HYDRAULIC PROPERTIES OF ROOTS OF LOBLOLLY PINE (*PINUS TAEDA* L.) SEEDLINGS

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CHAPTER - I

INTRODUCTION

Roots are axial multi-cellular structures of vascular plants that are usually present below ground and have strictly apical elongation growth. The distinguishing feature of the roots as compared to the shoots of vascular plants are the presence of a root cap and a more defined lineage of cells from the apical cells to tissues in the more mature parts of the roots. Roots have an endodermis, a protostele sometimes with a pith and an endogenous origin of laterals (Esau, 1965).

The traditionally recognized root functions are anchorage (Ennos, 1993; Bernston, 1994) and the uptake and longitudinal movement of water and mineral nutrients in the plant (Clarkson, 1985; Varney and Canny, 1993; Marschner, 1995). Roots are also involved in carbohydrate storage and root signals of soil conditions (Davies and Zhang, 1991). Roots are the major site of resistance to water flow to the shoot (Kramer and Boyer, 1995). They control the amount of soil water available to the plant; therefore, roots are a determining factor in the soil-plant-atmosphere continuum. Research has been made on root systems (growth, spatial distribution, anatomy) but hydraulic properties that characterize uptake and movement of water and nutrients in the root, are not well understood.

Water uptake by roots

Within the root, two pathways in series have to be considered. The radial pathway defines the movement of water from the soil to the lacunae of xylem tracheids, and the axial pathway controls the movement of water from the roots to the upper parts of the plant, through the xylem tracheids. To reach the tracheids, water has to move through a series of tissues each a potential barrier to flow (Fig. 1). First, water has to cross the epidermis, containing diffused suberin in its walls (Peterson *et al.*, 1978). As this layer of cells allows the passage of a dye molecule larger than water, the passage of water molecules should not be blocked by the epidermis.

Behind the epidermis is the multi-layered cortex (Esau, 1965). The outermost layer is designated a hypodermis. When Casparian bands are observed in the radial walls, this hypodermis is called exodermis. The rings of cortical cells are parenchyma cells and the innermost layer in the cortex is referred to as the endodermis. The cell walls of the endodermis may be modified by the presence of Casparian bands and/or suberin lamellae. Casparian bands form in the radial walls and the suberin lamellae in the inner surface of radial and tangential cell walls. Schreiber *et al.* (1999) found that Casparian bands were mainly

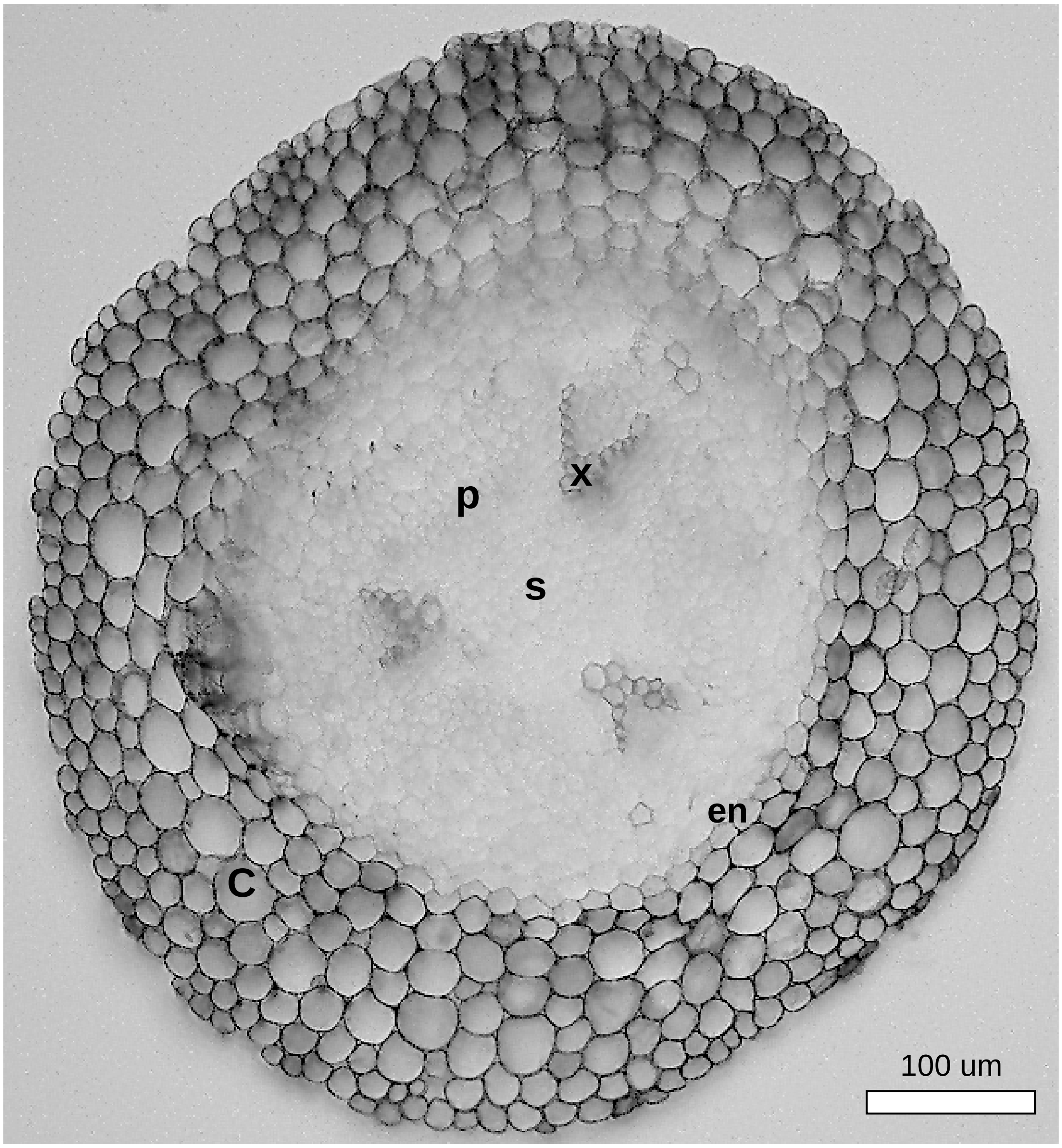


Fig. 1. Cross section at about 20 mm from the tip of a typical pine root (100X). The cortex (c) surrounds the central stele (s). The endodermis (en) is the last layer of cortical cells. Inside the stele, three xylem poles (x) are visible with phloem (p) between them.

composed of hydrophilic lignin, but also contained a lesser amount of hydrophobic substances like suberin, protein and carbohydrate. These results suggested that the Casparian bands would be fairly impermeable to ions and rather big polar solutes, but may allow some passage of water and small solutes (Clarkson and Robards, 1975; North and Nobel, 1991). The suberin lamella that is deposited after the Casparian bands, is mostly composed of hydrophobic substances such as polymers of phenols and fatty acids (Schreiber *et al.*, 1999). They are deposited between the plasma-membrane and the cell walls and are considered impermeable to water and solutes. In some species, it has been shown that the deposition of lamella is asynchronous, so that some endodermal cells develops lamellae and others not. The cells without the suberin lamellae are called passage cells (Peterson and Enstone, 1996) and are suspected to be the site of symplastic bypasses. The endodermis surrounds a group of tissues referred as the stele. The outermost layer of the stele is the pericycle, composed of parenchyma cells. Lateral roots and cork originate from this layer of cells. Inside the pericycle are the vascular tissues: phloem and xylem.

To reach the lacunae of the tracheary elements from the soil, three pathways are available to water flow: (1) apoplastic, (2) symplastic and (3) transcellular (Fig. 2). The apoplastic pathway contains the part of the plant outside the plasma membrane of the living cells (Münch, 1930), including cell walls, intercellular spaces and the lumenae of the tracheary elements. The symplast is the

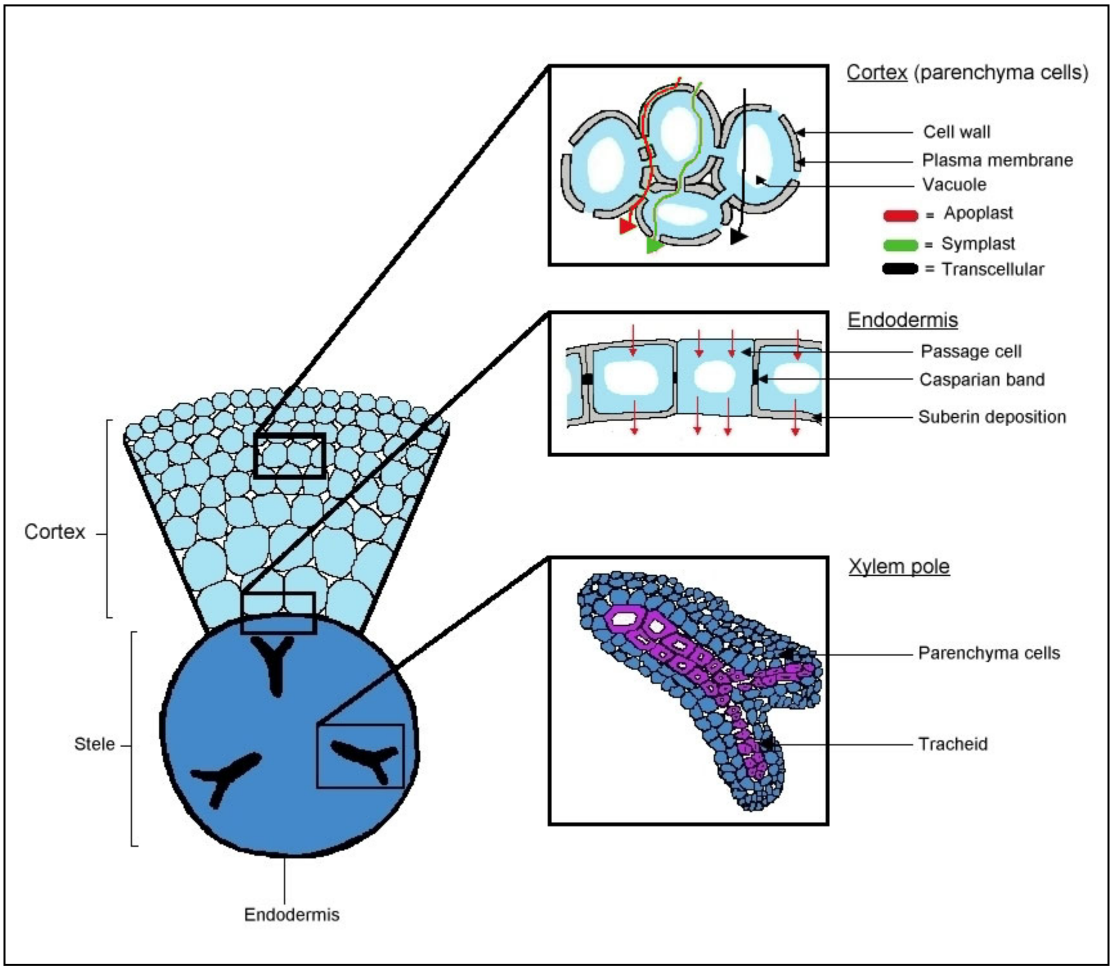


Fig. 2. Diagram representing the radial water pathways in the root.

continuum of cytoplasm connected by plasmodesmata, excludes the vacuole and requires the passage through one membrane. In the transcellular pathway, water crosses membranes to go from one cell to the next. Due to technical limitations, the transcellular and the symplastic pathways can not be measured separately with the current techniques.

Once in the lacunae of the tracheary elements inside the stele, water is under tension and is pulled toward the leaves of the transpiring plant. Xylem tracheids become functional when they die and the cell contents are absorbed. It has been observed that the xylem close to the tip of the roots is immature, resulting in a hydraulically isolated zone (McCully ad Canny, 1988; Peterson and Steudle, 1993; Frensch and Hsiao, 1993). In conifers, the tracheids are very short, about 3 mm long. Water enters tracheids through numerous small openings termed “pits” in the secondary walls. Secondary walls form an arch, resulting in a bowl-shaped chamber around the pits. This type of connection is called “bordered pit” (Fig. 3). At the center of each bordered pit is the “pit membrane”, which is formed from the original primary walls and middle lamellae. In the conifers, the pit membrane has been specially modified: the peripheral portions are digested such that only a loose network of cellulosic fibrils remains, and water can pass with a minimum of friction. This is the “margo”. The central region of the membrane, however, is thickened with secondary wall material and lignified and become the “torus”. The bordered pits are usually opposite each other but an alternate arrangement is also possible (Bailey, 1953). The alternating

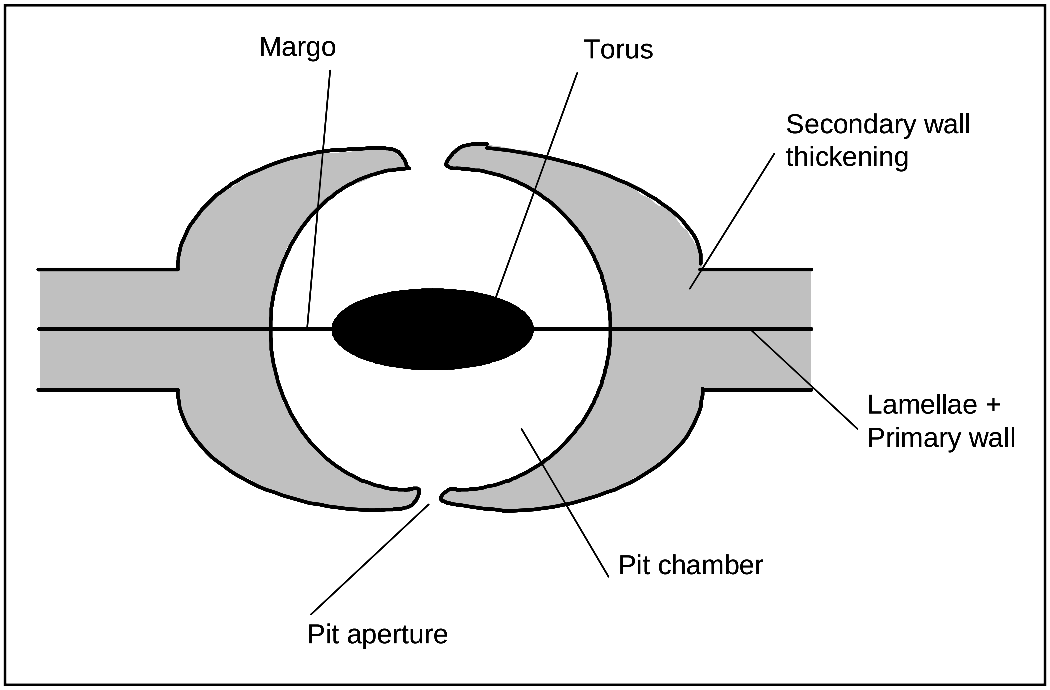


Fig. 3. Diagram of a bordered pit structure.

arrangement of pits occurs most frequently toward the overlapping ends of the tracheids where the pits are aggregated (Bannan, 1965b). Due to their shortness, for every ten millimeters of axial flow, water must cross many cell walls to pass through tracheids. According to Gibson *et al.* (1985), the bordered pits are the most important resistance to axial water flow in tracheid-bearing plants, representing about 70% of the total resistance to axial water flow in the fern *Pteris vittata*.

It appears that overall the main resistance to water transport occurs in the radial pathway, from the soil solution to the lacunae of xylem vessels through layers of tissues, and not in the axial path, within the vessels (Frensch and Steudle, 1989; Frensch, 1997; North and Nobel, 1991; Steudle and Peterson, 1998). Near the root tip, both radial and axial components have to be taken into account (Frensch and Hsiao, 1993; Melchior and Steudle, 1993). The axial conductivity may be reduced near the tip where the vessels are immature and in the meristematic zone (McCully and Canny, 1988; Peterson and Steudle, 1993; Frensch and Steudle, 1989).

1- Forces affecting water uptake into roots

In roots, water is not taken up actively, but instead moves passively through the roots in response to a water potential gradient set up by transpiration of the leaves and by osmosis. Thus a water continuum exists between the soil and the atmosphere as described in the tension-cohesion theory (Dixon and Joly, 1896). As a result water moves under tension in the xylem vessels. The existence of two parallel pathways (apoplastic and symplastic) for water movement across the root cylinder results in two different driving forces: osmotic and hydrostatic (Steudle and Peterson, 1998). Hydrostatic driving force occurs in transpiring plants, resulting in the movement of water in the apoplast which lacks membranes. Osmotic driving forces move water in roots and require membranes (cell-to-cell pathway). The osmotic force is most important at low flow as in non-transpiring plants. At low transpiration, most flow is cell-to-cell driven by osmotic forces and at high transpiration most flow is apoplastic driven by a hydrostatic gradient.

2- Potential barriers to water movement and their development

Along a developing root, the relative contribution of hydrostatic and osmotic flow may change when apoplastic barriers that modify the flow around root protoplasts are formed in the endodermis (Frensch *et al.*, 1996; Fig. 4). The passage of various substances is affected differently depending on the primary route by which they move. Suberization of the endodermis in more mature regions of the root is frequently associated with a reduction in water uptake (Clarkson and Robards, 1975; Melchior and Steudle, 1993). The classical view was that water uptake mostly occurs behind the root tips. Recent findings

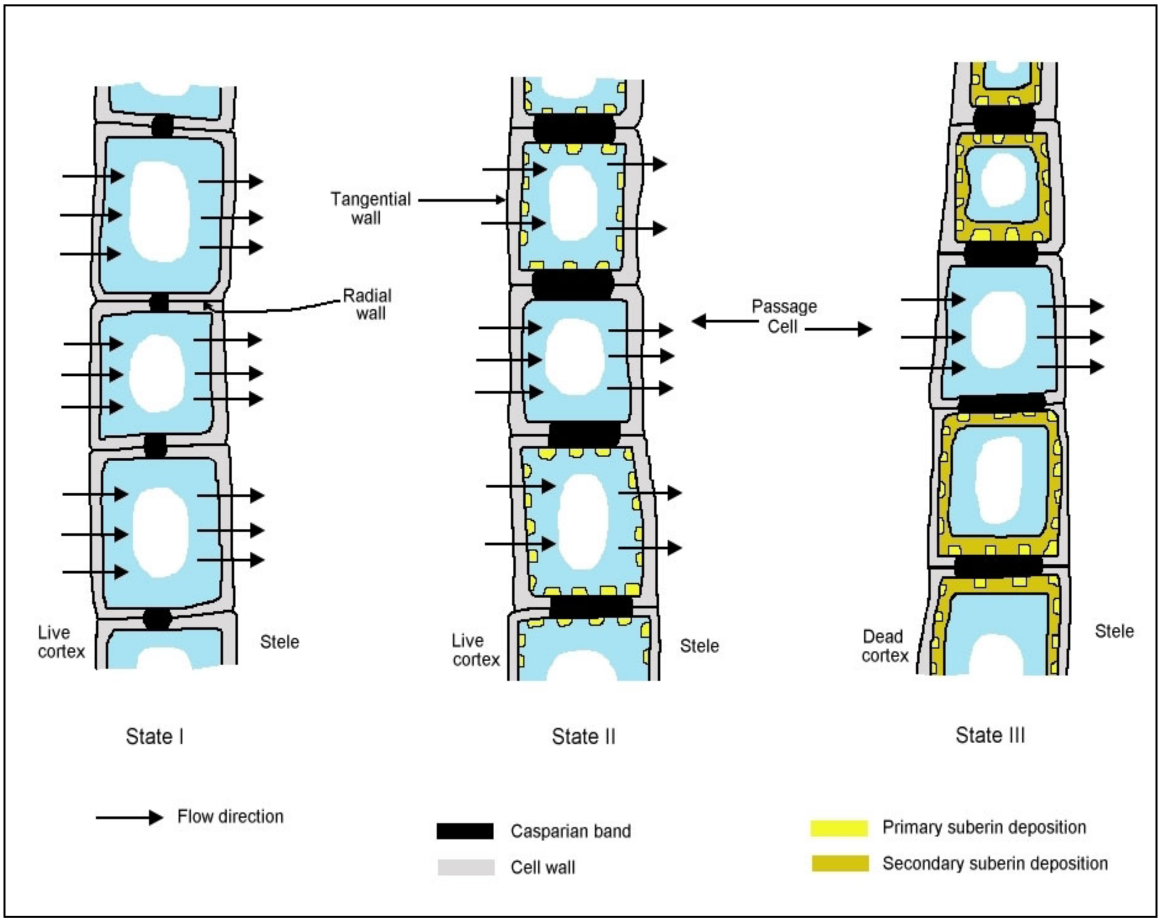


Fig. 4. Diagram representing the different developmental stages of the endodermis and their influence on a hypothesized water flow.

indicate the endodermis is the main barrier to ions but not to water (Steudle *et al.*, 1993). The different interactions of water and ions with the endodermis can be explained by a difference in membrane permeability. The development of hydrophobic barriers, such as Casparian bands in the endodermal radial walls (state I; Peterson and Enstone, 1996) reduces water movement into the stele, but not the ions as they mostly move symplastically (Peterson and Steudle, 1993). When suberin lamellae develop on the inner surfaces of all walls of endodermal cells (state II and for some species state III), the only way for water and ions to cross the endodermis is through intact plasmodesmata (Peterson and Enstone, 1996). As mentioned before, the endodermal cells mature asynchronically resulting in the presence of cells at the state I, called passage cells, next to suberized cells. These cells are usually aligned with the poles of the protoxylem facilitating the passage of water. As the endodermis mature (state II and III), the number of passage cells decreases until complete endodermal suberization, resulting in a very low water and ion uptake capacity. In some species, a cork layer forms below the suberized endodermis, and further decrease the absorptive ability of the root (McKenzie and Peterson, 1995). These differences in endodermal suberization stages and the progressive death of the cortex lead McKenzie and Peterson (1995) to define three zones: The white zone at the tip with little suberization, a more suberized condensed tannin zone and a completely suberized cork zone.

3- Uptake along the length of roots

Because changes in structure occur with age and environment, the anatomy of the root is non-uniform along its length, affecting the permeability to water and solutes (Wilcox, 1964; McCrady and Comerford, 1998; Fig. 5). The length of the various zones varies widely, depending on the species and growth conditions. Several studies (Kramer and Bullock, 1966; Chung and Kramer, 1975; Van Rees and Comerford, 1990) observed that sometimes root systems of field-grown trees contained very few growing tips during periods of high transpiration, suggesting that water absorption must occur through woody roots. The suberized roots in loblolly pine represented about 90% of the root system (Kramer and Bullock, 1966), but it was not clear whether their suberized roots were woody or just brown in color with no secondary growth. Wilson and Atkinson (1978) estimated that the proportion of brown (suberized and woody) root length ranged, for young *Malus pumila* Mill. trees from 15 to 100% of the total root length; The fact that a large proportion of the root system is composed of woody roots suggests that their contribution to uptake is significant for field-grown trees, particularly at certain times of the year. McFall *et al.* (1990, 1991) found a decrease in soil moisture around suberized pine roots growing in sand. Sanderson (1983) found in barley roots that the zone with suberin lamellae was the site of greatest absorption.

