phloem can be transferred to the xylem and then moved upward again. As discussed earlier, movement in phloem depends first on the ability of the substance to penetrate the membrane of phloem cells. The understanding of phloem loading and translocation is currently meager at best.

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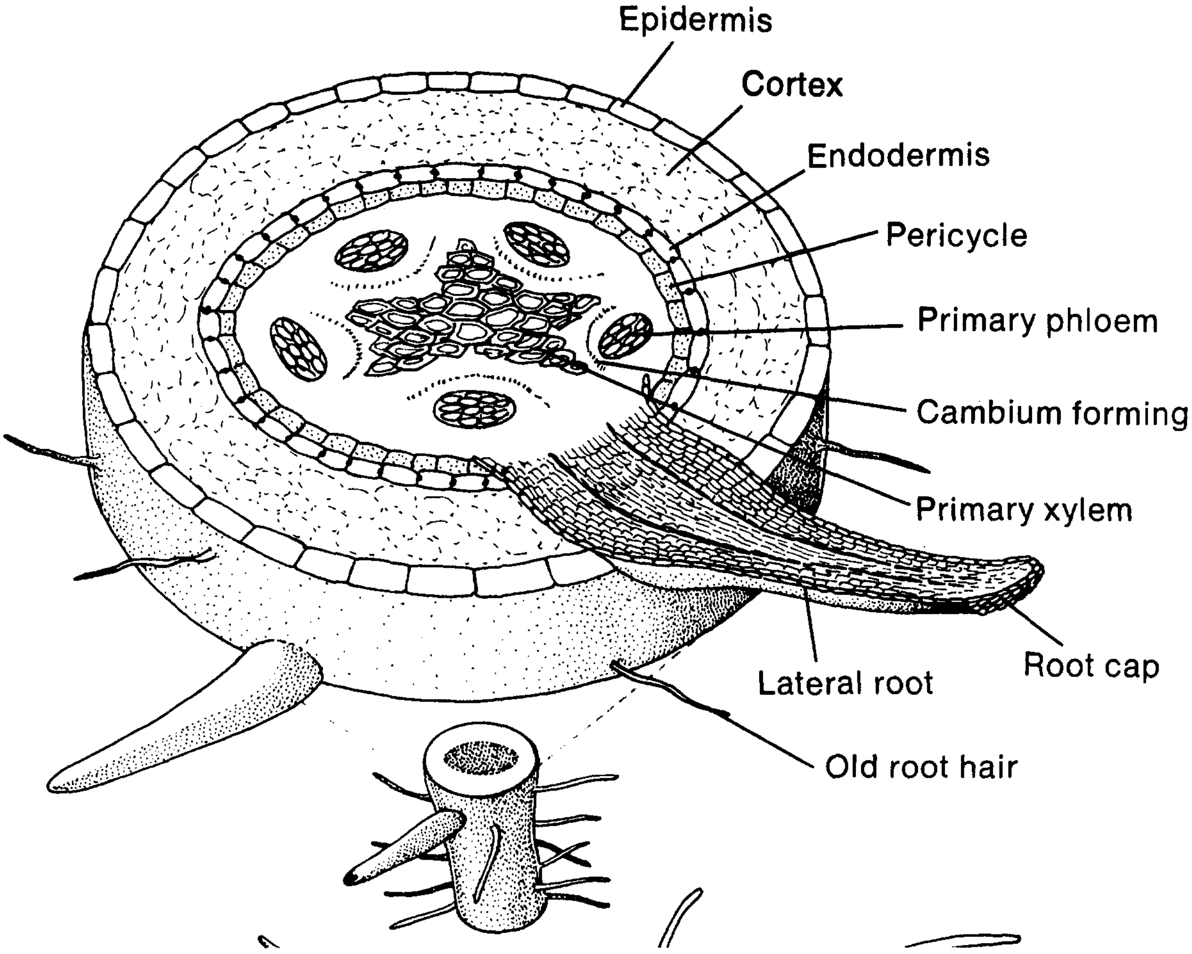

Figure 5. Diagram of young root showing tissue regions and the internal origin of lateral roots and cambium. (From Plants and Life, 1978, A. W. Haney with permission of Macmillan Publishing Co., Inc.).

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Abstract

JONOVIC, DONALD J. 1985. **Outside review helps stem a tide of trouble.** Am. Nurseryman 161(7): 73-74, 76, 80.

For most family companies, trouble is a creeping, seeping thing, not a sudden catastrophe. Flash floods could be dealt with, because most family business managers are used to handling unexpected gully washers. What defeats them is the slow drizzle, the gradually rising tide. A manager trying to cope with constant distraction and exhaustion doesn't manage very well at all. How does the concept of outside review apply? If the family business manager is already drowning, the last thing he would seem to need is another variable to deal with. Hard work does not inherently guarantee effectiveness. Too many family companies are closed corporations in practical as well as legal terms. Few solicit any kind of outside review of management decisions and policies. The only kind of expertise, knowledge, or advice available is the kind managers get from insiders who have been drawing on the same data base for almost a generation. The boss does have professional advisers: his attorney, accountant, banker, insurance agent, and so forth. At least they're around to keep him out of trouble. Results of a tendency to rationalize are the dusty, unsigned estate plan, the inadequate accounting system, the poorly administered pension fund, the confused insurance setup, and the lack of sophisticated cash management and financing.