Other experiments showed that most of the water was absorbed close to the tip,

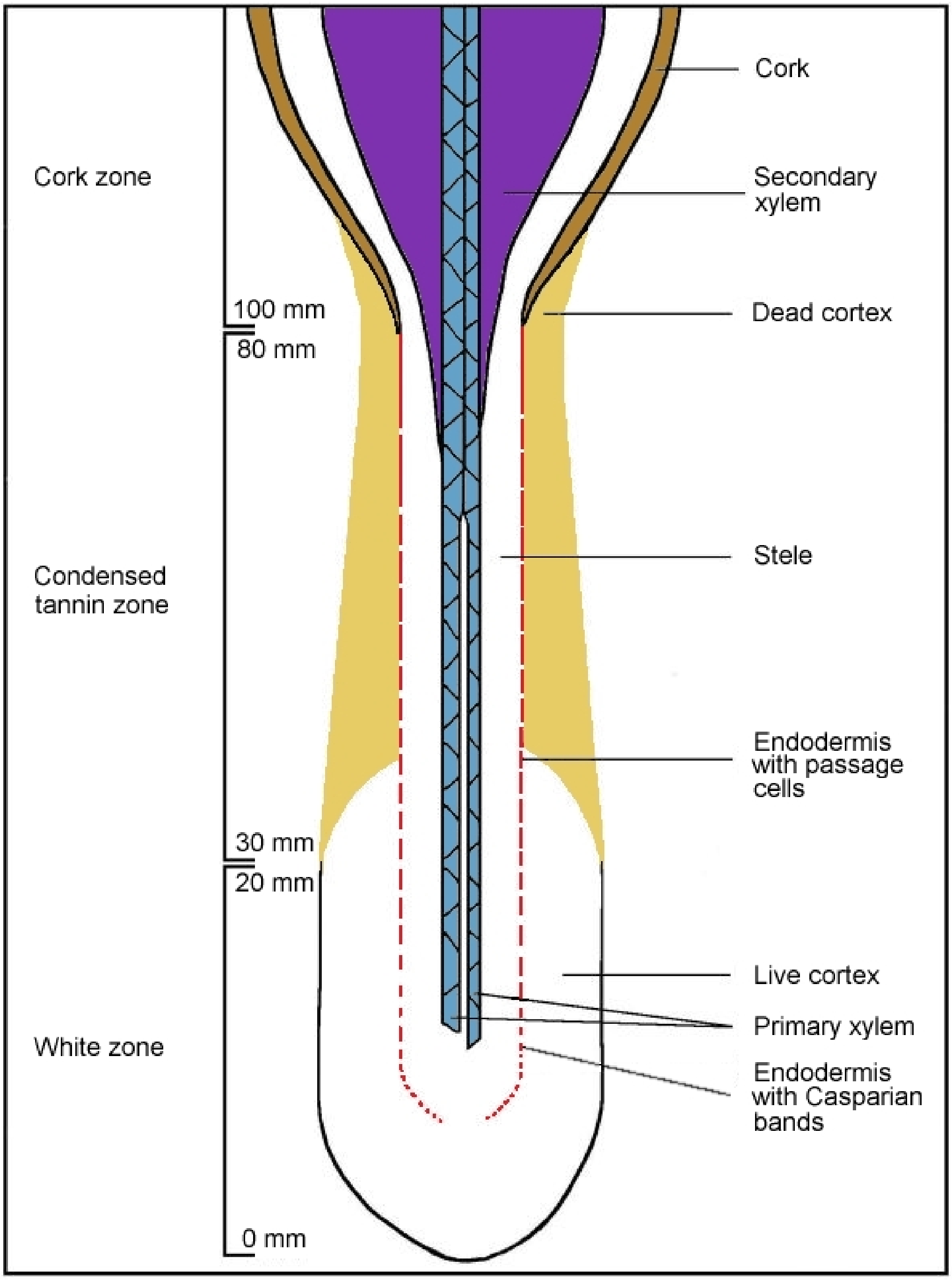


Fig. 5. Diagram representing the longitudinal structure of a loblolly pine root (redrawn from Peterson *et al.*, 1999).

behind the hydraulically isolated meristematic zone (McCully and Canny, 1988; Enstone and Peterson, 1992; Frensch and Hsiao, 1996). Steudle and Frensch (1989) found decreased water uptake more than 200 mm behind the root tip in maize. Melchior and Steudle (1993) also showed that the basal zones ($z > 140$ mm) of onion roots had a low contribution to water uptake. In A*gave deserti*, young roots showed greater water acquisition than older roots (North and Nobel, 1991).

4- Membranes and water channels

In some species, the main resistance to water uptake seems to be evenly distributed over the entire living tissues (Steudle *et al.*, 1993; Rieger and Litvin, 1999). During cell-to-cell transport, water flow has to cross many cell layers and two plasma membranes per cell layer, which results in high hydraulic resistance. Modifications in the cell-to-cell pathway may allow more flexible control of root water transport (Henzler and Steudle, 1995; Steudle, 2000). There is growing evidence that membranes have water channels called aquaporins. Aquaporins belong to an ancient family of membrane proteins, the Major Intrinsic Proteins (MIPs). Reizer *et al.* (1993) hypothesized that they derived from a single prokaryote gene transmitted to the eukaryotes. The polypeptide chain, approximately 30 kD in size, spans the membrane six times to form the water pore and facilitate the passive bi-directional flow of water through the membrane (Maurel, 1997; Tyerman *et al.*, 1999). Aquaporins are present in both the plasma membrane and the tonoplast for a wide range of plant tissues (Maurel, 1997). They seem to be very abundant in the apical growth zone (Chaumont *et al.*, 1998), whereas their presence is restricted to the endodermis and xylem parenchyma cells in mature regions (Barrieu *et al.*, 1998). This distribution has been found not only in maize roots, but also in tobacco (Yamada *et al.*, 1997) and sunflower roots (Sarda *et al.*, 1999). Mercurial reagents, such as $HgCl_2$, inhibit water flow in most aquaporins via non-specific interactions with cysteins residues at various positions (Shi and Verkman, 1996). This inhibition is reversed by 2-mercaptoethanol. Although it is known that some aquaporins are insensitive to mercurial treatment (Kammerloher *et al.*, 1994) and that mercurial inhibition is not specific to aquaporins, this inhibition/reversal makes possible the study of their role in root water uptake (Wan and Zwiazek, 1999; Barrowclough *et al.*, 2000). It is not known how aquaporins are regulated. It has been proposed that their activity could be controlled by phosphorylation (Johansson *et al.*, 1998) and other results show that the regulation could be under environmental control (Henzler *et al.*, 1999).

5- Composite model

Water flow across the root is driven by both hydrostatic and osmotic forces. The relative contribution of the two components varies, depending on conditions. The existence of two parallel pathways for water and solutes across the root cylinder is very important. The composite transport model (Steudle *et al.*, 1994b) explains the difference between osmotic and hydraulic water flow, the low root reflection coefficient (σ_{sr}) and the variability of root hydraulic resistance. The absence of membranes along the apoplastic path, results in a reflection coefficient close to zero. Osmotic gradients cannot induce water flow in the apoplast and water flow will be driven by hydrostatic force. In contrast, the cell-to-cell path requires water and solutes to cross membranes with selective properties (σ_{sr} close to unity) and water flow will be driven by osmotic pressure. At low or zero transpiration, water uptake is largely caused by osmotic forces (Steudle and Frensch, 1996). As the hydrostatic pressure gradient increases due to an increased tension in the xylem resulting from transpiration, the apoplastic flow increases and will eventually becomes the dominant path. The root reflection coefficient (σ_{sr}) indicates the passive selectivity of a membrane barrier. It is a measure of interactions between solutes and water within a membrane barrier. Its values range from zero (osmotic barrier has no selective properties at all) to unity (solutes are completely blocked by the barrier). Roots do not behave like ideal osmometers as plant cells do with a σ_{sr} close to unity. In fact, measurements show that root σ_{sr} is smaller than unity, ranging from 0.1 to 0.6 (Steudle and Peterson, 1998) depending on species, stage of development and growth conditions. Low root reflection coefficients result from apoplastic bypasses such as immature and permeable Casparian bands (Peterson and Enstone, 1996; Steudle *et al.*, 1993; Schreiber *et al.*, 1999). The low reflection coefficient in roots is due to the fact that two parallel pathways (apoplastic and cell-to-cell) with different selective properties (σ_{sr}) contribute to the overall water flow. As σ_{sr} of the apoplast is close to zero and σ_{sr} for cell-to-cell is close to 1, the overall (root) σ_{sr} should be somewhere between these two values.

6- Ectomycorrhizae

The term mycorrhiza refers to the intimate association or symbiosis between plant roots and specialized soil fungi that colonize the cortical tissue of roots. The majority of land plants form diverse symbiotic associations with fungi. The association is characterized by the movement of plant-produced carbon to the fungus and mineral ions acquired by the fungus to the plant. Mycorrhizal fungi form a link between plants and the soil. They usually proliferate both in the root and in the soil. The hyphae take up nutrients from the soil solution and transport them to the root. By this mechanism, mycorrhizae increase the effective absorptive surface area of the plant (Piché *et al.*, 1983, Rousseau *et al.*, 1994).

In pine, roots are associated with ectomycorrhizal fungi belonging to Basidiomycotina and Ascomycotina (Sylvia, 1990, 1998). Ectomycorrhizae are often found on shallow roots, immediately below the litter layer, into which the fungi extend their hyphae. Ectomycorrhizae produce a mantle of hyphae covering the surface of the root, plus a Hartig net of tissue extending into the root. The Hartig net is formed as hyphae from the fungus penetrate the root along the middle lamellae between the root cortical cell walls and never enter into them. Moreover the fungi do not penetrate into the stele (Clarkson and Robards, 1975). The fungi and the plants principally fuse walls, forming a complicated, three dimensional structure where it is difficult to determine where the plant wall ends and the fungal wall begins, thus facilitating exchanges with the plant. A consequence of the presence of the ectomycorrhizae in the root is a change in the shape of roots making them shorter, broader or forked with two white tips. Ectomycorrhizae tend to form on lateral feeder roots, rather than primary roots. Ectomycorrhizal fungi also produce rhizomorphs, slender hyphae that extend into the soil from the mantle. These strands can reach centimeters to meters out into the soil, enabling the fungi to extend the root capacity to take up water (Parke *et al.*, 1983; Mudge *et al.*, 1987) and mineral ions (Vogt *et al.*, 1991). However, it has been observed that ectomycorrhizal associations can have positive, negative or neutral effect on root water absorption (Sands and Theodorou, 1978; Dixon *et al.*, 1980; Dudridge *et al.*, 1980; Coleman *et al.*, 1990). To be effective in water and nutrient absorption, the hyphae must be distributed beyond the depletion zone (Marschner, 1986). A nutrient depletion zone develops when the nutrients are removed from the soil solution more rapidly than they can be replaced by diffusion (Sylvia, 1990).

Lateral roots

Longitudinally, the lateral root primordia are typically initiated just behind the root hair zone, but they can occur either closer to the apex or farther back (Blakely *et al.*, 1982, Mallory *et al.*, 1970). Apparently, the lateral root primordia do not arise from single cells in the pericycle but result from the division and reprogramming of parenchyma and pericycle cells located between the endodermis and the xylem within the stele of the mother root (Bell and McCully, 1970; Luxová, 1990). Lateral roots are initiated internal to the endodermis in the immediate vicinity of vascular tissues of the parent and grow out through mature tissues (endodermis, cortex) of the parent root. By the time the root emerges, a well-defined apical meristem has been established, and even a root cap may be present, giving a root structure to the laterals including a stele with xylem and phloem, endodermis and cortex.

As the lateral root begins to form its own endodermis, parenchyma cells at the point of origin of the root re-differentiate as a new endodermis that connects the endodermis of the parent root with that of the new lateral (Esau, 1940; Dumbroff and Peirson, 1971; Peterson *et al.*, 1981; McCully *et al.*, 1988). The xylem tissues of branch roots develop directly from provascular cells produced by their meristems. Lateral roots are very similar in structure to the parent root with xylem and phloem tissues at the center of the stele, an endodermis, and a cortex. The emergence of the root causes considerable damage to the cortex and the endodermis, and results in a transitory, localized apoplastic permeability that is a danger point for penetration by bacteria and fungi. Until the apoplastic barriers are restored (endodermis junction, filling of the rupture point with suberized and lignified cells), the break may represent an apoplastic pathway for water into the stele of the main root (Dumbroff and Peirson, 1971; Peterson *et al.*, 1993). Experiments with young laterals of broad bean showed that apoplastic pathways existed at the base of lateral roots shortly after they emerged from the main root (Peterson *et al.*, 1981). Peterson and Lefcourt (1990) pointed out the lack of Casparian bands and mature xylem in early stages of development of lateral roots in broad bean.

The emergence of lateral roots increased the radial hydraulic conductivity of the tissues outside the stele of *Opuntia fiscus-indica* (L.) (North and Nobel, 1995). Because of the existence of living tissue (at least for a time) and the small size of vascular elements, junction resistances (hydraulic constriction) probably exist because the new root xylem must be joined to already matured xylem tissues in the parent stele (Zimmermann, 1983; Luxová, 1990; North *et al.*, 1992; Shane *et al.*, 2000). As the xylem strands of the lateral root are opposite to the xylem pole of the main root, abundant parenchyma cells are found between the new stele and the old one; these cells are able to differentiate into tracheary elements to establish the connection (McCully, 1975).

Branch-root xylem joins the main-root xylem through smooth elbows in the upward (proximal) direction, but distal connections are much less distinct. The vascular cambium forms after branch root development and lays down continuous xylem between the main root and the proximal side of the lateral root so that the new xylem forms a continuous conductive tissue where water can be carried inward and upward. On the distal side, the vascular cambium of the lateral root builds concentric layers of xylem tissues, but the vessels appear to make a “T-junction” as they meet the xylem of the main root (Kepler, 1983). There appears to be less resistance to upward than downward passage of water where a woody branch root joins the main root. Water in a woody root, then, moves in a definite group of xylem tissues from branch to parent root and upward in a ‘cablelike’ arrangement (Esau, 1965; Kepler, 1983).

The classical view is that most of the water is absorbed near the tip. However, little water enters through the meristematic regions (Frensch and Steudle, 1989), probably because of a lack of functional xylem. The xylem becomes functional farther back, but suberization and lignification of the endodermis usually reduce the permeability of older regions. Indeed, numerous studies have shown that the older proximal parts even when suberized also absorb water but generally at a reduced rate (Kramer and Bullock, 1966; Sanderson, 1983; MacFall *et al.*, 1990; Varney and Canny, 1993). Addoms (1946) observed absorption of weak aqueous dye solutions by older, suberized roots of yellow poplar, sweet gum, and shortleaf pine. She observed that these roots did not appear to absorb unless younger branch roots were excised and the wounds sealed. This suggests that the absorption by older roots is masked by the water flow into branch roots, or would occur only if the necessity arose, perhaps due to the increased xylem tension caused by the inability to feed the transpirational stream by the removed branch roots.

Aloni *et al.* (1998) observed that lateral roots of dicotyledonous species were more permeable to fluorescent berberine than the main roots. In contrast, McFall *et al.* (1991) showed that lateral roots of Loblolly pine seemed not to be the predominant path of water into the taproot, although they provided a path of low resistance to water flow. In maize roots, the development of laterals seemed to have only a small effect on water uptake (Steudle and Frensch, 1989). These older parts, however, have generally much higher capacity for axial transport due to the secondary xylem development, resulting in a basipetal increase in root diameter (Wenzel *et al.*, 1989; Wang *et al.*, 1991; Krasowski and Owens, 1999)

Hydraulic properties of the xylem

Water evaporates from a plant through its stomata. This water is replaced by uptake through the roots and transported in xylem conduits to the site of evaporation. Thus the efficiency of the root water transport system (the xylem vessels and/or tracheids) can significantly affect water movement by imposing conductivity constraints (Tyree and Ewers, 1991). The Hagen-Poiseuille equation has been widely used to predict conductances and flows in the xylem (Zimmermann, 1971, 1983; Milburn, 1979; Nobel, 1983).

To describe fluid movement in the xylem quantitatively, we need to relate the flow to the driving force causing the movement. The flow rate (F, $m^3\ s^{-1}$) through a capillary is proportional to the applied pressure gradient (dP/dx, $MPa\ m^{-1}$) and the hydraulic conductivity (K_h, $m^4\ s^{-1}\ MPa^{-1}$)

$$F = K_h * \frac{dP}{dx} \qquad (1)$$

The best known theoretical result describing flow of a viscous fluid in a tube is that of Hagen and Poiseuille (Streeter and Wylie, 1985). They found that the volume of a fluid moving in unit time along a cylinder is proportional to the fourth power of its radius, and that the movement depends linearly on the drop in hydrostatic pressure. For flow in a cylinder of radius r, and hence cross-sectional area πr^2, the volume flowing per unit time and area (F) is

$$F = \frac{\Pi r^4}{8\eta} * \frac{dP}{dx} \qquad (2)$$

Where r is the radius (m) of the cylinder, η is the viscosity of the solution (Pa s), and dP/dx is the gradient of the hydrostatic pressure. Combining equation (1) and (2) gives

$$K_h = \frac{\Pi r^4}{8\eta} \qquad (3)$$

Poiseuille's law is obtained from the general principles of hydrodynamics provided that some precise conditions are fulfilled. The rigidity and continuity of walls must be assured; the fluid entry or exit along the walls of the pipe must be negligible; the radius of the pipe must be constant. This equation also assumes that the fluid in the cylinder moves in layers, or *laminae*, each layer gliding over the adjacent one (Streeter and Wylie, 1985). Such laminar movement occurs only if the flow is slow enough to meet a number deduced by Reynolds in 1883. This number can help to indicate whether the flow is laminar or turbulent. It indicates the ratio of inertial forces which tends to keep things moving to viscous forces due to frictional interactions, which tend to slow things down. Specifically, the dimensionless quantity $\rho Fd/\eta$ must be less than 2000 (ρ is the solution density and d is the cylinder diameter); otherwise, flow becomes turbulent, and Poiseuille's law is no longer valid. Consequently, in an ideal capillary, Poiseuille laminar flow is stationary at the wall of the cylinder, and its velocity increases toward the center of the tube.

However, tracheary elements in plants differ from ideal capillaries. Vessels are of finite length and some of them are very short. Water must move many times from one element to the next, laterally through the membrane of the bordered pit areas in the case of tracheids, and longitudinally through perforation plates in the case of vessels. Also the walls are often not very smooth, and may contain irregularities such as warts and ridges. The flow is therefore not ideally paraboloid but more complex.

Two types of conducting cells can be distinguished in the xylem: the vessel members found in angiosperms and the more primitive tracheids in angiosperms, gymnosperms and the lower vascular plants. Vessel members are composed of stacked columns of short, wide cells whose end walls are partly or completely dissolved (perforation plate) during late stages of cell maturation forming long xylem vessels (continuous tube). The ends usually taper to a point, which causes lateral movement of water where two vessels, the ending and the continuing one, run side by side. This structure allows conductances to be nearly 100 % of that predicted for ideal pipes (Dimond, 1966; Zimmermann, 1971). Compared to vessel members, most of the tracheids are shorter and tapered at the ends, causing water to move frequently laterally from one tracheid to the other.

Lateral movement of water between vessels or tracheids occurs through circular bordered pits. These pits are composed of an overarching secondary wall (the circular border) exposing in its center a large membrane area (the primary wall) across which water moves. Coniferous trees such as loblolly pine have different bordered pits. The center of the pit membrane remains more or less unchanged (slightly thicker), while its outer portion loses the wall matrix substances. A cellulosic network of fibril bundles then remains which appears quite permeable. This system is referred as a torus (central, thick pit membrane) and a margo (peripheral, porous pit membrane), surrounded by a circular border.

According to Poiseuille’s law for ideal capillaries (Gibson *et al.*, 1985; Zimmermann, 1983), hydraulic conductivity should be proportional to the sum of the vessel radii, each raised to the fourth power. Xylem conductances and flow have been routinely predicted with this equation (Zimmermann, 1971, 1983; Milburn, 1979; Nobel, 1983). However, studies have indicated that measured values of hydraulic conductance per unit length differ from predicted values (Gibson *et al.*, 1984, 1985; Calkin *et al.*, 1985; Gibson *et al.*, 1985; Zimmermann, 1971). Although measured xylem hydraulic conductivity was equal to Hagen-Poiseuille prediction in certain vessel-bearing angiosperms (Dimond, 1966; Zimmermann, 1983), in most vessel- and tracheid-bearing plants measured hydraulic conductivities are much less than those predicted from xylem diameters (Table 1).

Various explanations for these discrepancies have been proposed which can be roughly separated in two groups. The first group has tried to explain deviations within the Hagen-Poiseuille analogy by variations in vessel diameters, the role of scalariform perforation plates (Schulte and Castle, 1993; Ellerby and Ennos, 1998) and vessel ends (Chiu and Ewers, 1993), or the existence of air-embolisms or other physical blockages in xylem vessels (Sperry *et al*, 1988). The second group has focused on the inadequacies of the Hagen-Poiseuille analogy due to the implicit assumptions (Giordano *et al*, 1978) or even questioned the cohesion-tension theory of sap flow in plants (reviewed by Tyree, 1997; Canny, 1995; Milburn, 1996; Zimmermann *et al*, 1993).

Table 1: Hydraulic conductivity of xylem of various species in percent of the theoretical value of ideal capillaries of the same diameter

Plant species	**Hydraulic conductivity as a percentage of the calculated Poiseuille value**	**Author**
Pteris vittata (fern) stem	50	Calkin *et al.* (1985)
Angiosperm		
Vitis vinifera (grapevine), 3 years old	100	Berger (1931)
Aristolochia siphon (Dutchman's pipe), 2 years old	100	Berger (1931)
Phaseolus vulgaris L.cv. Ouay (bean) roots	40	Sands *et al.* (1982)
Crataegus coccinea (hawthorn)	21.7	Münch (1943)
Ruscus hypoglossum L. terete stems	66	Schulte and Gibson (1988)
Drimys wintera petiole	52	Schulte and Gibson (1988)
Trochodendron aralioides petiole	88	Schulte and Gibson (1988)
Rhododendron ferrugineum, 3 years old	20	Berger (1931)
Dendranthemaxgrandiflorum (chrysanthemum) stem	70	Nijsse *et al.* (2001)
Ferocactus acanthodes roots	77-93	North and Nobel (1992)
Opuntia Ficus-indica roots	68-91	North and Nobel (1992)
Fagus (beech) root wood	37.5	Riedl (1937)
Betula (birch) root wood	34.8	Riedl (1937)
Salix (willow) root wood	34.8	Riedl (1937)
Quercus (oak) root wood	53-84	Riedl (1937)
Corylus avellana (azelnut)	33.3	Münch (1943)
Populus robusta (poplar)	21.7	Berger (1931)
Gymnosperm		
Dioon spinulosum Dyer. (cycad) petiole	32	Schulte and Gibson (1988)
Ginkgo biloba L. petiole	6	Schulte and Gibson (1988)
Podocarpus nagi (Thunb.) young stem	18	Schulte and Gibson (1988)
Abies pectinata (fir)	26-43	Münch (1943)
Pinus taeda L. (loblolly pine) roots	55	Sands *et al.* (1982)
Model of bordered pit	70	Lancashire and Ennos (2002)

In conifers, water movement occurs through the closed-ended tracheids. Consequently, water must move laterally through bordered pits with a torus/margo system to enter the lower half and leave the upper half of the tracheids on the way up to the leaves. Such structure might be responsible for the differences between measured and theoretical axial conductivity. Two reasons may explain the increased resistance (Calkin *et al.*, 1986). The first reason is the narrowness of the ends. A tracheid has three different components: a tube (more or less cylindrical) with a constant diameter and the two tapering ends, where diameter decrease gradually. As water flow through a cylinder is correlated to the fourth power of its diameter (Poiseuille), the tapering of the ends decrease water flow by increasing the lumen resistance to water movement. The second reason is the lateral movement through the bordered pits, which adds another resistance component in series with the pipe resistance of the cell lumen (Calkin *et al*, 1986; Schulte and Gibson, 1988). All the available evidence suggests that pit resistance can be significant. In a range of gymnosperms and angiosperms it has been estimated to account for between 12-70% of the total resistance (Schulte and Gibson, 1988; Zimmermann, 1971). Furthermore, these authors found that the relative importance of pit resistance increased with tracheid diameter.

Most of the water transport in the direction of the shoot occurs in the xylem tracheids. The hydraulic resistance of the xylem is an important characteristic that determines the rate at which water can be supplied to the shoot

(Zimmermann, 1983). The classical view is that most of the water is absorbed near the tip. However, numerous studies have shown that the older proximal parts, even when suberized, also absorb water, but generally at a reduced rate (Kramer and Bullock, 1966; Sanderson, 1983; Varney and Canny, 1993). These older parts have high axial conducting capacities due to the secondary growth. Indeed ontogenetic gradients exist along the roots. At the tip of the root, tracheids begin as parenchyma cells derived from the procambium (primary growth), and initially have dense protoplasm, small vacuoles and thin primary walls (O'Brien, 1981; Barnett, 1981). The cells enlarge, becoming more vacuolated and retaining just the primary wall until they are full sized. As the deposition of the secondary wall starts the cytoplasm begins autolysis. Tracheids are dead cells when mature and functional. Any region not covered by lignified secondary wall is subjected to a partial enzymatic degradation, resulting in the primary wall being just a mat of fibrils (O'Brien, 1981). Such areas are referred as the pit fields, but the mechanism explaining how the secondary wall of one cell matches that of the adjacent cell remains unknown. The primary xylem is composed of the protoxylem, which differentiates while young and close to the root apex, and the metaxylem, which is older at the time of differentiation and has, consequently, much larger cells (Brouwer *et al*, 1981; Torrey and Clarkson, 1975). The first cells to differentiate are the most exterior and are small. After these come cells that are progressively larger and are located deeper within the stele. Such organization, with the protoxylem exterior and the metaxylem toward the center of the root stele, is called an exarch xylem. Roots with one protoxylem pole is referred as monarch, two (diarch), three (triarch), four and more (polyarch). Loblolly pine (*Pinus taeda* L.) roots are usually diarch and sometimes triarch.

As the plant develops and becomes larger, more water and nutrients are required. The root system begins to branch and produce higher order laterals. As the distal parts of roots become branched and increase their absorptive power, the extra water that is absorbed must be moved through the established proximal portions of the root, and extra conducting capacity is needed. By undergoing secondary growth, plants produce new tracheary elements to increase the root transport capacity.

Rationale

As the plant grows, the complexity of the root system increases to provide anchorage and optimize water and mineral uptake capacity. Root system complexity is the result of response to heterogeneity of the soil environment for nutrients (Fitter, 1994) and moisture (Callaway, 1990; Bell and Sultan, 1999). Anatomical and morphological characteristics such as the size and shape of the tip, length, diameter, secondary growth, branching density, casparian band and suberization respond to the soil environment (Pages *et al.*, 1993). It would be interesting to learn how anatomical and morphological structures are involved in water transfer.

Loblolly pine (*Pinus taeda* L.) is the leading timber species in the United States. It is found on more than 13.4 million hectares over 14 southern and mid-Atlantic states (Schultz, 1997) and represents half of the total volume of southern pine growing stock (approximately 1.4 billion m^3) and about 80 % of all pine seedlings planted in the southern United States. Besides the economic value, loblolly pine plays a major role for wildlife habitat, erosion control, water quality improvement, and recreational opportunities.

The *P. taeda* root system is characterized by having a taproot, horizontal laterals, sinker roots and fine roots (Carlson *et al.*, 1988; Harrington *et al.*, 1989). The taproot (TAPR) grows downward into the soil and mainly provides support and anchorage for the shoot and the first-order lateral roots (FOLRs). The FOLRs spread out horizontally into the shallow soil. The sinker roots and other second-order laterals (SOLRs) arise from the FOLRs. Sinker roots grow vertically downward. In loblolly pine, most of the roots are located in the top 20-cm of the soil (Kramer and Bullock, 1966). The presence of surface lateral roots may be beneficial to the tree growth because these surface roots can take advantage of light summer showers that do not penetrate the soil layers surrounding deeper roots (Carlson *et al.*, 1988).

The roots of *P. taeda* can be divided into three zones: white, condensed tannin and cork (McKenzie and Peterson, 1995a, b; Peterson *et al.*, 1999). The white zone is the distal and youngest part of the root, from 0 to about 40 mm from the tip. It appears white and possesses all tissues: meristematic tissue involved in active cell division and multiplication, cortex with developing endodermis, pericycle, maturing xylem and phloem. The condensed tannin (CT) zone is basal to the white and is brown. This color is due the dead cortical cells whose walls contain condensed tannins. The last zone, the cork zone, shows the production of cork cells interior to the endodermis. These cells are similar to the bark of the shoot and comprise a multilayered tissue of dead cells with suberin lamellae deposited on their walls. This layer is thought to have Casparian band-like structures in the primary wall (McKenzie and Peterson, 1995b).

Enstone *et al.* (2001) observed, in pouch- and pot-grown *P. taeda* seedlings, that the Casparian band appeared in the endodermis approximately 7 mm from the tip and that all endodermal cells possess a Casparian band at 10 mm from the tip. They also observed that the suberin lamellae developed progressively and asynchronously until 80% of the endodermal cells at the beginning of the tannin zone 30-40 mm from the apex were suberized. This percentage remained constant over the CT zone until the cork zone, where almost all endodermal cells possess a suberin lamellae (130mm from the root tip). The white zone, with its living cortex and not yet fully developed endodermis (developing Casparian band and abundant passage cells), was thought to have the largest potential for radial water and ion uptake due to a large plasmalemma surface in contact with the soil solution. Although tracheids can be detected close to the tip, they do not become conductive until 5 mm from the tip.

The development of the suberin lamellae in the endodermis, the progressive death and abrasion of the cortical cells in the CT zone resulted in a decrease in absorbing membrane surface area in this zone. This may lead to an increase of the resistance to radial water uptake. The presence of the cork layer and the almost totally suberized endodermis in the cork zone should further increase the radial resistance to water flow. This increasing resistance to radial water transport occurs while the longitudinal transport capacity is greatly increasing due to an increasing number of conductive tracheids resulting from secondary growth.

As the plant develops and becomes larger, more water and nutrients are required. The root system begins to branch and produce higher order laterals. As the distal parts of roots become branched thereby increasing their absorptive power, the extra water that is absorbed must be moved through the established proximal portions of the root, and extra conducting capacity is needed. By undergoing secondary growth, plants produce new tracheary elements to increase the root transport capacity. Therefore, the hydraulic resistance of the xylem is an important characteristic that determines the rate at which water can be supplied to the shoot (Zimmermann, 1983). The hydraulic conductivity of the xylem water transport system depends on the hydraulic conductivity within the conduit lumina and the hydraulic conductivity of the inter-conduit connections (bordered pits). Thus diameter and length of the conduits and how they are interconnected determines the xylem network efficiency of a vascular system. The usual assumption in root conductivity research is that xylem axial conductivity is more than adequate to transport water entering the root through radial transport (Landsberg and Fowkes, 1978). There is some doubt that this is true all along the root, especially near the tip, and in cases where xylem cavitation has occurred.

Objectives

The overall objective of this study was to quantify limitations to water uptake by *P. taeda* root systems. This required determining the ontological changes in root anatomical features and relating them to conductivity for different root types. I investigated: 1.) the changes in morphological characteristics of a loblolly pine seedling root system during its first year of growth in a nursery, 2.) the hydraulic properties of the seedling root xylem, and 3.) the changes in root water uptake capacity during root growth and development. The new knowledge produced from this study will be of great value for improving water transfer models at the plant and ecosystem level. It will also aid in determining how cultural treatments and genetic improvement can be used to optimize tree water uptake capacity.

Chapter II contains details about the root morphological and anatomical changes of the TAPR, FOLRs and SOLRs during the first year of growth in the nursery. Chapter III contains details about the seasonal changes of the tracheid characteristics in the different zones and the contribution of the tracheid components to the total tracheid resistance. In Chapter IV, the root, axial and radial hydraulic conductivity were determined for each root zones in *P. taeda* seedlings during its first year in the nursery. Axial conductivity results were compared with theoretical conductivity determined from anatomical characteristics. Conductivity data and root system morphology established in Chapter II were combined into a model to determine the uptake capacity of the root system and the distribution of uptake capacity to white, CT and cork zone.

REFERENCES

Addoms, R.M. 1946. Entrance of water into suberized roots of trees. Plant Physiol. 21: 109-111.

Aloni, R., D.E. Enstone and C.A. Peterson 1998. Indirect evidence for bulk water flow in root cortical cell walls of three dicotyledonous species. Planta 207:1-7.

Bailey, I.W. 1953. Evolution of the tracheary tissue of land plants. Am. J. Bot. 40: 4-8.

Bannan, M.W. 1965. The length, tangential diameter, and length/width ratio of conifer tracheids. Can. J. Bot. 43:967-984.

Barnett, J.R. 1981. Secondary xylem cell development. *In*: Xylem cell development, ed. J.R. Barnett. Castle House Publications, Ltd.:Kent, England.

Barrieu, F., F. Chaumont and M.J. Chrispeels 1998. High expression of the tonoplast aquaporin Zm TI1 in epidermal and conducting tissues of maize. Plant Physiol. 117: 1153-1163.

Barrowclough, D.E., C.A. Peterson and E. Steudle 2000. Radial hydraulic conductivity along developing onion roots. J. Exp. Bot. 51(344): 547-557.

Bell, D.L. and S.E. Sultan 1999. Dynamic phenotypic plasticity for root growth in *Polygonum*: a comparative study. Am. J. Bot. 86:807-819.

Bell, J.K. and M.E. McCully 1970. A histochemical study of lateral root initiation and development in *Zea mays*. Protoplasma 70:179-205.

Bernston, G.M. 1994. Modeling root architecture: are there tradeoffs between efficiency and potential of resource acquisition? New Phytol. 127:483-493.

Blakely, L.M., M. Durham, T.A. Evans and R.M. Blakely 1982. Experimental studies on lateral root formation in radish seedling roots. I. General methods, developmental stages, and spontaneous formation of laterals. Bot. Gaz. 143:341-352.

Brouwer, R., O. Gasparikova, J. Kolek and B.C. Loughman 1981. Structure and function of plant roots. Martinus Nijhoff / Dr W. Junk Publishers: The Hague.

Calkin, H.W., A.C. Gibson and P.S. Nobel 1985. Xylem water potentials and hydraulic conductances in eight species of ferns. Can. J. Bot. 63:632-637.

Calkin, H.W., A.C. Gibson and P.S. Nobel 1986. Biophysical model of xylem conductance in tracheids of the fern *Pteris vittata*. J. Exp. Bot. 37(180):1054-1064.

Callaway, R.M. 1990. Effects of soil water distribution on the lateral root development of three species of California oaks. Am. J. Bot. 77:1469-1475.

Canny, M.J. 1995. Apoplastic water and solute movement: new rules for an old space. Annu. Rev. Plant Physiol. Plant Mol. Biol. 46:215-236.

Carlson, W.C., C.A. Harrington, P. Farnum and S.W. Hallgren 1988. Effects of root severing treatments on loblolly pine. Can. J. For. Res. 18:1376-1385.

Chaumont, F., F. Barrieu, E.M. Herman and M.J. Chrispeels 1998. Characterization of a maize tonoplast aquaporin expressed in zones of cell division and elongation. Plant Physiol. 117:1143-1152.

Chiu, S.T. and F.W. Ewers 1993. The effect of segment length on conductance measurements in *Lonicera fragrantissima*. J. Exp. Bot. 44:175-181.

Clarkson, D.T. 1985. Factors affecting mineral nutrient acquisition by plants. Annu. Rev. Plant Physiol. 36:77-115.

Clarkson, D.J. and A.W. Robards 1975. The endodermis, its structural development and physiological role. *In*: The development and function of roots. Edited by J.G. Torrey and D.T. Clarkson. Academic Press, London, pp. 415-436.

Coleman, M.D., C.S. Bledose and B.A. Smith 1990. Root hydraulic conductivity and xylem sap levels of zeatin riboside and abscisic acid in ectomycorrhizal Douglas fir seedlings. New Phytol. 115:275-284.

Davies, W.J. and J. Zhang 1991. Root signals and the regulation of growth and development of plant in drying soil. Annu. Rev. Plant Physiol. Plant Mol. Biol. 42: 55-76.

Dimond, A.E. 1966. Pressure and flow relations in vascular bundles of the tomato plant. Plant Physiol. 41:119-131.

Dixon, H.H. and J. Joly 1896. On the ascent of sap. Philos. Trans. R. Soc. Lond. B Biol. Sci. 186:563-576.

Dixon, R.K., S.G. Pallardy, H.G. Garrett and G.S. Cox 1980. Comparative water relations of container-grown and bare-root ectomycorrhizal *Quercus velutina* seedlings. Can. J. Bot. 61:1559-1565.

Dudrige, J.A., A. Malibari and D.J. Read 1980. Structure and function of mycorrhizal rhizomorph with special references to their role in water transport. Nature 287:834-836.

Dumbroff, E.B. and D.R. Peirson 1971. Probable sites for passive movement of ions across the endodermis. Can. J. Bot. 49:35-38.

Ellerby, D.J. and A.R. Ennos 1998. Resistances to fluid flow of model xylem vessels with simple and scalariform perforation plates. J. Exp. Bot. 49:979-985.

Ennos, A.R. 1993. The function and formation of buttresses. Trends Ecol. Evol. 8:350-351.

Enstone, D.E. and C.A. Peterson 1992. A rapid fluorescence technique to probe the permeability of the root apoplast. Can. J. Bot. 70:1493-1501.

Enstone, D.E., C.A. Peterson and S.W. Hallgren 2001. Anatomy of seedling tap roots of Loblolly pine (*Pinus tadea* L.). Trees 15:98-111.

Esau, K. 1965. Vascular differentiation in plants. John Wiley and Sons: New York.

Fitter, A.H. 1994. Architecture and biomass allocation as component of the plastic response of root system to soil heterogeneity. *In*: Exploitation of environmental heterogeneity by plants: ecophysiological processes above- and belowground, Caldwell M.M., Pearcy R.W., eds. SanDiego: Academic Press. pp. 305-323.

Frensch, J. 1997. Primary responses of root and leaf elongation to water deficits in the atmosphere and soil solution. J. Exp. Bot. 48(310):985-999.

Frensch, J. and E. Steudle 1989. Axial and radial hydraulic resistance to roots of maize (*Zea mays* L.). Plant Physiol. 91:719-726.

Frensch, J. and T.C. Hsiao 1993. Hydraulic propagation of pressure along immature and mature xylem vessels of roots of *Zea mays* measured by pressure probe techniques. Planta 190:247-254.

Frensch, J., T.C. Hsiao and E. Steudle 1996. Water and solute transport along developing maize roots. Planta 198:348-335.

Gibson, A.C., H.W. Calkin and P.S. Nobel 1984. Xylem anatomy, water flow and hydraulic conductance in the fern *Cyrtomium falcatum*. Am. J. Bot. 71:564-574.

Gibson, A.C., H.W. Calkin and P.S. Nobel 1985. Hydraulic conductance and xylem structure in tracheid-bearing plants. I.A.W.A. Bull. 6:293-302.

Gibson, A.C., H.W. Calkin, D.O. Raphael and P.S. Nobel 1985. Water relations and xylem anatomy of ferns. Proc. R. Soc. Edin. 86B:81-92.

Giordano, R., A. Salleo, S. Salleo and F. Wanderling 1978. Flow in xylem vessels and Poiseuille’s law. Can. J. Bot. 56:333-338.

Harrington, C.A., J.C. Brissette and W.C. Carlson 1989. Root system structure in planted and seeded loblolly and shortleaf pine. For. Sci. 35:469-480.

Henzler, T. and E. Steudle 1995. Reversible closing of water channels in *Chara* internodes provides evidence for a composite transport model in the plasma membrane. J. Exp. Bot. 46:199-209.

Henzler, T., R.N. Waterhouse, A.J. Smyth, et al. 1999. Diurnal variations in hydraulic conductivity and root pressure can be correlated with the expression of putative aquaporins in the roots of *Lotus japonicus*. Planta 210:50-60.

Johansson, I., M. Karlsson, V.K. Shukla, M.J. Chrispeels, C. Larsson and P. Kjellbom 1998. Water transport activity of the plasma membrane aquaporin PM28A is regulated by phosphorylation. Plant Cell 10:451-460.

Kammerloher, W., U. Fischer, G.P. Piechottka and A.R. Schäffner 1994. Water channels in the plant plasma membrane cloned by immunoselection from a mammalian expression system. Plant J. 6(2):187-199.

Kepler, B. 1983. Managing root systems for efficient water use: axial resistances to flow in root systems – anatomical considerations. *In*: Limitations to efficient water use in crop production. H.M. Taylor et al. (ed.) ASA, CSSA, and SSSA, Madison, WI. pp. 115-125.

Kramer, P.J. and J.S. Boyer 1995. Water Relations of plants and soil. Academic Press, New York. 495p.

Kramer, P.J. and H.C. Bullock 1966. Seasonal variations in the proportions of suberized and unsuberized roots of trees in relation to the absorption of water. Am. J. Bot. 53:200-204.

Krasowski, M.J. and J.N. Owens 1999. Tracheids in white spruce seedling's long lateral roots in response to nitrogen availability. Plant Soil 217:215-228.

Landsberg, J.J. and Fowkes N.D. 1978. Water movement trough plant roots. Ann. Bot. 42:493-508.

Luxová, M. 1990. Effect of lateral root formation on the vascular pattern of barley roots. Botanica acta 103:305-310.

MacFall, J.S., G.A. Jonnson and P.J. Kramer 1990. Observation of a water depletion region surrounding Loblolly pine roots by magnetic resonance imaging. Proc. Natl Sci. USA 87:1203-1207.

MacFall, J.S., G.A. Jonnson and P.J. Kramer 1991. Comparative water uptake by roots of different ages in seedlings of Loblolly pine (*Pinus taeda* L.). New Phytol. 119:551-560.

Mallory, T.E., S.H. Chiang, E.G. Cutter and E.M.Jr. 1970. Sequence and pattern of lateral root formation in five selected species. Am. J. Bot. 57:800-809.

Marschner, H. 1995. Mineral nutrition of higher plants. Academic Press, Second edition.

Maurel, C. 1997. Aquaporins and water permeability of plant membranes. Annu. Rev. Plant Physiol. Plant Mol. Biol., 48:399-429.

McCrady, R.L. and N.B. Comerford 1998. Morphological and anatomy relationships of loblolly pine fine roots. Trees 12:431-437.

McCully, M.E. 1975. The development of lateral roots. *In*: The development and functions of roots. Edited by J.G. Torrey and D.T. Clarkson. Academic Press, London, pp. 105-124.

McCully, M.E. and M.J. Canny 1988. Pathways and processes of water and nutrient movement in roots. *In:* Structural and functional aspects of transports in roots. pp. 3-14.

McKenzie, B.E. and C.A. Peterson 1995a. Root browning in *Pinus Banksiana* Lamb. and *Eucalyptus pilularis* Sm. Anatomy and permeability of the White and Tannin Zones. Botanica Acta 108:127-137.

McKenzie, B.E. and C.A. Peterson 1995b. Root browning in *Pinus Banksiana* Lamb. and *Eucalyptus pilularis* Sm. Anatomy and permeability of the Cork Zone. Botanica Acta 108:138-143.

Melchior, W. and E. Steudle 1993. Water transport in Onion (*Allium cepa* L.) roots. Changes of axial and radial conductivities during root development. Plant Physiol. 101:1305-1315.

Milburn, J.A. 1979. Water flow in plant. Longman, London.

Milburn, J.A. 1996. Sap ascent in vascular plants: challengers to the cohesion theory ignore the significance of immature xylem and the recycling of Munch water. Ann. Bot. 78:399-407.

Münch, E. 1943. Durchlässigkeit der Siebröhren für Druckströmungen. Flora, 136:223-262.

Mudge, K.W., K.S. Diebolt and T.H. Whitlow 1987. Ectomycorrhizal effect of host plant response to drought stress. J. Environ. Hort. 5:183-187.

Nobel, P.S. 1983. Biophysical plant physiology and ecology. W.H. Freeman, San Francisco.

Nobel, P.S. and M. Cui 1992. Hydraulic conductances of the soil, the root-soil air gap, and the root : changes for desert succulents in drying soil. J. Exp. Bot. 43:319-326.

North, G.B. and P.S. Nobel 1991a. Drought-induced changes in hydraulic conductivy and structure in roots of *Ferocactus acanthodes* and *Opuntia ficus-indica*. New Phytol. 120:9-19.

North, G.B. and P.S Nobel 1991b. Changes in hydraulic conductivity and anatomy caused by drying and rewetting roots of *Agave desertii* (Agavaceae). Am. J. Bot. 78:906-915.

North, G.B. and P.S. Nobel 1995. Hydraulic conductivity of concentric root tissues of *Agave deserti* Engelm. Under wet and drying conditions. New Phytol. 130:47-57.

O'Brien, T.P. 1981. The primary xylem. *In*: Xylem cell development, ed. J.R. Barnett. Castle house Publications, Ltd.: Kent, England.

Pages, L., J. Kervella and J. Chadoeuf 1993. Development of the root system of young peach trees *Prunus persicae* L. Batsch: a morphometrical analysis. Ann. Bot. 71:369-375.

Parke, J.L., R.G. Linderman and C.H. Black 1983. The role of ectomycorrhizae in drought tolerance of Douglas fir seedlings. New Phytol. 95:83-95.

Peterson, C.A. and D.E. Enstone 1996. Function of passage cells in th endodermis and exodermis of roots. Physiology Plant. 97:592-598.

Peterson, C.A. and B.E.M. Lefcourt 1990. Development of endodermal Casparian band and xylem in lateral roots of broad bean. Can. J. Bot. 68:2729-2735.

Peterson, C.A. and G.J. Moon 1993. Effect of lateral root outgrowth on the structure and permeability of the onion root exodermis. Botanica Acta 106:411-418.

Peterson, C.A. and E. Steudle 1993. Lateral hydraulic conductivity of early metaxylem vessels in *Zea mays* L. roots. Planta 189:288-297.

Peterson, C.A., M.E. Emanuel and G.B. Humphreys 1981. Pathways of movement of apoplastic fluorescent dye tracers through the endodermis at the site of secondary root formation in corn (*Zea mays*) and Broad bean (*Vicia faba*). Can. J. Bot. 59:618-625.

Peterson, C.A., D.E. Enstone and J.H. Taylor 1999. Pine root structure and its potential significance for root function. Plant Soil 217:205-213.

Peterson, C.A., R.L. Peterson and A.W. Robards 1978. A correlated histochemical and ultrastructural study of the epidermis and hypodermis of onion roots. Protoplasma 96:1-21.

Piché, Y., R.L. Peterson, M.J. Howarth and J.A. Fortin 1983. A structural study of the interaction between the ectomycorrhizal fungus *Pisolithus tinctorius* and *Pinus strobes* roots. Can. J. Bot. 61:1185-1193.

Reizer, J., A. Reizer and M.H.Jr. Saier 1993. The MIP family of integral membrane channel proteins: sequence comparisons, evolutionary relationships, reconstructed pathway of evolution, and proposed functional differentiation of the 2 repeated halves of the proteins. Crit. Rev. Biochem. Mol. Biol. 28:235-257.

Rieger, M. and P. Litvin 1998. Root system hydraulic conductivity in species with constrasting root anatomy. J. Exp. Bot. 50:201-209.

Rousseau, J.V.D., D.M. Sylvia and A.J. Fox 1994. Contribution of ectomycorrhiza to the potential nutrient-absorbing surface area of pine. New Phytol. 128:639-644.

Sands, R. and C. Theodorou 1978. Water uptake by mycorrhizal roots of radiata pine seedlings. Aust. J. Plant Physiol. 5:301-309.

Sarda, X., D. Tousch, K. Ferrare et al. 1999. Characterization of closely related δ-TIP genes encoding aquaporins which are differentially expressed in sunflower roots upon water deprivation through exposure to air. Plant Mol. Biol. 40:179-191.

Sanderson, J. 1983. Water uptake by different region of the barley root. Pathways of radial flow in relation to the development of the endodermis. J. Exp. Bot. 34(140):240-253.

Schreiber, L., K. Hartmann, M. Sjrabs and J. Zeier 1999. Apoplastic barriers in roots: chemical composition of endodermal and hypodermal cell walls. J. Exp. Bot. 50(337):1267-1280.

Schulte, P.J. and A.L. Castle 1993. Water flow through vessel perforation plates – a fluid mechanical approach. J. Exp. Bot. 44:1135-1142.

Schulte, P.J. and A.C. Gibson 1988. Hydraulic conductance and tracheid anatomy in six species of extant seed plants. Can. J. Bot. 66:1073-1079.

Schultz, R.P. 1997. Loblloly pine: the ecology and culture of Loblolly pine. Agriculture handbook, 173p.

Shane, M.W., M.E. McCully and M.J. Canny 2000. Architecture of branch-root junctions in maize: structure of the connecting xylem and the porosity of pit membranes. Ann. Bot. 85:613-624.

Shi, L.-B. and A.S. Verkman 1996. Selected cystein point mutations confer mercurial sensitivity to the mercurial-insensitive water channel MICW/AQP-4. Biochem. J. 35:538-544.

Sperry, J.S., J.R. Donnelly and M.T. Tyree 1988. Seasonal occurrence of xylem embolism in sugar maple (*Acer saccharum*). Am. J. Bot. 75:1212-1218.

Steudle, E. 1994. Water transport across roots. Plant Soil 67:79-90.

Steudle, E. 2000. Water uptake by roots: effects of water deficit. J. Exp. Bot. 51(350):1531-1542.

Steudle, E. and J. Frensch 1996. Water transport in plants: role of the apoplast. Plant Soil 187:67-79.

Steudle, E. and C.A. Peterson 1998. How does water get through roots? J. Exp. Bot. 49:775-788.

Steudle, E., M. Murrman and C.A. Peterson 1993. Transport of water and solute across maize roots modified by puncturing the endodermis. Further evidence for the composite transport model of the root. Plant Physiol. 1063:335-349.

Streeter, V.L. and E.B. Wylie 1985. Fluid mechanics. 8th ed. McGraw-Hill, New York.

Sylvia, D.M. 1990. Distribution, structure, and function of external hyphae of vesicular-arbuscular mycorrhizal fungi. *In*: J.E. Box and L.H. Hammond (eds). Rhizosphere Dynamics. Westview Press, Boulder, CO. pp. 144-167.

Sylvia, D.M. 1998. Mycorrhizal symbiosis. *In*: D.M. Sylvia, J. Fuhrmann, P.G. Hartel and D. Zuberer (eds). Principles and Applications of Soil Microbiology. Prentice Hall, New Jersey. pp. 408-426.

Torrey, J.G. and D.T. Clarkson 1975. The development and function of roots. Academic Press: London.

Tyerman, S.D., H.J. Bohnert, C. Maurel, E. Steudle et al. 1999. Plant aquaporins: their molecular biology, biophysics and significance for plant water relations. J. Exp. Bot. 50:1055-1071.

Tyree, M.T. 1997. The cohesion-Tension theory of sap ascent: current controversies. J. Exp. Bot. 48:1753-1765.

Tyree, M.T. and F.W. Ewers 1991. The hydraulic architecture of trees and other woody plants. New Phytol. 119:345-360.

Van Rees, J.C. and N.B. Comerford 1990. The role of woody roots of slash pine seedlings in water and potassium absorption. Can. J. For. Res. 20:1183-1191.

Varney, G.T. and M.J. Canny 1993. Rates of water uptake into the mature root system of maize plants. New Phytol. 123:775-789.

Vogt, K.A., D.A. Publicover and D.J. Vogt 1991. A review of the role of mycorrhizae in forest ecosystems. Agr. Ecosyst. Environ. 35:171-190.

Wan, X. and J.J. Zwiazek 1999. Mercuric chloride effects on root water transport in aspen seedlings. Plant Physiol. 121:939-946.

Wang, X.L., M.J. Canny and M.E. McCully 1991. The water status of the roots of soil-grown maize in relation to the maturity of their xylem. Physiol. Plant. 82:157-162.

Wenzel, C.L., M.E. McCully and M.J. Canny 1989. Development of water conducting capacity in the root systems of young plants of corn and some other C4 grasses. Plant Physiol. 89:1094-1101.

Wilcox, H.E. 1968. Morphological studies of the root of red pine *Pinus resinosa* L., growth characteristics and patterns of branching. Am. J. Bot. 64:18-24.

Wilson, S.A. and D. Atkinson 1978. Water and mineral uptake by fruit tree roots. *In*: Symposium on root physiology and symbiosis, Sept. 11-15, Nancy. Edited by A. Riedacker and J. Gagnaire-Michard, Proceedings IUFRO, Nancy, France. pp. 372-382.

Yamada, S., D.E. Nelson, E. Ley, S. Marquez and H.J. Bohnert 1997. The expression of an aquaporin promoter from *Mesembryanthemum crystallinum* in tobacco. Plant Cell Physiol. 38:1326-1332.

Zimmermann, M.H. 1971. Transport in the xylem. *In*: Trees: Structure and function. Eds M.H. Zimmermann and C.L. Brown. Springer-Verlag, New York. pp. 169-200.

Zimmmermann M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin.

CHAPTER II

ANATOMICAL AND MORPHOLOGICAL TRAITS OF THE *PINUS TAEDA* SEEDLING ROOT SYSTEM

SUMMARY

Roots of *P. taeda* roots were comprised of three zones – white, condensed tannin (CT) and cork zones – previously described (McKenzie and Peterson, 1995a and b; Enstone et al., 2000). The white zone had a live cortex and plentiful passage cells conductive to water and ion uptake. The CT zone had reduced cortex and passage cells. The cork zone had secondary xylem production and was clad in cork cells to facilitate upward transport of water. The root system was composed of a vertical taproot (TAPR), many horizontal first-order lateral roots (FOLRs) and even more second-order lateral roots (SORLs). Lateral roots comprised most of the root length (75 to 99%) and surface area (63 to 95%) throughout the year. White zone was a rather small portion of root length and area, comprising 4% of the length and 12% of the root system surface area. Rapid CT zone production increased its contribution to the root system to

63% of the length and 44% of the surface area by November. The basal cork zone comprised 33% of the length and 44% of the surface area of the root system in November. Tracheid diameter increased dramatically from the white to CT zone and in this zone appeared to reach a maximum diameter because no further increase was observed in the cork zone. The TAPR had traits associated with high capacity for axial water transport; it was composed mostly of cork zone and had a very large number of large diameter tracheids relative to lateral roots. The lateral roots had traits associated with high uptake capacity; they were small diameter with few small diameter tracheids and were composed mostly of CT zone.

INTRODUCTION

Because changes in structure occur with age and environment, the anatomy of an individual root is non-uniform along its length (Esau, 1977, Wilcox, 1964, McCrady and Comerford, 1998). The three anatomical zones (white, CT and cork) described by McKenzie and Peterson (1995a, b) and Taylor and Peterson (2000) have also been found in *Pinus taeda* (Enstone *et al.*, 2001). The white zone starts from the tip. It has a cortex with a partially suberized endodermis and plentiful non-suberized passage cells, a few conductive xylem elements and phloem. Proximal to the white zone is the condensed tannin (CT) zone with a brown color. The cortical cells are dead and progressively sloughed, the endodermis becomes progressively suberized and more conductive xylem and phloem are formed. The cork zone is marked by the initiation of the secondary growth of the vascular cambium in the stele and cork cambium below the endodermis.

Each zone with its distinctive internal structure should have consequences for ion and water uptake. The white zone with live and abundant non-suberized passage cells (Peterson and Steudle, 1993; Steudle and Peterson, 1998) should have a high absorptive capacity. The white zone may be relatively more important for ion than water uptake, because the plentiful membranes of the cortex provide ion transporters and a long pathway for water movement. Progressive suberization of the endodermis in the CT zone should reduce its radial conductive ability. On the other hand, the dead cortex provides a low resistance pathway for water up to the endodermal passage cells. The layer of cork surrounding the stele may further decrease the amount of water entering the root in the cork zone.

In contrast to this idea of increasing resistance from the tip to the base, Kramer and Bullock (1966) and McFall *et al.* (1991) revealed that suberized roots were able to absorb significant amounts of water. Consequently the question arises whether the cork zone has a high resistance compared to the white and CT. Also the number of tracheids increases from the white to the cork, first as part of the primary development and then as produced by the secondary growth. According to Tyree *et al.* (1994), the anatomy of the conduits determines their hydraulic efficiency. The diameter is an important parameter as wide conduits are more efficient in water transportation than narrow conduits (Zimmermann, 1983). It is not known whether the tracheid characteristics change with the development of the root.

The root system of one year-old seedlings include a vertical taproot (TAPR) that has undergone advanced secondary growth, horizontal first-order lateral roots (FOLR), and second-order lateral roots (SOLR), with and without mycorrhizae. Such heterorhizy corresponds to differences in morphological parameters that could vary during the growing season as the root system grows. Prior research has developed the concepts and tools for describing root zones (McKenzie and

Peterson, 1995a, b and Enstone *et al.*, 2001) with supposed uptake functions. The objective of the research presented here was to determine the distribution of these root zones in *P. taeda* seedlings and learn whether there are developmental and seasonal patterns in their production. The study was conducted over the period June to November on first-year *P. taeda* seedlings grown under operational procedures in a forest tree nursery. These were ideal conditions for excavation of intact root systems. The information sought in this study is essential for achieving the ultimate goal of predicting uptake capacity of the entire root system.

MATERIALS AND METHODS

Plant material

Seedlings were obtained from a single open-pollinated Oklahoma family of genetically improved *P. taeda*. Seeds were sown in the first week of May 2002 at the Oklahoma State Forest Regeneration Center near Washington, Oklahoma. They germinated in 10 – 15 days. The standard nursery beds were 1.4 m wide and 180 m long aligned in the east-west direction (Fig. 1). They consisted of slightly raised flat-topped mounds. Seedlings were grown at a density of approximately 200 m^{-2} in 7 parallel rows oriented along the length of the beds. Seedlings were grown in the nursery beds from May until harvest in mid-winter. The major cultural operations were fertilization, watering and pesticide application when needed. Lateral root pruning and undercutting were done in early October.

For this study, seedlings were harvested every month from June to November. They were harvested from three replicates located at a minimum of 50 m apart in the three different beds (Fig. 2). A 1 m length of 10 cm diameter PVC pipe was used to take a 50-60 cm deep core of soil containing five to six trees. Four pipes per replication were collected (Fig. 3). The whole TAPR and its laterals were obtained. Beginning in August the laterals were too long to be extracted with the 10 cm-diameter pipes and a 30 cm-diameter pipe was used to collect a core of

Fig. 1. Loblolly pine seedlings growing on beds at the Oklahoma State Forest Regeneration Center.

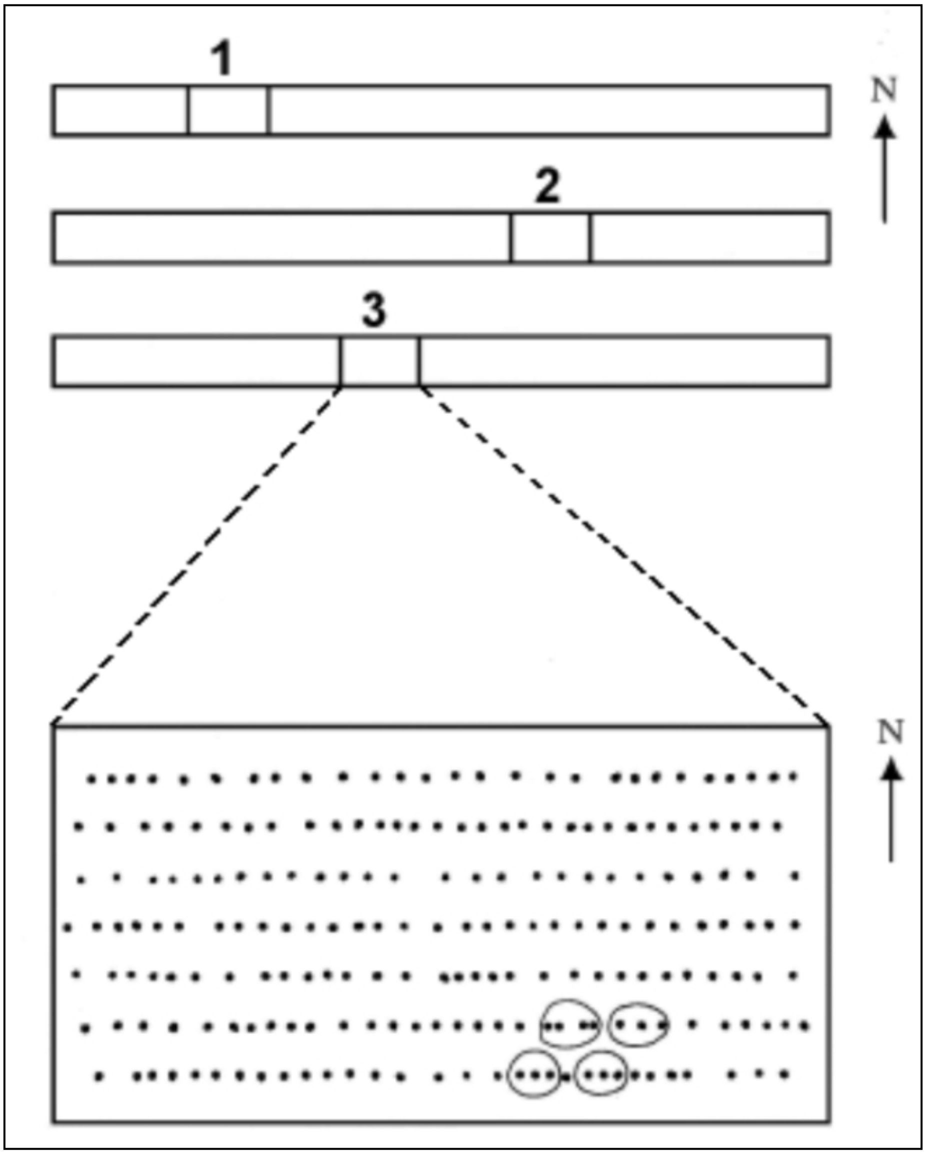


Fig. 2. Diagram representing the repartition of the three replicates and the sampling of trees. Four pipes were used to randomly samples trees.

Fig. 3. Collection of seedlings by Insertion of four pipes up to 50 cm.

soil at a depth of 30 cm.

The pipes with soil and roots inside were brought back to Stillwater and stored at 6°C until measurements were made. The day before washing, pipes were taken out of the cold room and kept at ambient temperature. The top of the pipes was filled with water and left to infiltrate overnight to facilitate the extraction of the soil core. The next day, the root systems were carefully separated from the soil with water and brought to the laboratory in containers filled with water for conductivity and morphological measurements. Lateral roots were extracted from the big pipe using the same technique.

Root system morphology

The three most intact root systems were selected among the trees collected with the four pipes within each bed. In this way nine root systems (3 trees x 3 replicates) were collected and analyzed each month. The TAPRs were intact from base to tip with all laterals. The tips of long lateral roots were very fragile and were often lost in later harvests. The roots were kept under water during all the observations, to avoid any shrinkage. Starting from the tip of the main root, the TAPR was separated into the white, CT and cork zones and each zone was cut in 2 cm-length segments. The white and CT zones were distinguished according to visual inspection based on criteria from McKenzie and Peterson (1995a) and personal communication (Prem Kumar and Steve Hallgren). The white zone was obviously white and the CT zone was brown. The white zone had a healthy intact cortex and the CT zone was characterized by gradual death and sloughing of cortical cells. Histochemical tests found tannin deposits in cortical walls in the CT zone of *Pinus banksiana* (McKenzie and Peterson, 1995a). The cork zone was clearly different from the CT zone. The cork zone was distinguished by being stiffer, having more and larger lateral roots and showing evidence of a periderm. The evidence of periderm was splitting of the outer surface of the root to reveal an interior layer lighter in color than the surface. Length and diameter of all first-order lateral roots (FOLRs) and second-order lateral roots (SOLRs) were measured for each taproot (TAPR) segment. The diameters were measured using a microscope with an eyepiece micrometer and a caliper when the roots were too large. These data were used to calculate total root length and surface area by zone and type for a seedling.

Tracheids

Every month, crystal violet (0.01%) was drawn into TAPR, FOLR and SOLR segments from the different zones by applying a negative pressure at the basal end of the segments. As a result, the walls of the conductive tracheids were stained in blue-violet (Fig. 4). While viewing cross-sections under a bright field illumination microscope, the diameters of the conductive tracheids were estimated by fitting a circle inside each tracheid using the ImagePro Plus

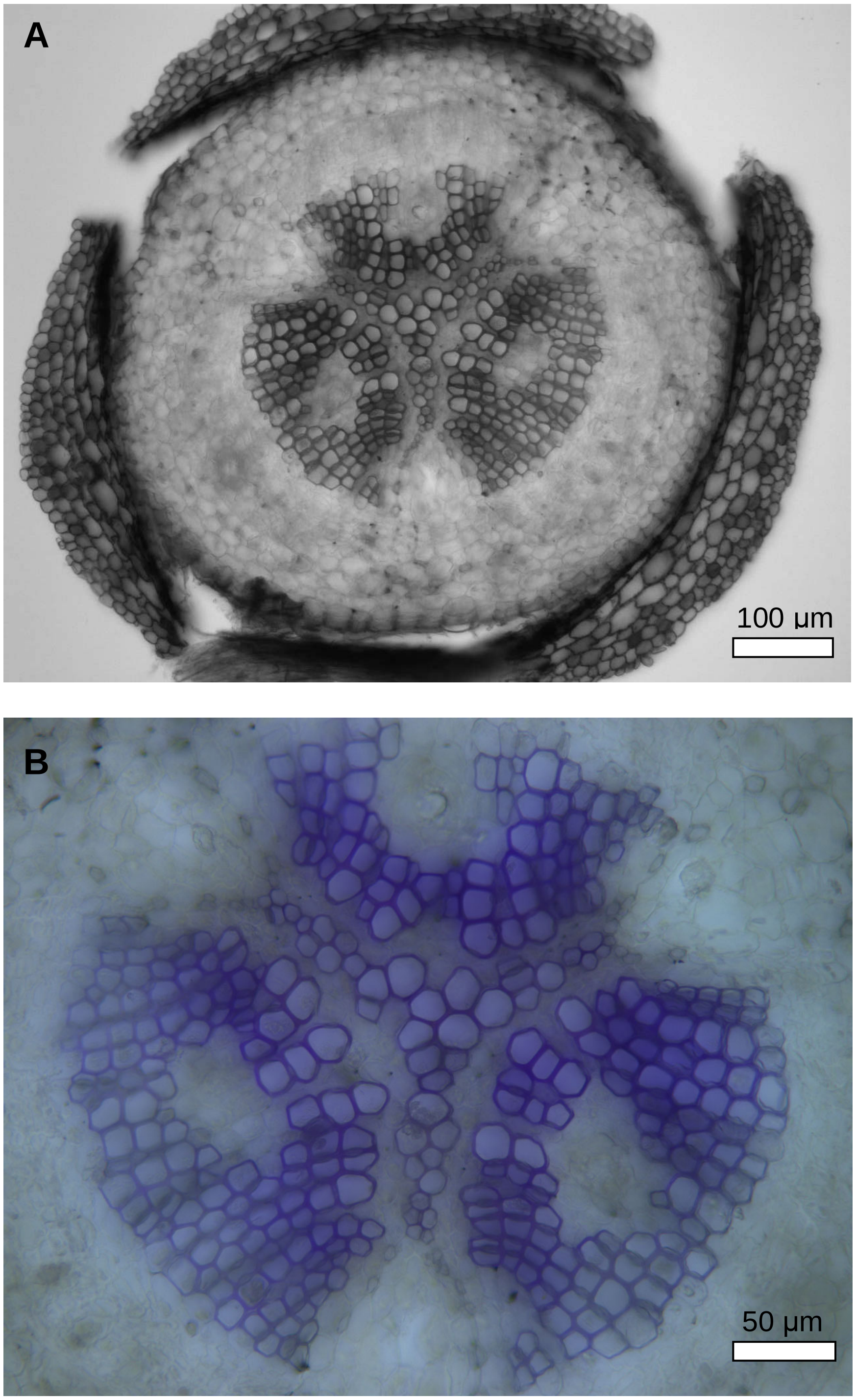


Fig. 4. Cross section of a typical pine root in the CT zone. (A) The root with partially sloughed cortex (100X). (B) A closer view of the xylem stained with 0.01% crystal violet (200X).

software. When the number of tracheid was over two hundred, the tracheid number and diameter was estimated using the surface area of the conductive stele and the number and diameter of conductive tracheids within four sub-samples inside the stele.

Data analysis

Roots and root segments were collected from three different beds representing three replicates. Statistical analyses were performed using SAS (1999); means and standard errors were calculated at $p \leq 0.05$ (SAS, 1999). Mean separations were made using LSD. Results were plotted against harvest date by root type and zone.

RESULTS

Root morphology

The largest root was the TAPR. The longest TAPR grew to 350 mm by June and over 600 mm by September (Fig. 5). Undercutting reduced its length to 150 mm in October and it grew to 450 mm in November. The longest FOLR in June was just under 50 mm (Fig. 6). By September the longest FOLR was nearly 250 mm. Root pruning reduced the FOLR length to about 160 mm in October and new growth increased the length to just over 400 mm by November. SOLRs did not appear until August and they grew rapidly to a maximum length of just over 60 mm in September (Fig. 7). The longest SOLR was reduced to near 20 mm in October by root pruning. New root growth had increased the length of the longest SOLR to nearly 100 mm in November.

Total seedling root length was already 1 m in June (Fig. 8) and it increased steadily to nearly 15 m in November despite pruning in October. FOLRs were the major part of root length in June. SOLRs did not appear until August. The distribution of root length in November was 5% TAPR, 31% FOLRs and 64% SOLRs. The dominant root zone was most often the CT zone and by November the distribution of root length by zone was 4% white zone, 63% CT zone and 33% cork zone (Fig. 9).

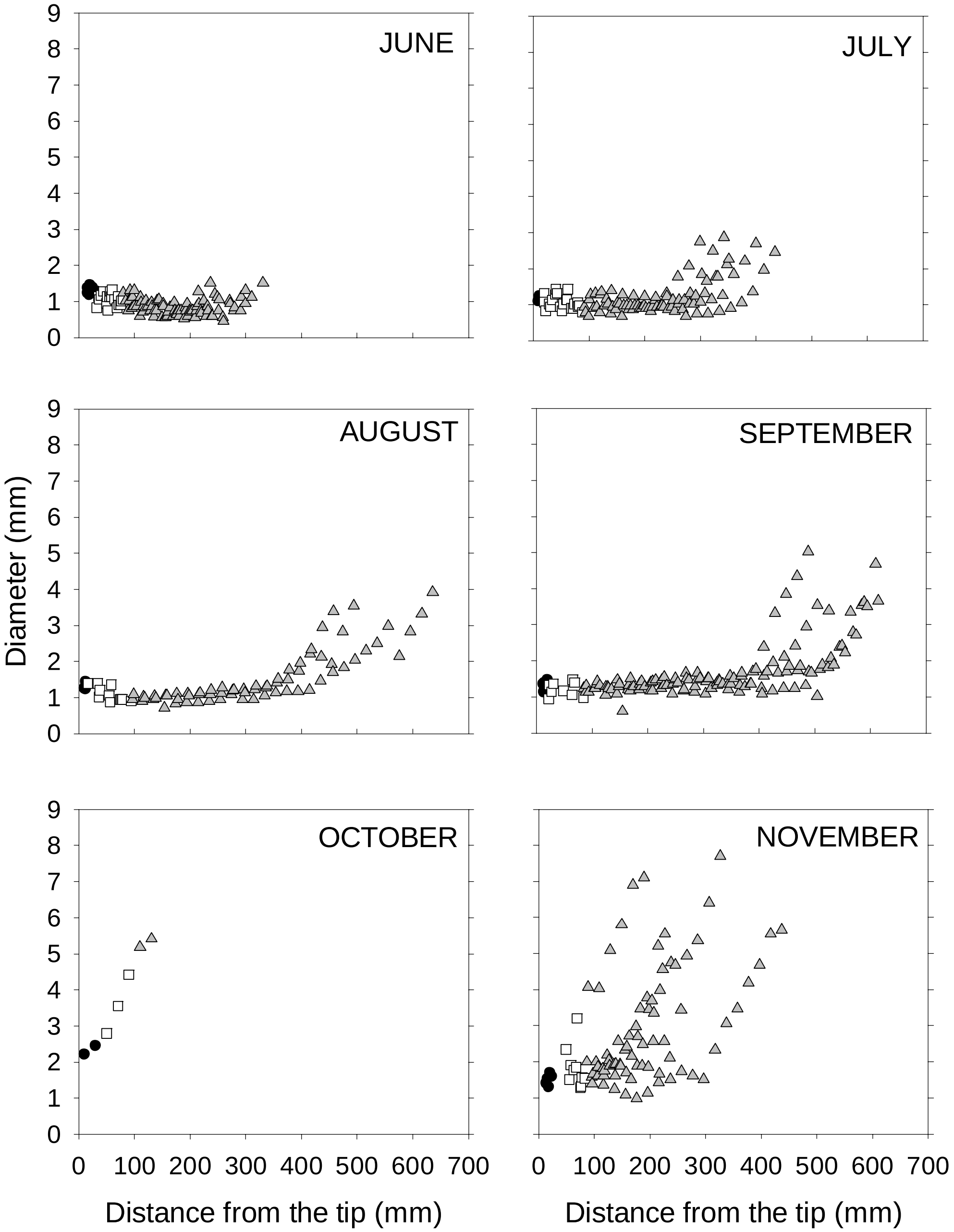


Fig. 5. Changes in TAPR diameter for the white zone (●), CT zone (□) and cork zone (△).

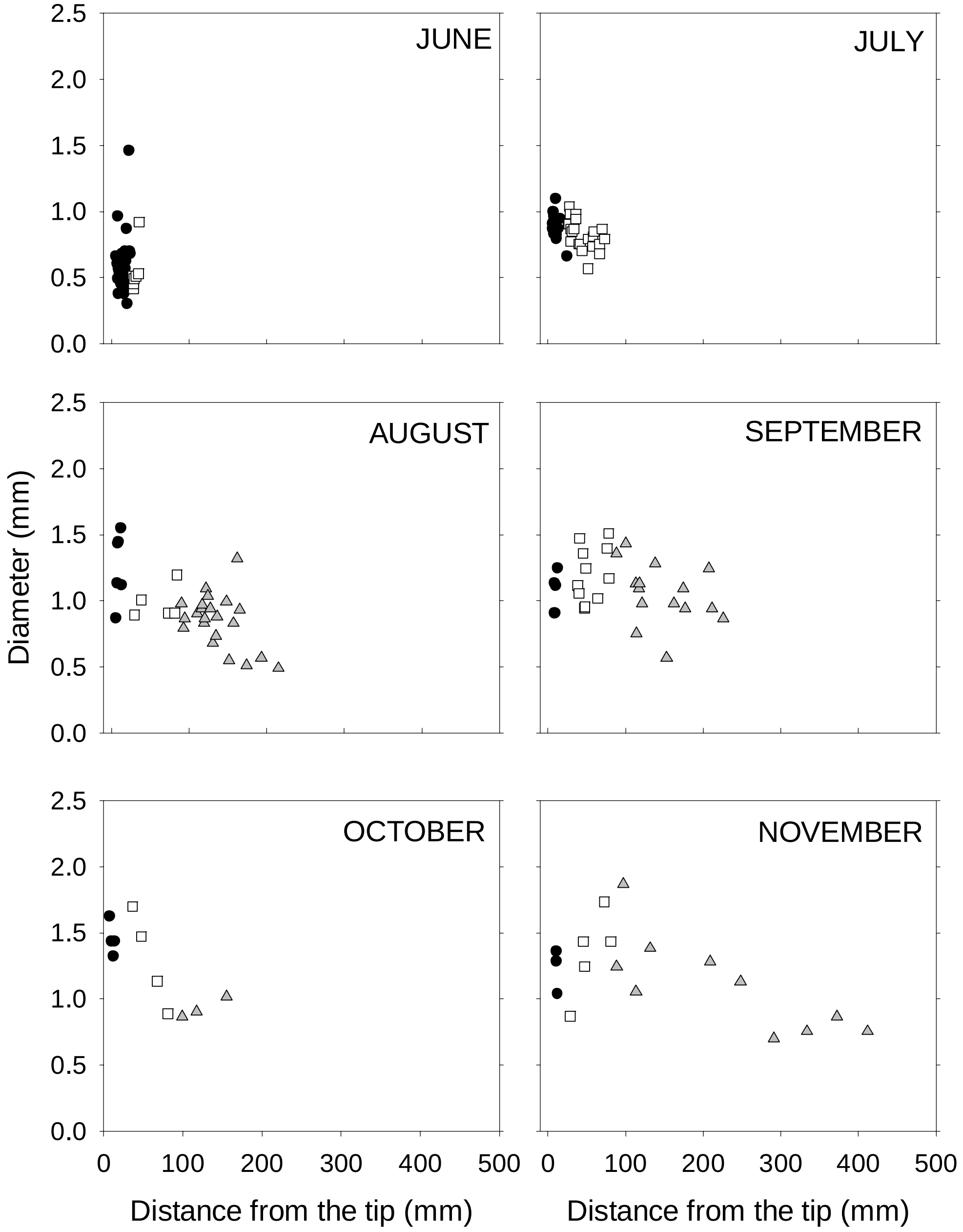


Fig. 6. Changes in FOLR diameter for the white zone (●), CT zone (□) and cork zone (▲).

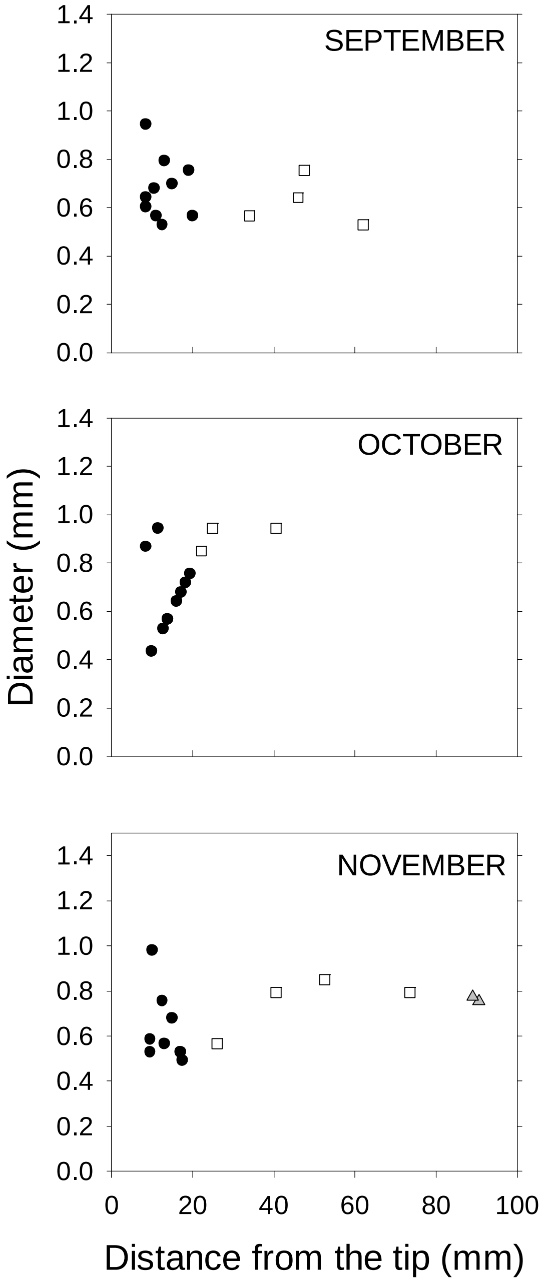


Fig. 7. Changes in SOLR diameter for the white zone (●), CT zone (□) and cork zone (▲).

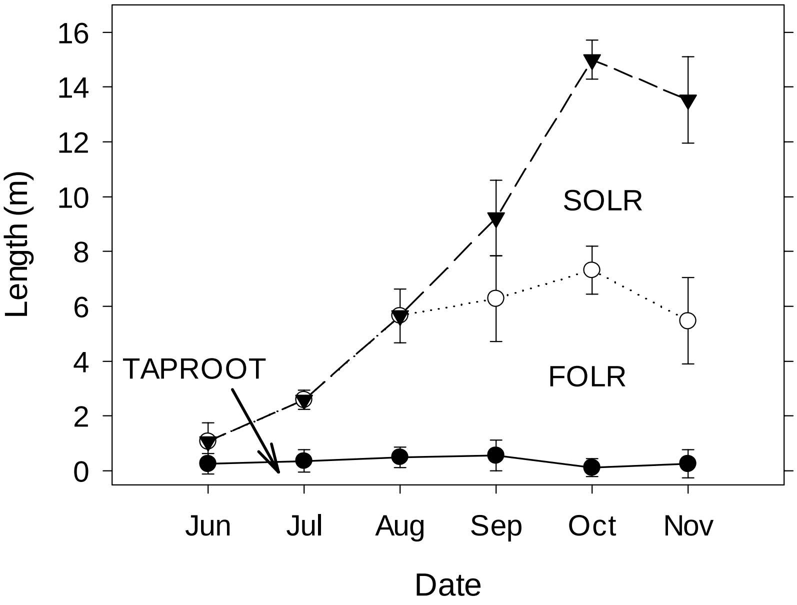


Fig. 8. Changes in cumulative length *P. taeda* root system and its distribution to TAPR, FOLRs and SOLRs. Mean +/- SE, n=3

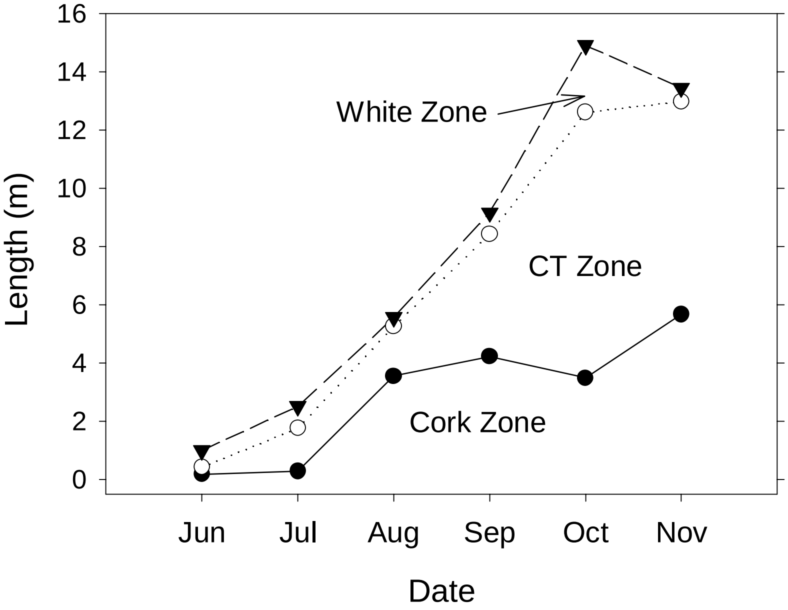


Fig. 9. Changes in cumulative length of *P. taeda* root system and its distribution to cork, CT and white zone. Mean+/- SE, n=3

The TAPR diameter in June ranged from 0.5 to 1.5 mm (Fig. 5). It was slightly larger at the tip, declined to a minimum near 200 mm behind the tip and then gradually increased toward the base. This pattern was evident in July and August. There was an abrupt increase in TAPR diameter commencing at approximately 300 mm in July and 350 mm in August. TAPR diameter reached 3 mm in July and 4 mm in August at the base. The September TAPR had a distal portion with gradually increasing diameter in the range of 1.0 to 1.5 mm and an abrupt increase in diameter beginning at 400 mm reaching a basal diameter of 5 mm. Undercutting in October eliminated all roots less than 2 mm diameter; consequently, root diameter showed a steep increase from 1.5 at the tip to 8.0 mm at the base in November. FOLR diameter generally ranged from 0.5 to 1.5 mm and showed a slight decline from the tip to the base, especially in November when lengths approached 400 mm (Fig. 6). SOLRs were not common until September and diameter ranged from 0.5 to 1.0 mm (Fig. 7).

Total surface area of the seedling varied similarly to the length. It increased to over 0.05 m^2 in November (Fig. 10). In November SOLRs dominated the root system with 53% of the surface area, FOLRs were 42% and the TAPR was only 5%. The CT zone was usually dominant. By November the white zone represented 12% of the seedling surface area and the CT and cork zones were 44% each (Fig. 11).

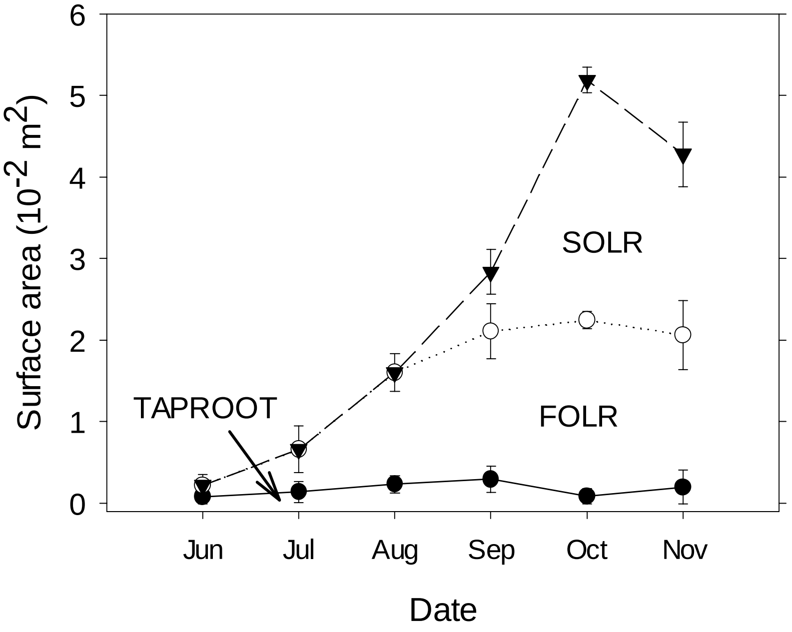


Fig. 10. Changes in cumulative surface area of *P. taeda* root system and its distribution to TAPR, FOLRs and SOLRs. Mean +/- SE, n=3.

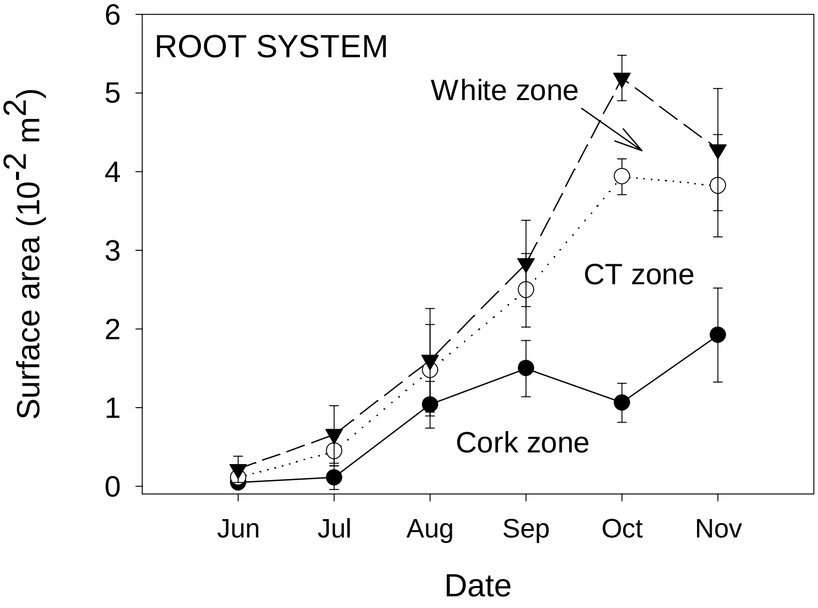


Fig. 11. Changes in cumulative surface area of *P. taeda* root system and its distribution to cork, CT and white zone. Mean +/- se, n=3.

Tracheids

The number of conductive TAPR tracheids in a root cross section ranged from 10 to 100 in the white zone over most of the year except in October when there were over 300 in some roots (Fig. 12). The CT zone contained 30 to 300 conductive tracheids except in October when the number ranged from 300 to 1,000. The number of conductive tracheids in the cork zone increased steeply in the proximal direction along its length. The cork zone had 30 to 300 tracheids in June and the number increased to the range of 1,000 to 30,000 in November. FORL had 3 to 25 conducting tracheids in the white zone in June and the number did not increase beyond 25 in later months (Fig. 13). The FORL CT zone had 10 to 25 conductive tracheids in June. The number gradually increased to 20 to 30 in November. Cork zone did not develop in FORL until August and it had 20 to 60 conducting tracheids. SORL had 10 to 30 conducting tracheids in the white zone, 15 to 30 in the CT zone and just over 35 in the cork zone (Fig. 14).

The diameter of conductive tracheids in the white zone of TAPR was 17 to 22 µm in June and July, 20 to 25 µm in August and September and 25 to 30 µm in October and November (Fig. 15). Diameter of conducting TAPR tracheids in the CT zone was 25 to 30 µm in June through September and it increased to 30 to 35 µm in October and November. The cork zone conducting tracheids fell in the range of 25 to 35 µm. Almost all the conducting tracheids of the FOLR white zone fell in the diameter range of 8 to 13 µm, and the diameter tended to be

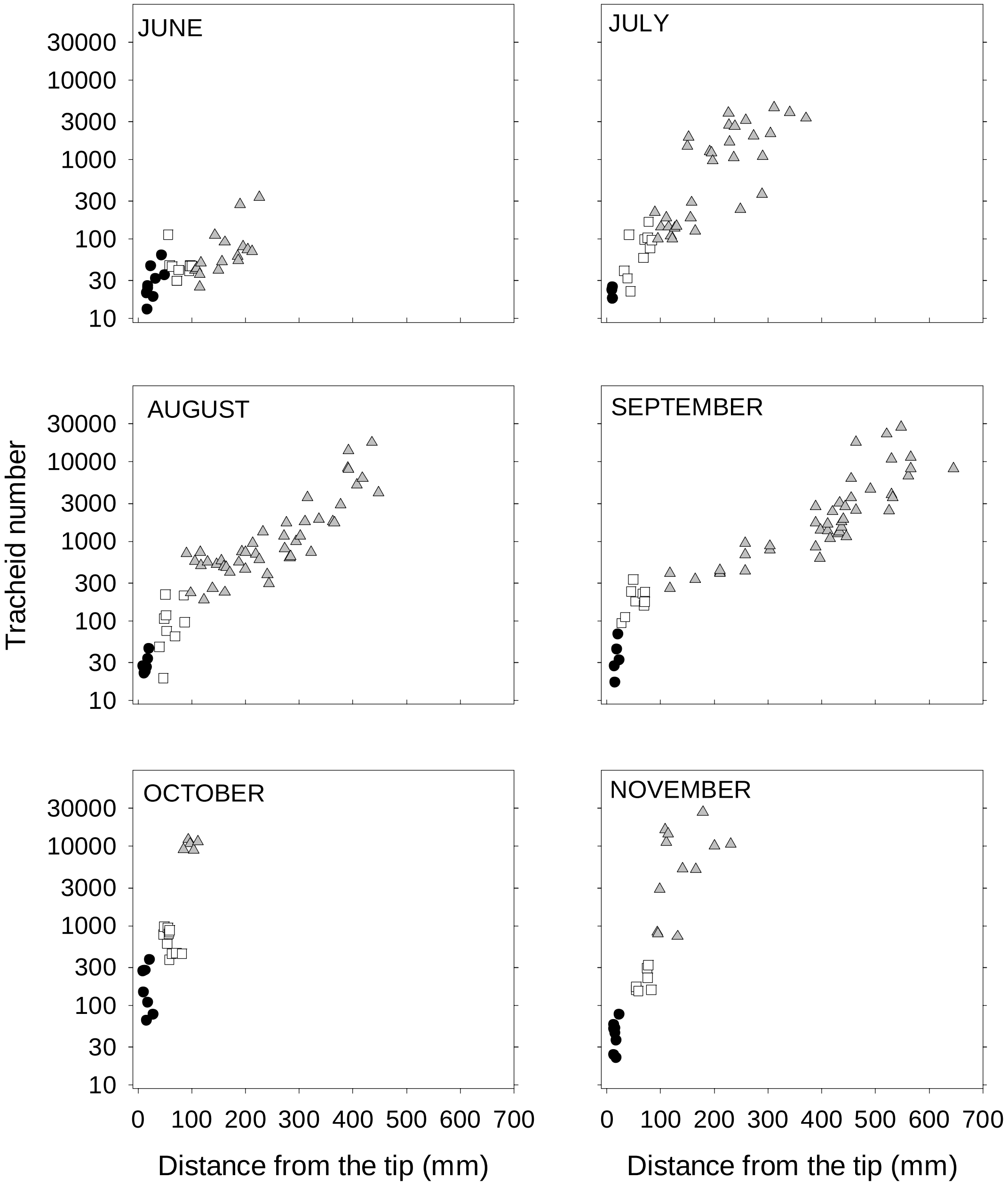


Fig. 12. Changes in TAPR conductive tracheid number for white (●), CT (□) and cork zone (▲).

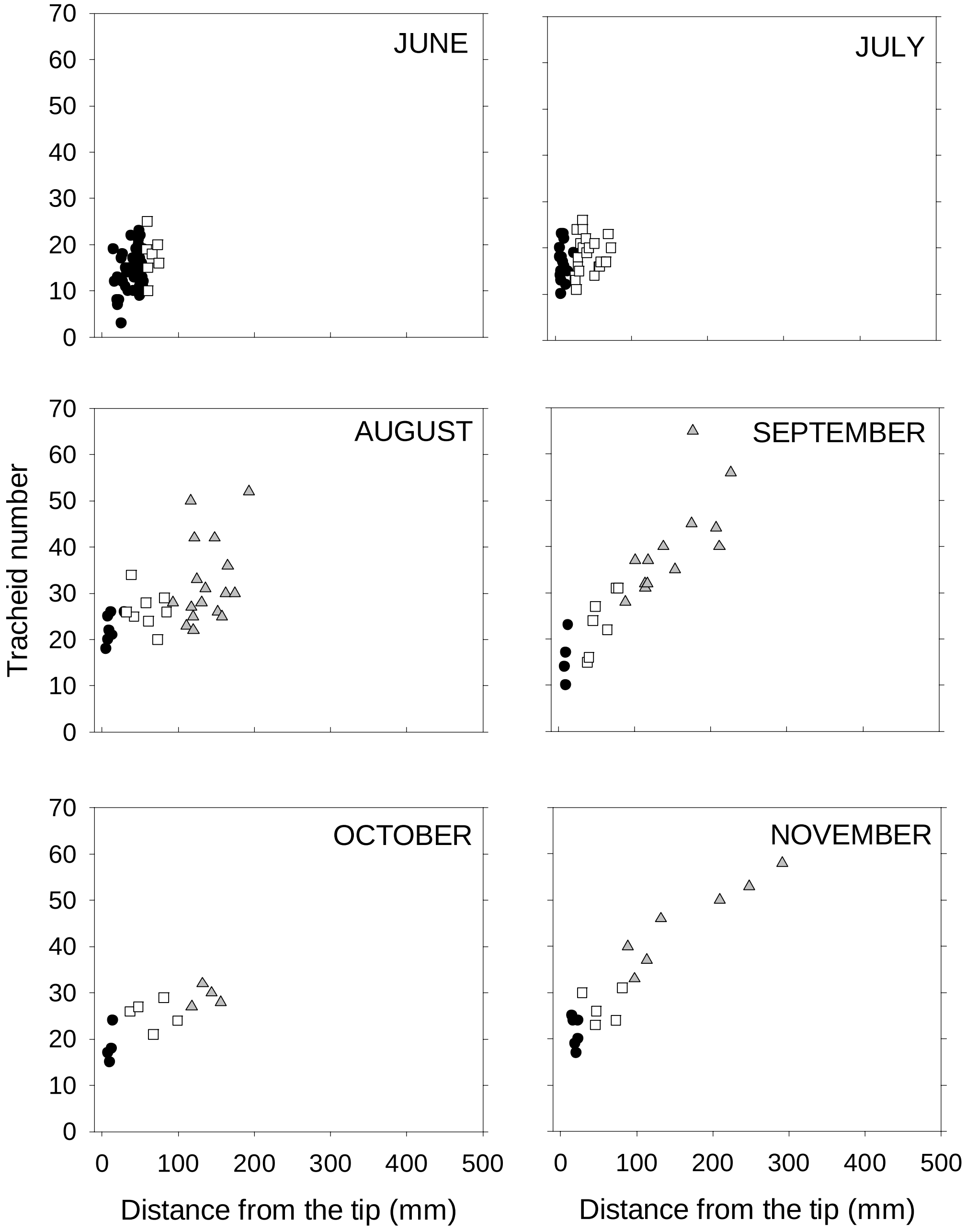


Fig. 13. Changes in FOLR conductive tracheid number for white (●), CT (□) and cork zone (▲).

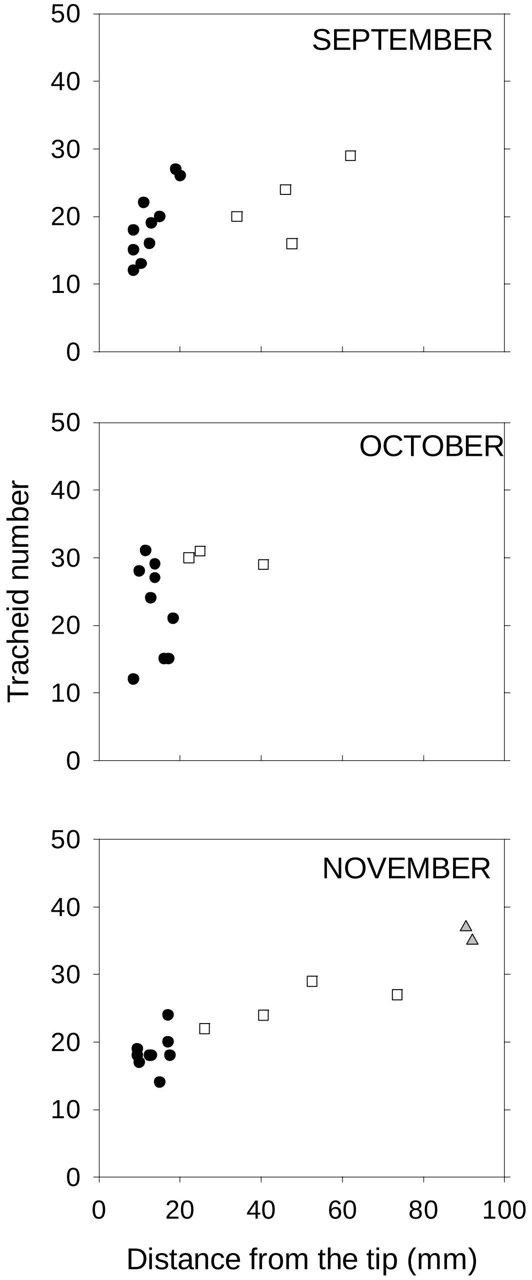


Fig. 14. Changes in SOLR conductive tracheid number for white (●), CT (□) and cork zone (▲).

greater later in the year (Fig. 16). The diameter of FOLR CT zone conducting tracheids was 10 to 14 µm and cork zone conducting tracheids were slightly larger at 10 to 16 µm. The SOLR white zone had conducting tracheids mostly in the range of 8 to 10 µm with some reaching 12 µm in November (Fig. 17). The SOLR CT and cork zone had conducting tracheids in the range of 10 to 12 µm.

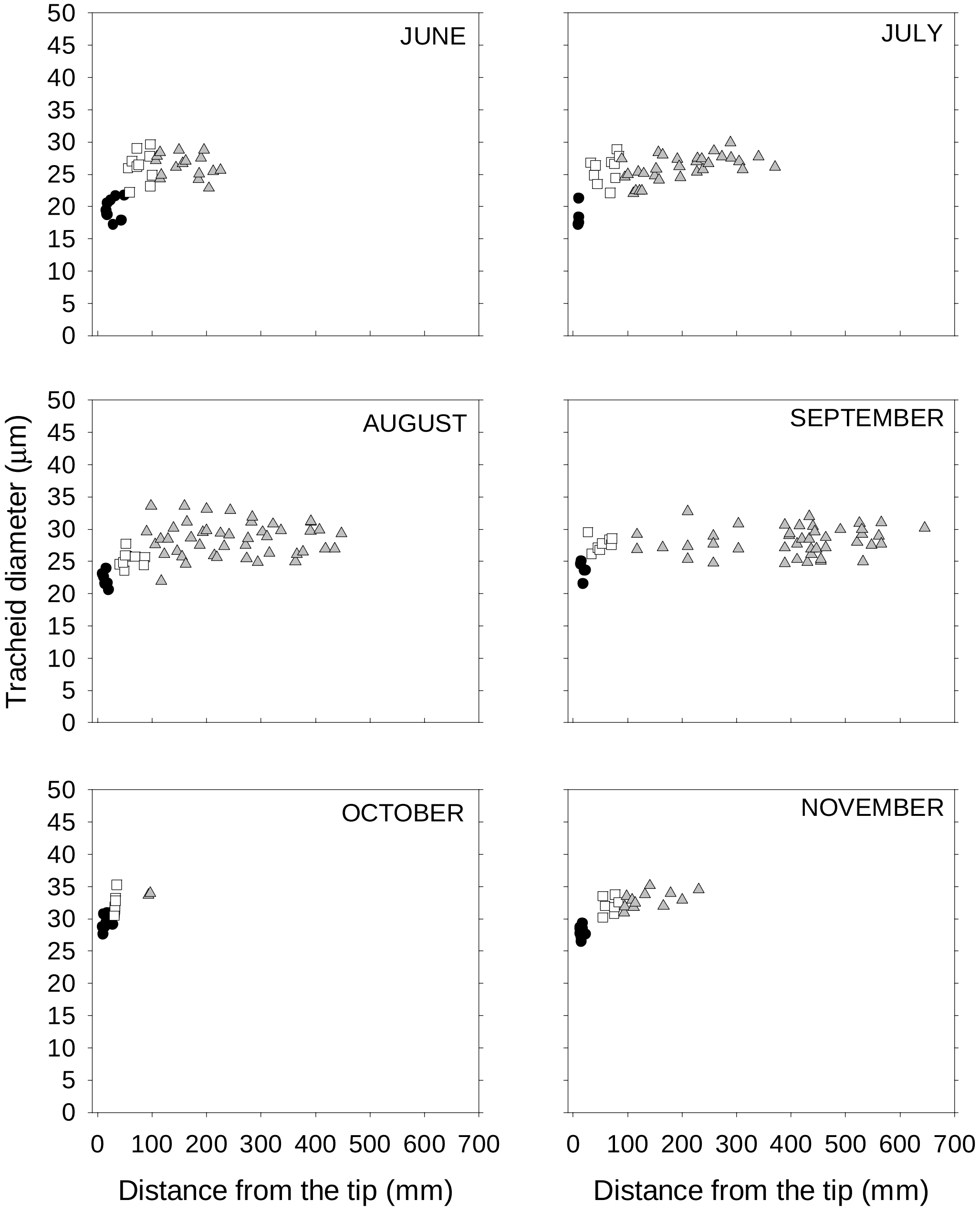


Fig. 15. Changes in TAPR conductive tracheid diameter for white (●), CT (□) and cork zone (▲).

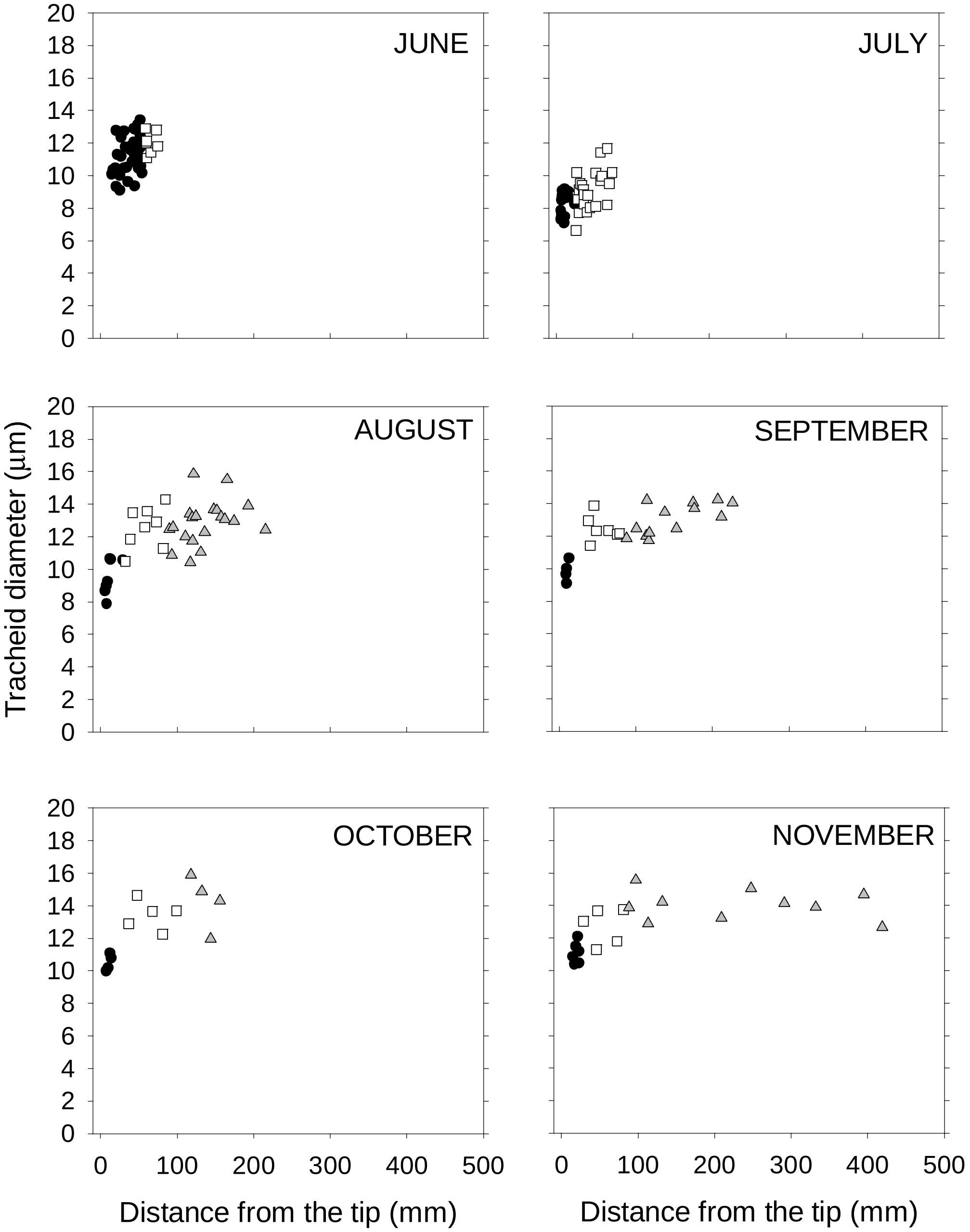


Fig. 16. Changes in FOLR conductive tracheid diameter for white (●), CT (□) and cork zone (▲).

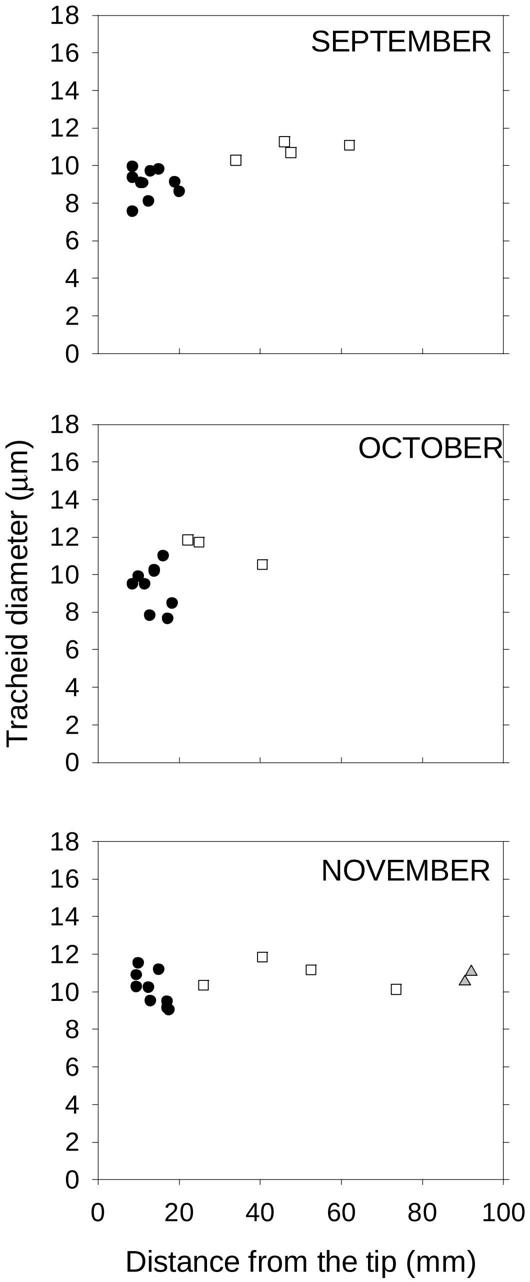


Fig. 17. Changes in SOLR conductive tracheid diameter for white (●), CT (□) and cork zone (▲).

DISCUSSION

Root length is an important characteristic in determining the ability of roots to absorb water and nutrients (Levitt, 1980; Bowen, 1985). The contribution of the different root zones varied among the root types. The major contributor to TAPR length was the cork zone followed by the CT and white zones. This could indicate that in addition to absorbing water, the TAPR mainly functioned as a conduit for water absorbed by laterals. The dominance of the cork zone would help to reduce water losses to the soil as water was pulled toward the shoot. The FOLR length was mainly composed of CT and the cork zone. Hence their capacity to absorb water was greater than TAPR because the CT zone possessed passage cells allowing water to enter the root. The SOLRs had very little cork zone, indicating a high potential for water uptake.

The white zone was not a large part of the root system length, although it was considered the most important zone involved in absorption of water and nutrients (Taylor and Peterson, 2000). The explanation may be that the newly produced white roots became CT zone and the older region of CT zone became in turn cork zone. This resulted in a decrease in the absorptive area and an increase in the length of the CT and cork zones. The production of white roots was similar to the rate of transformation to CT and cork zone, resulting in an increase in the length of CT and cork zone and a nearly constant amount of white zone.

Most of the root system length was lateral roots (75 to 99%). This agreed with the structure of the loblolly pine root system as a TAPR supporting horizontal laterals, sinker roots and fine roots described by Carlson *et al.* (1988) and Harrington *et al.* (1989). Lyford (1980) and Eis (1978) observed that the TAPR growth rate usually slowed as the growth rate of the lateral roots increased. A study by Nobel and Sanderson (1984) found lateral roots accounted for about 70% of the total root length for *Ferocactus acanthodes*. The increasing length of the root system showed that an increasing amount of soil was explored by these lateral roots resulting in an improved capacity to absorb water. This also indicated most of the water was absorbed by the laterals as they had a high individual absorptive potential. However, Sanderson (1982) calculated that the lateral roots of barley would only account for one quarter of the total uptake of water by the plant compared to the two thirds reported by Graham *et al.* (1974). This was surprising, as the barley lateral roots represented nearly three quarters of the total root length. In my study, as lateral roots represented 75 to 99% of the root system length, it was expected that their rate of water uptake was high.

Eissenstat (1992) and Fitter and Hay (1987) reported that root surface area is the most important trait in explaining the significance of roots in their capacity to explore soil for water and nutrients. TAPR surface area was dominated by the cork zone. White and CT zones were small but may have been highly efficient in the absorption of water, because of the presence of passage cells in the CT zone, and the abundant living cortical cells in the white zone. The cortex cells provided a large surface area to exploit the soil solution. The lateral roots represented most of the root surface area (63 to 95%). This agreed with Kramer and Bullock (1966) who found that roots with a diameter less than 1.3 mm represented 67% of the mature loblolly pine root system surface area. Our lateral roots, at 1 mm and less in diameter, were comparable to the roots described by Kramer and Bullock. They also calculated that loblolly pine suberized roots represented about 97% of the root system surface area. However the term “suberized roots” employed by Kramer and Bullock needs to be clarified. Their suberized roots included all roots with a brown color and a suberin lamellae detected with Sudan III. This would correspond to the CT and cork zones defined by recent studies (McKenzie and Peterson, 1995a, b; Enstone *et al.*, 2001). Therefore, the surface area of “suberized roots” found by Kramer and Bullock was very similar to the values found in this study (96% in November).

Undercutting and root pruning reduced root length in October. Rapid growth replaced all the lost roots and increased root length 20% above the amount before pruning by November. It has been documented that injury can cause the production of abundant root tips. In noble fir (Wilcox, 1955) and paper birch (Horsley and Wilson, 1971), when the main root tip was injured it was replaced by a number of roots with a large diameter tip. Chauhan and Mishra (1996) observed an increase in the number of lateral roots in undercut and pruned seedlings. This production of new lateral root branches from cut ends resulted in an augmentation of the length and surface area of the root system. The more fibrous root system had a better capacity to explore the soil solution (Eissenstat and Van Rees, 1994; Lynch, 1995). Varney and Canny (1993) found FOLRs absorbed 88% of the total water due to their large surface area.

The diameter depends on the type of the root, its maturity or age and the environment (Enstone *et al.*, 2001; McCrady and Comerford, 1998). The larger diameter of the TAPR reflected its different roles: anchorage, collection of the water from the FOLRs and transport of this water to the shoot. The TAPR was characterized by a progressive decrease in diameter in the first 300 mm from the tip of the root followed by a strong increase up to the base. The slowly decreasing diameter was probably due to the progressive death and shedding of the cortical cells (Peterson *et al.*, 1999; Enstone *et al.*, 2001). This zone was also the site of emergence of the lateral roots, whose xylem was connected to the TAPR xylem, enabling the upward movement of water from lateral to TAPR. However this addition of FOLRs did not affect the TAPR diameter in the CT zone. In older roots, in addition to the presence of laterals, the production of secondary xylem by the vascular cambium was responsible for the strong radial growth of the TAPR (Esau, 1965). The cells of the vascular cambium surround the xylem, produce tracheids centripetally and phloem centrifugally, progressively crushing the existing parenchyma. The TAPR increased its diameter with the production of new tissues.

The lateral roots showed some differences. Their diameter was smaller than the TAPR, with the SOLR diameter being smaller than the FOLR diameter. The smaller size of the lateral roots reflected their function to explore as much soil as possible to find water and nutrients (Carlson *et al.*, 1988; Varney and Canny, 1993). As in the TAPR, the smaller diameter of the FOLRs was caused by the death and sloughing of the cortical cells. A strong increase in diameter could happen later if the FOLRs become sufficiently long for large amounts of secondary xylem to develop. The SOLR diameter remained constant, implying that the cortical sloughing was not significant.

There are at least two ways to increase the transport efficiency of a system of given length. One is by producing more xylem cross-sectional area, and the other is to change anatomical features which affect conductivity such as vessel diameter, length and number. Our study showed that *P. taeda* was doing both. The number of tracheids and their diameter increased along the axis of the TAPR and FOLRs. Changes in transectional area and shape of the xylem along the axis had been also observed in ferns (Bower, 1935; Bierhorst, 1971; Ogura, 1972; Beck *et al.*, 1982, Gibson *et al.*, 1984). No such changes were observed in SOLRs. In the TAPR the tracheid diameter was smaller in the white zone compared to CT and cork zones. This was caused by the differentiation of the primary xylem, producing small tracheids when the root was young and larger one (metaxylem) as the root grew older and developed lateral roots. The secondary growth also produced tracheids that were similar to the metaxylem.

Petioles of *Ginkgo biloba* and *Drimys wintera* also showed an increase of the tracheid diameter in secondary growth (Schulte and Gibson, 1988).

In *P. taeda* seedlings, the number and the small size of the tracheids in the white zone of the TAPR seemed to be sufficient to transport water upwardly as the axial conductivity was not limiting water flow (Chapter IV). In the TAPR CT zone, tracheid number and diameter increased as the FOLRs that conducted water to the TAPR began to develop. In the TAPR cork zone, FOLRs were produced which in turn produced SOLRs. Consequently, the TAPR needed a larger transport capacity to accommodate the increased flow. It seemed that instead of augmenting the diameter of the tracheids, the TAPR increased the number of conductive tracheids via secondary growth. The FOLRs also increased the number and width of its tracheids as it grew older and SOLRs developed. The SOLRs kept a constant number of tracheid with a constant diameter. The differences between TAPR and its laterals could have been due the youth of these roots. Lateral roots may have developed the TAPR characteristics later when their development was more advanced.

Hormones influence plant development. Auxin is transported through plant tissues, moving from cell to cell in a polar manner from leaves and buds to roots (Sachs, 1984, 1986). Roots act as a sink for the polar flow of auxin originating in the young leaves (Sachs, 1968). Xylem development is mainly controlled by auxin (Klee *et al., 1987;* Tuominen *et al.,* 1995; Berleth *et al.,* 2000; Aloni, 2001).

According to Aloni and Zimmermann (1983), the increase in the size of individual vascular elements from leaves to roots (Bailey, 1958; Zimmermann and Potter, 1982) can be explained by the decreasing auxin concentration progressively down the axis of the plant resulting in a slower differentiation rate that allows the production of fewer but larger vessels. However, this theory is principally based on observations of leaves and stems of trees. There has been very little research on seedling roots.

My study showed the *P. taeda* TAPR and FOLRs increased tracheid number and diameter from the white to the CT zone and greatly increased the tracheid number from the CT to older roots with no change in diameter. The TAPR had many times the number of tracheids found in the laterals and they were two to three times larger in diameter (Fig. 5-7 and 12-14). It was not clear whether these results conformed with the hypothesis of auxin control of tracheid number and size that was proposed for the shoot. It is possible basipetal auxin transport in roots and a supply of auxin from the shoot could favor the increased production of large diameter tracheids in the TAPR compared to FOLRs and SOLRs. In addition, local obstructions at the junctions between the TAPR and FOLRs and between FOLRs and SOLRs could restrict shoot-origin auxin movement to the lateral roots. Xylem restrictions at root junctions have been observed (Luxová, 1986, 1990; McCully and Canny, 1988; Aloni and Griffith, 1991; Shane et al., 2000) implying there may be restrictions to movement in the phloem as well which may affect auxin movement. In contrast, the high auxin content of mycorrhizal fungi appears to stunt root growth and could affect the xylem production in mycorrhizae as well as the sub-adjacent root which was most often the SOLR (MacDougal and Dufrenoy, 1944; Slankis, 1973).

CONCLUSIONS

- The TAPR had characteristics suggesting high capacity for water transport: (*i*) rapid secondary xylem production near the base, (*ii*) up to 10 times the number of tracheids as FOLRs for CT and cork zones of the same diameter and distance from the tip, and (*iii*) maximum tracheid diameters over twice that of FOLRs and nearly 3 times that of SOLRs.

- Lateral roots and especially SOLRs appeared to be well suited for uptake of water and mineral ions as they were comprised mostly of white and CT zone.

- Lateral roots represented most of the length (75-99%) and surface area (63-95%) of the root system. SOLRs did not appear until August and rapidly increased to nearly 50% of the root length and surface area by November.

- White zone was nearly a constant amount of root length and area which represented a decreasing percentage of the root system, 4% of length and 12% of surface area in November.

- CT zone was a dominant part of the root system reaching 63% of the length and 44% of the surface area in November.

- There appeared to be a maximum tracheid diameter specific to root zone and type, because tracheid diameter increased dramatically from the white to the CT zone especially in the TAPR and remained relatively constant throughout the CT and cork zones.

FUTURE RESEARCH

- The CT and cork zones represented most of the length and surface area of the root system. More details are needed to elucidate the adaptive advantage of these zones. The changes in the suberization of the CT in reaction to environmental changes need to be studied. The importance of lenticels, wounds and openings created by lateral root junctions in the cork zone needs further investigations.

- Lateral roots represented most of the length and surface area of the root system. They absorb water that is conducted toward the shoot by the taproot. More information is needed concerning taproot-lateral root and lateral root-lateral root junction as constrictions may increase resistance to water passing from one root to another.

- The diameter of the tracheids was different between the root zones and types resulting in different axial transport capacities. Are these differences only ontogenetic? Is tracheid diameter determined by internal controls such as hormones?

- Research on root anatomy and morphology should be extended to less controlled field conditions and older plants to learn more about environmental and ontogenetics effects.

REFERENCES

Aloni, R. 2001. Foliar and axial aspects of vascular differentiation: Hypotheses and evidence. J. Plant Growth Reg. 20:22-34.

Aloni, R. and M. Griffith 1991. Functional xylem anatomy in root-shoot junctions. Planta 184:123-129.

Aloni, R. and M.H. Zimmermann 1983. The control of vessel size and density along the plant axis – a new hypothesis. Differentiation 24:203-208.

Bailey, I.W. 1958. The structure of tracheids in relation to the movement of liquids, suspensions and undissolved gases. *In*: Thimann K.V. (ed.). The Physiology of Forest Tree. Ronald, New York, pp. 71-82.

Beck, C.B., R. Schmid and G. Rothwell 1982. Stelar morphology and the primary vascular system of seed plants. Bot. Rev. 48:491-815.

Berleth, T., J. Mattsson, C.S. Hardtke 2000. Vascular continuity and auxin signals. Trends Plant Sci. 5:387-393.

Bierhorst, D.W. 1971. Morphology of vascular plants. New York: Macmillan.

Bowen, G.D. 1985. Roots as a component of tree productivity. *In*: M.G.R. Cannell, and J.E. Jackson (eds.). Attributes of trees as crop plants. Institute of Terrestrial Ecology, Midlothian, Scotland. pp. 303-315.

Bower, F.O. 1935. Primitive land plants. Macmillan, London.

Carlson, W.C., C.A. Harrington, P. Farnum and S.W. Hallgren 1988. Effects of root severing treatments on loblolly pine. Can. J. For. Res. 18:1376-1385.

Chauhan, S.K. and V.K. Mishra 1996. Effect of undercutting on the biomass of *Ulmus villosa* seedlings. Indian J. For. 19(3):283-284.

Eis, S. 1978. Natural root forms of western conifers. *In*: Symposium on Root Form of Planted Trees, Victoria, B.C. Canada. pp. 23-27.

Eissenstat, D.M. 1992. Costs and benefits of constructing roots of a small diameter. J. Plant Nutr. 15:763-782.

Eissenstat, D.M and K.C. Van Rees 1994. The growth and function of pine roots. Ecol. Bull. 43:76-91.

Enstone, D.E., C.A. Peterson and S.W. Hallgren 2001. Anatomy of seedling tap roots of Loblolly pine (*Pinus tadea* L.). Trees 15:98-111.

Esau, K. 1965. Vascular differentiation in plants. John Wiley and Sons: New York.

Esau, K. 1977. Plant anatomy. Second edition. John Wiley & Sons, Inc., New York.

Fitter, A.H. and R.K.M. Hay 1987. Environmental physiology of plants. Academic Press, London.

Gibson, A.C., H.W. Calkin and P.S. Nobel 1984. Xylem anatomy, water flow and hydraulic conductance in the fern *Cyrtomium falcatum*. Am. J. Bot. 71:564-574.

Graham, J.P., D.T. Clarkson and J. Sanderson 1974. Water uptake by the roots of marrow and barley plants. Agricultural Research Council Letcombe Laboratory Annual Report, 1973:9-12.

Harrington, C.A., J.C. Brissette and W.C. Carlson 1989. Root system structure in planted and seeded loblolly and shortleaf pine. For. Sci. 35: 469-480.

Horsley, S.B. and B.F. Wilson 1971. Development of the woody portion of the root system of *Betula papyrifera*. Am. J. Bot. 58:141-147.

Jenkins, P.A. 1974. Influence of applied indolacetic acid and abscissic acid on xylem cell dimensions in *Pinus radiata* D. Don. *In*: Bieleski R.L., Ferguson A.R., Cresswell M.M (eds.) Mechanisms of Regulation of Plant Growth. R. Soc. N.Z., Wellington. pp. 737-742.

Klee, H.J., R.B. Horsch, M.A. Hinchee et al. 1987. The effects of overproduction of two *Agrobacterium tumefasciens* T-DNA auxin biosynthetic gene products in transgenic petunia plants. Genes Dev. 1:86-96.

Kramer, P.J. and H.C. Bullock 1966. Seasonal variations in the proportions of suberized and unsuberized roots of trees in relation to the absorption of water. Am. J. Bot. 53:200-204.

Levitt, J. 1980. Responses of plants to environmental stresses. II. Water, radiation, salt and other stresses. Academic Press, London.

Lyford, W.H. 1980. Development of the root system of Northern red oak (*Quercus rubra* L.). Harvard For. Paper 10.

Lynch, J. 1995. Root architecture and plant productivity. Plant Physiol. 109:7-13.

Luxová, M. 1986. The hydraulic safety zone at the base of barley roots. Planta 169:465-470.

Luxová, M. 1990. Effect of lateral root formation on the vascular pattern of barley roots. Botanica Acta 103:305-310.

MacDougal, D.J. and J. Dufrenoy 1944. Mycorrhizal symbiosis in *Aplectrum, Corallorhiza,* and *Pinus.* Plant Physiol. 19:440-465.

MacFall, J.S., G.A. Jonnson and P.J. Kramer 1990. Observation of a water depletion region surrounding Loblolly pine roots by magnetic resonance imaging. Proc.Natl Sci. USA 87:1203-1207.

MacFall, J.S., G.A. Jonnson and P.J. Kramer 1991. Comparative water uptake by roots of different ages in seedlings of Loblolly pine (*Pinus taeda* L.). New Phytol. 119:551-560.

McCrady R.L. and N.B. Comerford 1998. Morphological and anatomy relationships of loblolly pine fine roots. Trees 12:431-437.

McCully, M.E. and M.J. Canny 1988. Pathways and processes of water and nutrient movement in roots. Plant Soil 111:159-170.

McKenzie, B.E. and C.A. Peterson 1995a. Root browning in *Pinus Banksiana* Lamb. and *Eucalyptus pilularis* Sm. Anatomy and permeability of the White and Tannin Zones. Botanica Acta 108:127-137.

McKenzie, B.E. and C.A. Peterson 1995b. Root browning in *Pinus Banksiana* Lamb. and *Eucalyptus pilularis* Sm. Anatomy and permeability of the Cork Zone. Botanica Acta 108:138-143.

Nobel, P.S. and J. Sanderson 1984. Rectifier-like activities of roots of two desert succulents. J. Exp. Bot. 35:727-737.

Ogura, Y. 1972. Comparative anatomy of vegetative organs of the pteridophytes. Handbuch der Pflanzenanatomie, 7 (3). Berlin: Gebrüder Borntraeger.

Peterson, C.A. and E. Steudle 1993. Lateral hydraulic conductivity of early metaxylem vessels in *Zea mays* L. roots. Planta 189:288-297.

Peterson, C.A., D.E. Enstone and J.H. Taylor 1999. Pine root structure and its potential significance for root function. Plant Soil 217:205-213.

Sachs, T. 1968. The role of the root in the induction of xylem differentiation in pea. Ann. Bot. 32:391-399.

Sachs, T. 1984. Axiality and polarity in vascular plants. *In*: Barlow P.W., Carr D.J. (eds.). Positional Controls in Plant Development. Cambridge University Press, Cambridge. pp. 193-224.

Sachs, T. 1986. Cellular patterns determined by polar transport. *In*: Bopp M. (ed.). Plant Growth Substances. Springer, Berlin Heidelberg New York, Tokyo. pp. 231-235.

Salleo, S., M.A. Lo Gullo and L. Siracusano 1984. Distribution of vessel ends in stems of some diffuse- and ring-porous trees: the nodal regions as “safety zones” of the water conducting system. Ann. Bot. 54:543-552.

Sanderson, J. 1983. Water uptake by different region of the barley root. Pathways of radial flow in relation to the development of the endodermis. J. Exp. Bot. 34(140):240-253.

SAS 1999. The SAS for Windows, Release 8.0. SAS Institute Inc., Cary, NC 27513.

Savidge, R.A. and P.F. Wareing 1981. A tracheid-differentiation factor from pine needles. Planta 153:395-404.

Schulte, P.J. and A.C. Gibson 1988. Hydraulic conductance and tracheid anatomy in six species of extant seed plants. Can. J. Bot. 66:1073-1079.

Shane, M.W., M.E. McCully and M.J. Canny 2000. Architecture of branch-root junctions in maize: structure of the connecting xylem and porosity of pit membranes. Ann. Bot. 85:613-624.

Slankis, V. 1973. Hormonal relationships in mycorrhizal development. *In:* Ectomycorrhizae. G.C. Marks and T.T. Kozlowski, eds., Academic Press, New York. pp. 231-298.

Steudle, E. and C.A. Peterson 1998. How does water get through roots? J. Exp. Bot. 49:775-788.

Taylor, J.H. and C.A. Peterson 2000. Morphometric analysis of *Pinus banksiana* Lamb. root anatomy during a 3-month field study. Trees 14: 239-247.

Tuominen, H., F. Sitbon, C. Jacobsson, et al. 1995. Altered growth and wood characteristics in transgenic hybrid aspen expressing *Agrobacterium* *tumefasciens* T-DNA indoleacetic acid-biosynthetic genes. Plant Physiol. 109:1179-1189.

Tyree, M.T., S.D. Davis and H. Cochard 1994. Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? I.A.W.A. J. 15:335-360.

Varney, G.T. and M.J. Canny 1993. Rates of water uptake into the mature root system of maize plants. New Phytol. 123:775-789.

Wilcox, H. 1955. Primary organization of active and dormant roots of noble fir, *Abies procera*. Am. J. Bot. 41:812-821.

Wilcox, H. 1964. Xylem in roots of *Pinus resinosa* Ait. in relation to heterorhizy and growth activity. *In*: M.H. Zimmermann (ed.). The Formation of Wood in Forest Trees. Academic Press, New York. pp. 459-478.

Zimmmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin.

Zimmermann, M.H. and D. Potter 1982. Vessel-length distribution in branches, stems and roots of *Acer rubrum* L.. I.A.W.A. Bull. 3:103-109.

Zimmermann, M.H. and J.S. Sperry 1983. Anatomy of the palm *Rhapis excelsa* IX. Xylem structure of the leaf insertion. J. Arnold Arbor. Harvard Univ. 64:599-609.

CHAPTER - III

TRACHEID ANATOMY AND HYDRAULIC RESISTANCE IN *PINUS TAEDA* SEEDLING ROOTS

SUMMARY

The anatomy of the tracheid determines its hydraulic efficiency. Conifer tracheids are short (1-3 mm) and are closed by cell walls at both ends, compelling water to move from tracheid to tracheid through the pits in their side walls. Recently, it was observed that the loss of hydraulic conductivity from cavitation in conifers was mainly due to the anatomy of the tracheid pit membrane; conduit size was not the main factor (Sperry and Sullivan, 1992; Cochard, 1992). I determined tracheid characteristics in roots of *Pinus taeda* seedlings to learn how they affected xylem resistance to water flow. One objective was to learn the relative contribution to tracheid resistance of the different parts of the flow path through the tracheid. Another objective was to learn whether the tracheid characteristics and hence component resistances varied among the three root zones and in first-year seedling. Tracheids were longer and wider in the CT and cork zones and their number also increased from the white to the cork zone to accommodate water flow from the distal zone and

from the developing laterals. The TAPR bordered pit dimensions remained constant among zones and throughout the growing season. Pit resistance represented 82 to 97% of the tracheid resistance and the lumen resistance was 3 to18%. TAPR tracheid resistance was constant over the growing season despite the increase in diameter. This may have been due to the increase in the pit resistance because of their decreasing density. With a high resistance in the tapered ends, water movement from one tracheid to another occurred principally in the cylinder. TAPR tracheids may be less susceptible to cavitation than FOLRs but FOLR tracheids appeared to be more efficient to conduct water.

INTRODUCTION

Water uptake by terrestrial plants is determined by root tissue characteristics (Moreshet and Huck, 1991), and xylem anatomy is an important factor affecting water flow through roots (Tyree and Karamanos, 1981). Xylem development in relation to conductive capacity of roots has been extensively studied in agronomic crops (St. Aubin *et al.*, 1986; McCully and Canny, 1988; Wenzel *et al.*, 1989; Wang *et al.*, 1991) but rarely in conifers. Anatomical studies of Wilcox (1954, 1962, 1964) emphasized the development of primary tissues, including the xylem. Xylem differentiation in roots of *Abies alba* was described by Rypacek *et al.* (1976) but he limited his research to primary development. Only a few studies have been reported on the cambial growth, or wood formation in roots (Coutts, 1982; Liphshitz *et al.*, 1984).

The anatomy of the tracheid determines its hydraulic efficiency (Tyree *et al.*, 1994). Conifer tracheids are short (1-3 mm) and are closed by cell walls at both ends, compelling water to move from tracheid to tracheid through the pits in their side walls (Baily and Tupper, 1918; Esau, 1977). Crossing the xylem walls increases the resistance to axial flow (St. Aubin *et al.*, 1986; Sanderson *et al.*, 1988; Clarkson, 1991). Open xylem elements found in herbaceous plants and angiosperm trees present lower resistance to water flow (Passioura, 1988). Wide conduits are more efficient in water transport than narrow conduits (Zimmermann, 1983); however, that makes them more susceptible to cavitation

(Tyree *et al.*, 1994; Zimmermann, 1983). Recently, it was observed that the loss of hydraulic conductivity from cavitation in conifers was mainly dependent on anatomy of the tracheid pit membrane; conduit size was not the main factor (Sperry and Sullivan, 1992; Cochard, 1992). Two phenomena can limit xylem hydraulic conductivity. The first one is the cavitation or disruption of the water column and the second one is the displacement of the toruses against the pit apertures (Sperry and Tyree, 1990; Tyree *et al.*, 1994). When crossing through the pits, water has to move through margo pores which determine permeability. The pores also affect the hydraulic conductivity of tracheids and their vulnerability to cavitation.

I determined tracheid characteristics in roots of *Pinus taeda* seedlings to learn how they affected xylem resistance to water flow. One objective was to learn the relative contribution to tracheid resistance of the different parts of the flow path through the tracheid. Another objective was to learn whether the tracheid characteristics and hence component resistances varied with root type, root maturity and season of the year. The study was conducted over six months on first-year *P. taeda* seedlings grown in a forest tree nursery under operational conditions. The overall goal was to elucidate the contribution of the xylem to water uptake and transport capacity of the pine root system.

MATERIALS AND METHODS

Plant material

Seedlings were obtained from a single open-pollinated Oklahoma family of genetically improved *P. taeda*. Seeds were sown at the Oklahoma State Forest Regeneration Center near Washington, Oklahoma in the first week of May 2002 and they germinated in 10 – 15 days. The major cultural operations were fertilization, watering and pesticide application when needed. Lateral root pruning and undercutting were done in early October.

Seedlings were harvested every month from June to November. They were harvested from 3 replicates. PVC pipe was used to take a core of soil containing 5 to 6 trees with the whole tap root (TAPR) and its laterals. Four pipes per replication were collected. The pipes were stored at 6°C until measurements were made. The root systems were carefully separated from the soil using water and brought to the laboratory in containers filled with water.

Tracheid observation

TAPR was separated into white, CT and cork zones. The white and CT zones were distinguished according to visual inspection based on criteria from McKenzie and Peterson (1995a) and personal communication (Prem Kumar and

Steve Hallgren). The white zone was obviously white and the CT zone was brown. The white zone has a healthy intact cortex and the CT zone was characterized by gradual death and sloughing of cortical cells. Histochemical tests found tannin deposits in cortical walls in the CT zone of *Pinus banksiana* (McKenzie and Peterson, 1995a). The cork zone was clearly different from the CT zone. The cork zone was distinguished by being stiffer, having more and larger lateral roots and showing evidence of a periderm. The evidence of periderm was splitting of the outer surface of the root to reveal an interior layer lighter in color than the surface. The TAPR from June and November were analyzed to learn whether there were differences in tracheid dimensions between the beginning and the end of the growing season. Also the tracheids of first-order lateral roots (FOLRs) from November cork zone were measured as the high number of tracheids made them easy to observe in these roots.

For each zone, several segments about 1 cm long were immersed in a commercial bleach : water solution (1:3 by volume) for 2 hours or until the tissues were transparent. Then they were rinsed with water. Using a binocular microscope, the stele was separated from the cortex and opened to extract the xylem strands. Other tissues were removed to have a clear view of the xylem. The xylem strands were easy to detect as they had a silver-white coloration and were rigid compared to the other tissues. The non-tracheid tissues were removed with water and forceps to “clean” the slide. The xylem strands were carefully separated with forceps and spread on the slide. They were stained with

Toluidine blue (0.005% w/v) and viewed under a bright field microscope linked to a digital camera. The resulting digital images were analyzed using image analysis software (ImagePro Plus, Media Cybernetics, Silver Spring, MD, USA). Total length, length of the central cylinder and the tapered ends were measured (Fig. 1). Diameter and number of pits of each part were also measured.

Bordered pit observations with Scanning Electron Microscope (SEM)

After the separation of the TAPR into the three zones, 10 to 20 segments 1 cm long from each zone were stored in glutaraldehyde (first fixative). Then they were fixed a second time in 1% osmium tetroxide, dehydrated in a graded series of ethanol solutions and then critical-point dried. The segments were coated with a layer of carbon, and viewed with the SEM (JEOL JXM 6400). SEM observations produced digital images of the bordered pit that could be distorted because of the viewing angle depended on the tilt of the tracheid relative to the position of the electron detector. Assuming that the pits were perfectly round, the largest observed diameter of the ellipse representing a distorted view of the pit would be equal to its real diameter. Thus only this dimension was measured and analyzed. These images were analyzed using image analysis software (ImagePro Plus, Media Cybernetics, Silver Spring, MD, USA) (Fig. 2).

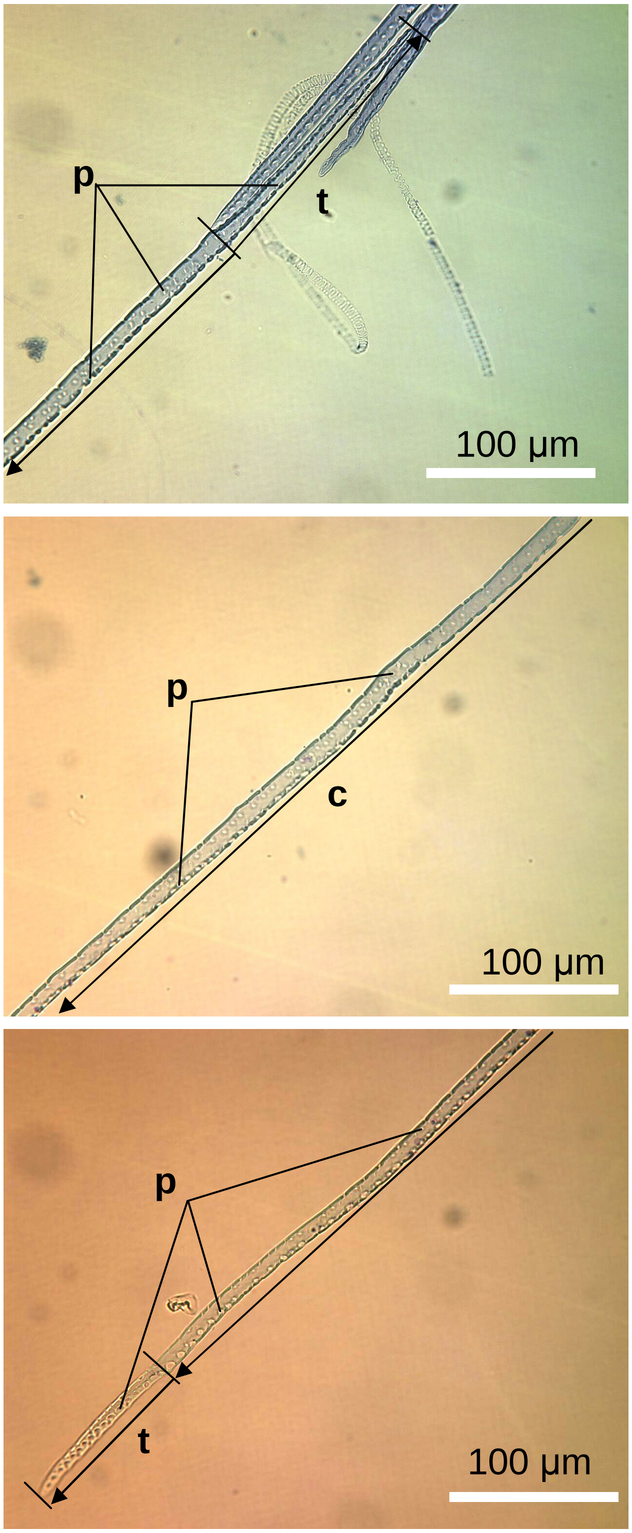


Fig. 1. Tracheid obtained by maceration of root segment (200x). The tracheid is composed of two tapered ends (t), a cylinder part (c) and is perforated by bordered pits (p).

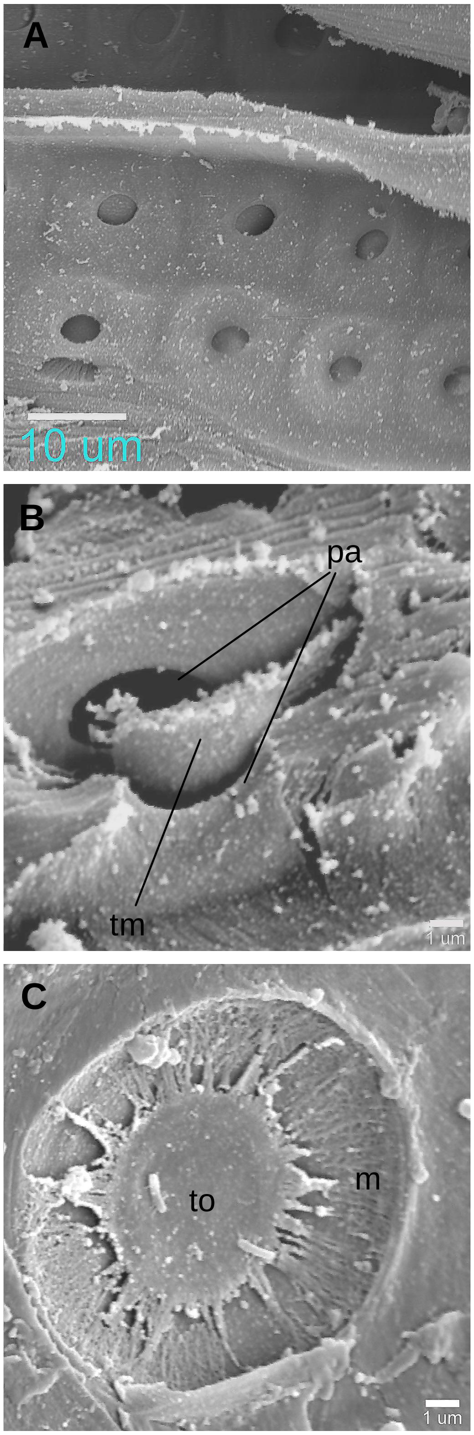


Fig. 2. SEM images of *P. taeda* bordered pits. (A) two rows of bordered pits (2,200x). (B) Internal structure of a bordered pit. pa = pit aperture, tm = torus and margo (7,500x). (C) Internal torus and margo structure. to = torus, m = margo (10,000x).

Resistances

Xylem resistance was simulated using a model incorporating resistances to flow through tracheid lumens, pit canal, and pit membranes (Gibson *et al.*, 1985; Calkin *et al.*, 1986; Lancashire and Ennos, 2002). Assuming a 50% overlapping of the tracheids, water has to travel half the length of the tracheid before crossing a pit to enter the next tracheid (Fig. 3-4). The tracheid resistance to fluid flow is the sum of two components: the half-cylinder (R^c) and one tapered end (R^t) resistances.

$$R_{tracheid} = R^c + R^t \quad (1)$$

In turn the resistance of the half cylinder is composed of a lumen resistance (R^{cl}) and a resistance from the pits on the walls of the half-cylinder (R^{cps}). The tapered end resistance is also composed of a lumen resistance (R^{tl}) and a total pit resistances (R^{tps}).

$$R_{tracheid} = (R^{cl} + R^{cps}) + (R^{tl} + R^{tps}) \quad (2)$$

Water moves in parallel through each of the pits in the half-tracheid, so the total pit resistance for the cylinder lumen and the tapered end are given by the expressions

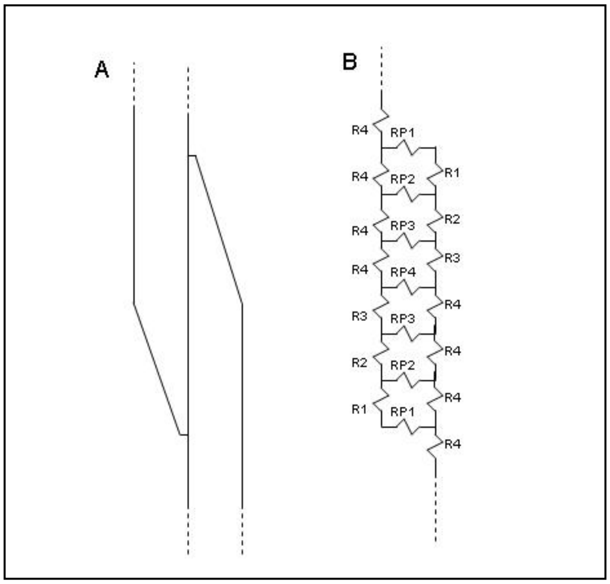


Fig. 3. Diagram showing two overlapping tracheids (A) and the analogue electrical circuit (B). Ri represents the tracheid lumen resistance and RPi represents the bordered pit resistance (from Calkin *et al.,* 1986)

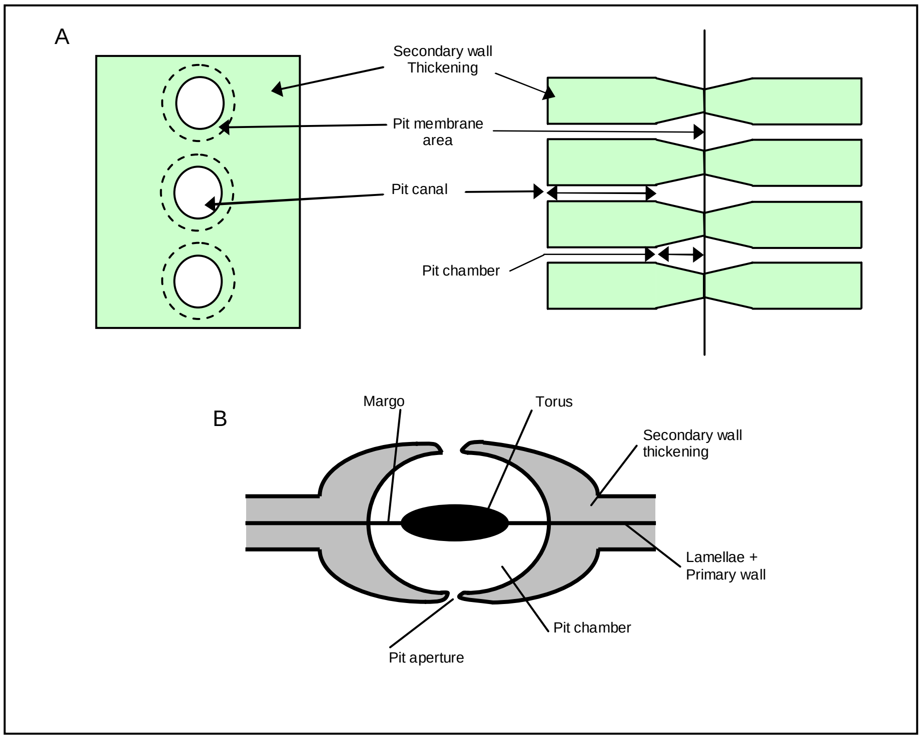


Fig. 4. Diagram of the internal structure of a bordered pit. (A) Tangential section through a tracheid wall showing several bordered pits. (B) Radial section through several bordered pits (modified from Calkin *et al.,* 1986).

$$R^{cps} = \frac{2R^{cp}}{N_c} \quad \text{and} \quad R^{tps} = \frac{2R^{tp}}{N_t} \quad (3)$$

where N_c and N_t are the number of pits in the entire cylinder and the tapered ends and R^{cp} and R^{tp} are the resistances of an individual pit of the cylinder and tapered end, respectively. Individual pit resistance (R_i^p) is composed of a pit canal and membrane resistance in series.

$$R_i^p = R_i^{pc} + R_i^{pm} \quad (4)$$

where R_i^{pc} and R_i^{pm} are the resistances of the ith pit canal and pit membrane, respectively.

R^{cl}, R^{tl}, and R_i^{pc} were calculated by the Hagen-Poiseuille equation (Streeter and Wylie, 1985):

$$K_h = \frac{\Pi r^4}{8\eta}$$

Where K_h was the conductivity, r was the radius and η was the viscosity of water. The inverse of K_h was calculated as resistance. The tapered end was divided into 10 sections for which the resistance was calculated separately and summed to determine R^{tl}. R_i^{pc} was calculated using the length of the pit canal including the pit chamber ignoring the greater diameter of the chamber. To determine R_i^{pm}

required using calculated and measured resistances. $R_{tracheid}$ was derived from measured axial hydraulic conductivity (K_h) (Chapter IV). The conductivity of one tracheid was calculated by dividing the K_h measured for a root segment by the number of conductive tracheids in its cross-section. Resistance of one tracheid was calculated as the inverse of its conductivity and one half of this value was the resistance of a half tracheid ($R_{tracheid}$). The equations above were used to calculate R_i^{pm} by subtraction from the calculated values for component resistances and the measured value for $R_{tracheid}$.

Analysis of data

There were three replicates. Each replicate comprised three to five trees. The three root zones were sampled separately for at least ten tracheids from each tree. At least ten bordered pits were examined by SEM for each root zone from two to three trees per replicate. Statistical analyses were performed using SAS; means and standard deviations were calculated at $p \leq 0.05$ (SAS 1999). Mean separations were carried out using LSD.

RESULTS

TAPR CT and cork zone tracheid had similar dimensions and their length, diameter and pit number were about 1.1 to 1.5 times greater compared to the white zone (table 1). The greater length was mainly due to the cylindrical part. The tracheid diameter remained uniform along the length of the central cylinder and tapered rapidly at the ends. All tracheid traits remained unchanged from June to November except the diameter. The diameter of TAPR tracheids increased nearly 60% in the white zone and 25% in the CT and cork zones from June to November. Tracheids from November's FOLR cork zone were smaller than TAPR cork zone tracheids and had fewer pits.

In June, the pit density in the TAPR cylinder was over 30% greater in the white zone compared to the CT and cork zones (table 2). November cylinder pit densities were similar in the three zones. The tapered end had a pit density 4 to 7 times greater than the cylinder in June and November. The pit density in the tapered end of CT and cork zones was always much less than in the white zone. FOLR tracheids from the November cork zone had densities in the cylinder and tapered end nearly twice those in the TAPR.

There were no differences in pit dimensions among zones (white, CT and cork) and between months (June and November) (table 3). The mean pit diameter was 8.5 µm and the diameter of the pit canal was half as large. The diameter of the

Table 1. Comparison of the dimensions of the tracheids in the three zones (White, CT and Cork) of the TAPR and FOLR from June and November (mean+/- standard error, letters indicate significant differences within column, $p \leq 0.005$, n=3)

	Tracheid length (mm)	Cylinder length (mm)	Tapered end length (mm)	Cylinder diameter (mm)	# pits / tracheid	# pits / cylinder	# pits / tapered end
TAPR							
June							
W	1.33 (0.15)^{b}	1.23 (0.26)^{b}	0.052 (0.05)^{b}	0.018 (0.001)^{d}	153 (5.4)^{b}	117 (10.4)^{b}	18 (0.5)^{b}
CT	2.09 (0.06)^{a}	1.92 (0.14)^{a}	0.084 (0.01)^{a}	0.026 (<0.001)^{c}	240 (1.02)^{a}	194 (6.0)^{a}	23 (0.4)^{a}
C	2.11 (0.04)^{a}	1.94 (0.05)^{a}	0.086 (0.004)^{a}	0.026 (<0.001)^{c}	242 (3.4)^{a}	200 (0.9)^{a}	21 (0.9)^{a}
November							
W	1.34 (0.01)^{b}	1.22 (0.006)^{b}	0.057 (<0.001)^{b}	0.028 (<0.001)^{b}	156 (1.9)^{b}	120 (1.2)^{b}	18 (0.2)^{b}
CT	2.10 (0.03)^{a}	1.92 (0.03)^{a}	0.090 (<0.001)^{a}	0.032 (<0.001)^{a}	245 (19.6)^{a}	201 (3.0)^{a}	22 (0.4)^{a}
C	2.09 (0.02)^{a}	1.91 (0.02)^{a}	0.090 (<0.001)^{a}	0.033 (0.001)^{a}	243 (3.8)^{a}	199 (3.7)^{a}	22 (0.2)^{a}
FOLR							
November							
C	1.56 (0.03)	1.44 (0.03)	0.061 (0.001)	0.019 (<0.001)	196 (7.5)	164 (6.8)	17 (0.6)

Table 2. Tracheid pit density in the three zones (white, CT and cork) of the TAPR from June and November and in the cork zone of the FOLR from November (mean +/- standard error, letters indicate significant differences within column, $p \leq 0.05$, n=3.

	TAPR Cylinder (Pits/mm^2)	**TAPR** Tapered end (Pits/mm^2)	**FOLR** Cylinder (Pits/mm^2)	**FOLR** Tapered end (Pits/mm^2)
June				
W	1680^a	12069^a		
CT	1237^b	6629^b		
C	1262^b	5726^b		
November				
W	1018^c	6976^b		
CT	952^c	4790^b		
C	919^c	4591^b	1909	9231

Table 3. Structural dimensions of the bordered pit of the three zones: white, CT and cork in June and November (mean +/- standard error). None of the means within a column were different at $p \leq 0.05$, n=3.

	Diameter Pit (μm)	Diameter Canal (μm)	Diameter Margo+torus (μm)	Diameter torus (μm)	Canal+ cavity depth (μm)	Canal length (μm)
June						
W	8.05 (1.14)	4.82 (1.86)	8.22 (1.05)	5.10 (1.23)	1.91 (0.36)	0.98 (0.17)
CT	8.39 (1.40)	4.41 (0.95)	8.29 (0.84)	4.96 (1.72)	1.81 (0.19)	0.89 (0.35)
C	8.11 (1.18)	4.33 (1.54)	8.68 (0.86)	4.68 (1.06)	1.83 (0.17)	0.96 (0.12)
November						
W	8.80 (0.99)	4.32 (1.28)	7.92 (2.08)	4.81 (1.43)	1.84 (0.23)	0.97 (0.19)
CT	8.69 (1.67)	4.84 (1.33)	8.88 (1.02)	4.88 (1.05)	1.88 (0.16)	1.01 (0.20)
C	8.95 (1.05)	4.05 (1.08)	8.53 (1.18)	4.88 (1.18)	1.85 (0.16)	0.99 (0.18)

torus was similar to the pit diameter. The torus diameter was close to 5 µm which was slightly bigger than the diameter of the pit canal thus allowing an efficient sealing of the opening. The mean distance from the torus to the canal was 1.85 µm and the canal length was 0.96 µm.

The resistance of the TAPR tracheid was similar in the cork zone in June and November and appeared to decline in the white and CT zones (Table 4). FOLR had a tracheid resistance smaller than that of TAPR tracheids. The pit component was the major resistance (82-97%) to water flow in TAPR tracheids (Table 5) and was fairly constant from June to November. The pits of the tapered end represented 63-80% of the tracheid resistance, the pits in the cylinder 16-22%, the tapered end lumen around 2% and the tracheid lumen nearly 4%. FOLR tracheid resistance was also dominated by the pits but to a lesser extant (64%).

Table 4. Calculated resistances of the tracheid components from the TAPR and FOLR (10^9 MPa s m^{-4})

	Tracheid	Tracheid Lumen	Tapered end Lumen	Pits of the cylinder	Pits of a tapered end	1 pit	Pit canal	Pit membrane
TAPR								
June								
W	1.79	0.23	0.09	0.35	1.12	20.22	0.07	20.14
CT	1.68	0.08	0.05	0.30	1.25	28.75	0.09	28.65
C	1.93	0.08	0.05	0.31	1.48	31.15	0.11	31.24
November								
W	1.16	0.04	0.02	0.25	0.84	15.18	0.11	15.07
CT	0.71	0.04	0.02	0.12	0.54	11.78	0.07	11.71
C	2.04	0.03	0.02	0.36	1.63	35.77	0.15	35.63
FOLR								
November								
C	0.80	0.22	0.07	0.09	0.42	7.20	0.15	7.05

Table 5. Calculated resistances of the tracheid components of the TAPR and FOLR as percentage of the resistance of a tracheid. FOLR bordered pits were assumed similar to the TAPR.

	Tracheid	Tracheid Lumen	Tapered end lumen	Pits	Pits of the cylinder	Pits of a tapered end
TAPR						
June						
W	100	13	5	82	19	63
CT	100	5	3	92	18	75
C	100	4	2	94	16	77
November						
W	100	3	2	95	22	73
CT	100	5	3	92	17	76
C	100	2	1	97	18	80
FOLR						
November						
C	100	27	9	64	11	53

DISCUSSION

Several studies found that tracheid number, length and diameter increased basipetally (Bower, 1935; Bierhorst, 1971; Ogura, 1972; Beck *et al.*, 1982; Gibson *et al.*, 1984). Petioles of *Ginkgo biloba* L. and *Drimys winteri* J. R. & G. Forst. showed a basipetal increase of the tracheid size (Schulte and Gibson, 1988). FOLR first appeared and became prominent in the CT zone of TAPR. In the cork zone of TAPR, there were more longer FOLRs and SOLRs were produced. The development suggested increasing capacity to transport water in TAPR. It appeared that instead of augmenting the diameter of the tracheids, the TAPR increased the number of conductive tracheids via secondary growth (Chapter II). Zimmermann (1978) described the hydraulic properties of the xylem as a tradeoff between hydraulic efficiency and hydraulic safety. The hydraulic efficiency increases with width of the conduit and decreases in pit resistance (Zimmermann, 1978; Tyree *et al.*, 1994). Hydraulic safety concerns the resistance of the xylem against cavitation. It appeared that *P. taeda* seedling increased xylem hydraulic efficiency by increasing tracheid size from the white to the CT zone and from June to November. However the similar tracheid size between the CT and cork zone in June and in November showed that the plant favored the hydraulic safety of its roots by limiting the tracheid size (Bailey and Tupper, 1918). To compensate, the number of tracheid was greatly increased by secondary growth.

Bannan (1965) measured tracheid length and diameter in lateral and sinker roots of *Picea glauca, Pinus strobus* and *Larix laricina*. *P. taeda* tracheids from the TAPR and FOLRs were similar in length and diameter to sinker root tracheids of *Picea glauca*, but they were 2.4 to 4.3 times smaller in length and 1.3 to 2.9 smaller in diameter compared to the tracheids of lateral roots from *Pinus strobus*, *Picea glauca*, *Larix laricina.* Dinwoodie (1962) and Hartley (1960) observed a positive relationship between height growth and stem tracheid length in species seedlings. In trees, however, the correlation was not significant as the tracheid size seemed to reach a maximum. In this study, the youth of the *P. taeda* seedlings may be the reason for the small size of the TAPR and FOLR compared to lateral roots of *Pinus strobus*, *Picea glauca*, *Larix laricina.* One can suppose that the size of the tracheids in loblolly pine seedling would increase as the tree root system grows until a maximum size is reached.

The number of pits per tracheid was slightly smaller than the values found in *Tsuga canadensis* (Bailey and Tupper, 1918; Zimmermann, 1983). The tracheids measured in this study were sufficiently smaller in length and diameter, so the pit density was much higher. This seems to be beneficial to the transport of water from one tracheid to another as it increased the number of pathways between them. The bordered pit observed in *P. taeda* seedling root had the typical circular structure with a net-like membrane, a central torus and the surrounding arched domes. The circular bordered pit observed in this study was twice as small as that of *Tsuga canadensis* (Lancashire and Ennos, 2002). The canal diameter was similar to *T. canadensis*. However the torus had a diameter twice smaller than in *T. canadensis*.

Previous attempts to compare measured hydraulic conductivity with values predicted from the Hagen-Poiseuille equation (Tyree and Zimmermann, 1971, Giordano *et al.*, 1978; Woodhouse and Nobel, 1982; Calkin *et al.*, 1984) indicated that the Poiseuille equation significantly overestimated the hydraulic conductivity of xylem vessels. The difference was explained by: (1) the properties of the xylem that reduced conductivity such as wall roughness and (2) blockage of xylem by cavitation. Tracheids are conduits of uniform diameter with two tapered ends. Water moves from one tracheid to another by crossing the permeable margo of the circular bordered pits present in the radial walls. The two components responsible for total tracheid resistance to flow have been assumed to be the tracheid lumen and either the pit membrane pores of the margo or the entire bordered pit pair (Petty, 1970; Petty and Puritch, 1970; Smith and Banks, 1971). The bordered pit membrane resistance found in this study is slightly higher than the values in the literature. Bolton and Petty (1975) showed that in Sitka spruce sapwood, the pit membranes pores contributed 81% of the resistance to liquid flow while the tracheid lumen accounted for 16% and the pit canal for only 3% of the total resistance. The significant pit canal resistance was probably due to a narrower diameter which increased the resistance. Lancashire and Ennos (2002) calculated a tracheid resistance of *Tsuga canadensis* to be 15 to 43 times lower than the one found in this study. They also estimated that in a typical tracheid, pits should account for about one-third of the total resistance which agreed with another study which reported values ranging from 12-70% mostly for ferns (Schulte and Gibson, 1988). It has been found that the relative importance of pits depends on tracheid diameter; the wider the tracheid the greater the importance of the pits (Schulte *et al.*, 1987; Schulte and Gibson, 1988). Surprisingly we found the pit resistances to be greater than 80%, despite smaller tracheid dimensions and a similar number of pits compared to Ennos (2002). However our pits were twice as narrow and more importantly the membrane surface area was 6 times smaller. This probably caused the higher resistance of our pits, assuming a similar number and diameter of membrane pores. It appeared that the principal reason for the difference between *P. taeda* and *T. canadensis* resistances was due to the bordered pit dimensions. Most of the pit resistance was found in the tapered ends, which implied that little water movement occured in the tapered ends. Most of the water must pass from one tracheid to another in the cylindrical part of the tracheid.

Tracheid resistance was fairly uniform from June to November in the cork zone. The increase in K_h between June and November (Chapter IV) was associated with a large increase in the number of tracheids. Despite the increase in the tracheid lumen diameter, the tracheid resistance did not change. This was due to the dominance of the pit resistance component. The tracheid resistance was composed of the lumen resistance and the pit membrane resistance. The lumen resistance decreases with the increasing diameter while the membrane resistance depends on the membrane surface area and pit number and diameter. Schulte and Gibson (1988) observed that pit membrane diameter and pit number increased with tracheid diameter which diminished the pit resistance as more primary wall (pit membrane) area was exposed for water flow. However in the present study, the TAPR pit dimensions did not change and although their number increased, the pit density decreased. As a result the decreasing resistance caused by wider tracheid lumens was counterbalanced by the increased membrane resistance caused by the decreasing pit density, giving a fairly constant tracheid resistance between June and November.

The advantage of the high pit resistance was that cavitations would be trapped by the pits between the tracheids and would not spread. The resistance of the membrane was linked to the size of the pore (Ennos and Lancashire, 2002). The pore size must be sufficiently small to hold an air-water meniscus against pressures which can deflect the membrane and seal the pit aperture with the torus (Chapman *et al.*, 1977; Sperry and Tyree, 1990). However the pore size must also be big enough to let water move from one tracheid to the next. Air seeding through membrane pits has cited as the likely major cause of xylem cavitation and subsequent failure to conduct water (Zimmermann, 1983). The high resistance of the pits was compensated by the redundancy of the tracheids (Zimmermann, 1978b; Carlquist, 1980), enabling the TAPR to conduct water and nutrients during development of the seedling while being protected from embolism.

The low $R_{tracheid}$ in FOLR cork zone in November compared to TAPR was associated with a relatively smaller membrane resistance. This may have increased hydraulic efficiency and reduced resistance to cavitation. This may be a protection mechanism against drought as the lateral root tracheids would cavitate before TAPR tracheids as water potential decreased. The loss of FOLR could reduce the risk of further cavitation in TAPR and water loss back to the dry soil (Luxová, 1990; Franco and Nobel, 1992; North et al., 1992). In addition, it has been suggested the early loss of fine roots to cavitation during drought can actually maximize water extraction from the soil and may protect the plant against the cost of refilling and replacing larger roots (Hacke et al., 2000).

CONCLUSIONS

- Tracheid size increased from the white to CT zone suggesting an increase in K_h. Any increase in K_h in the CT and cork zones would have to come strictly from increased tracheid number as there were no further changes in tracheid and bordered pit dimensions or bordered pit number.

- The increase in TAPR tracheid number for all three zones from June to November was the only change in xylem characteristics as tracheid and bordered pit dimensions did not change.

- Bordered pit dimensions were conserved across all zones and months for TAPR. The bordered pits were the largest source of resistance to water flow in the tracheids.

- The balance between safety / efficiency was different between TAPR and FOLR. TAPR high pit resistance to air seeding and water flow was counterbalanced by its high number of tracheids. FOLR tracheids seemed to be more efficient in water transport and more susceptible to cavitation.

FUTURE RESEARCH

- The pit membrane is responsible for most of the resistance of the tracheid. Further investigations are needed to elucidate the role of the membrane pores in the resistance to water flow.

- Similar research should be extended to older trees in field conditions.

REFERENCES

Bailey, I.W. and W.W. Tupper 1918. Size variation in traceary cells: I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms and angiosperms. Proc.Natl Acad. Sci. USA 54: 149-204.

Bannan, M.W. 1965b. The length, tangential diameter, and length/width ratio of conifer tracheids. Can. J. Bot. 43: 967-984.

Beck, C.B., R. Schmid and G. Rothwell 1982. Stelar morphology and the primary vascular system of seed plants. Bot. Rev. 48: 491-815.

Bierhorst, D.W. 1971. Morphology of vascular plants. New York: Macmillan.

Bolton, A.J. and J.A. Petty 1975. A model describing axial flow of liquids through conifer wood. Wood Sci. Tech. 12: 37-48.

Bower, F.O. 1935. Primitive land plants. Macmillan, London.

Calkin, H.W., A.C. Gibson and P.S. Nobel 1984. Xylem water potentials and hydraulic conductances in eight species of ferns. Can. J. Bot. 63: 632-637.

Calkin, H.W., A.C. Gibson and P.S. Nobel 1986. Biophysical model of xylem conductance in tracheids of the fern *Pteris vittata*. J. Exp. Bot. 37 (180): 1054-1064.

Carlquist, S. 1980. Further concepts in ecological wood anatomy, with comments on recent work in wood anatomy and evolution. Aliso 9: 499-553.

Chapman, D.C., R.H. Rand and J.R. Cooke 1977. A hydrodynamic model of bordered pits in conifer tracheids. J. Theor. Biol. 67: 11-24.

Clarkson, D.T. 1991. Root structure and sites of ion uptake. *In*: Plant roots. The hidden half. Eds Y. Waisel, A. Eshel and U. Kafkafi. Marcel Dekker, Inc., New York, Basel, Hong Kong. pp. 417-453.

Cochard, H. 1992. Vulnerability of several conifers to air embolism. Tree Physiol. 11: 73-83.

Coutts, M.P. 1982. The tolerance of tree roots to water logging: 5. Growth of woody roots of sitka spruce and lodgepole pine in water logged soil. New Phytol. 90: 467-476.

Dinwoodie, J.M. 1962. Tracheid and fiber length in timber. A review of literature. Forestry 34:125-144.

Esau, K. 1977. Plant anatomy. Second edition. John Wiley & Sons, Inc., New York.

Franco, A.C. and P.S. Nobel 1992. Influences of root distribution and growth on predicted water uptake and interspecific competition. Oecologia, 82: 151-157.

Gibson, A.C., H.W. Calkin and P.S. Nobel 1984. Xylem anatomy, water flow and hydraulic conductance in the fern *Cyrtomium falcatum*. Am. J. Bot. 71: 564-574.

Gibson, A.C., H.W. Calkin and P.S. Nobel 1985a. Hydraulic conductance and xylem structure in tracheid-bearing plants. I.A.W.A. Bull. New Series, 6: 293-302.

Gibson, A.C., H.W. Calkin, D.O. Raphael and P.S. Nobel 1985b. Water relations and xylem anatomy of ferns. Proc. R. Soc. Edin. 86B: 81-92.

Giordano, R., A. Salleo, S. Salleo and F. Wanderling 1978. Flow in xylem vessels and Poiseuille's law. Can. J. Bot. 56: 333-338.

Hacke U.G., J.S. Sperry, B.E. Ewers, D.S. Ellsworth, K.V.R. Schäfer and R. Oren 2000. Influence of soil porosity on water use in *Pinus taeda.* Oecologia 124:495-505.

Hartley, W.R. 1960. Nutrient and tracheid length in seedlings of *Pinus radiata* D. Don. Com. For. Rev. 39: 474-482.

Lancashire, J.R. and A.R. Ennos 2002. Modelling the hydrodynamic resistance of bordered pits. J. Exp. Bot. 53 (373): 1485-1493.

Liphshitz, N., S. Lev-Yadun, R. Rossen and Y. Waisel 1984. The annual rhythm of activity of the lateral meristems (cambium and phellogen) in *Pinus halapensis* mill. and *Pinus pinea* L.. I.A.W.A. 5: 263-274.

Luxová, M. 1990. Effect of lateral root formation on the vascular pattern of barley roots. Bot. Acta 103: 305-310.

McCully, M.E. and M.J. Canny 1988. Pathways and processes of water and nutrient movement in roots. *In*: Structural and functional aspects of transports in roots. pp. 3-14.

Moreshet, S. and M.G. Huck 1991. Dynamics of water permeability. *In*: Plant roots. The hidden half. Eds Y. Waisel, A. Eshel and U. Kafkaki. Marcel Dekker, Inc., New York, Basel, Hong Kong. pp. 605-626.

North, G.B., F.W. Ewers and P.S. Nobel 1992. Main root-lateral root junctions of two desert succulents: changes in axial and radial components of hydraulic conductivity during drying. Am. J. Bot. 79: 1039-1050.

Ogura, Y. 1972. Comparative anatomy of vegetative organs of the pteridophytes. Handbuch der Pflanzenanatomie, 7 (3). Berlin: Gebrüder Borntraeger.

Passioura, J.B. 1988. Water transport in and to roots. Annu. Rev. Plant Physiol. Plant Mol. Biol. 39: 245-265.

Petty, J.A. 1970. Permeability and structure of the wood of Sitka spruce. Proc. R. Soc. London B175: 149-157.

Petty, J.A. and G.S. Puritch 1970. The effects of drying on the structure and permeability of the wood *Abies grandis*. Wood Sci. Tech. 4: 140-154.

Rypacek, V., O. Hauck and J. Vyslouzil 1976. Conducting tissue differentiation in seedlings of some forest tree species. Scr. Fac. Sci. Nat. Univ. Purkynianane 6: 103-112.

Sanderson, J., F.C. Whitbread and D.T. Clarkson 1988. Persistent xylem cross-walls reduce the axial hydraulic conductivity in the apical 20 cm of barley seminal root axes: implications for the driving force of water movement. Plant Cell Environ. 11: 247-256.

SAS 1999. The SAS for Windows, Release 8.0. SAS Institute Inc., Cary, NC 27513.

Schulte, P.J. and A.C. Gibson 1987. Xylem anatomy and hydraulic conductance of *Psilotum nudum*. Am. J. Bot. 74 (9): 1438-1445.

Schulte, P.J. and A.C. Gibson 1988. Hydraulic conductance and tracheid anatomy in six species of extant seed plants. Can. J. Bot. 66: 1073-1079.

Smith, D.N.R. and W.B. Banks 1971. The mechanism of flow of gases through coniferous wood. Proc. R. Soc. London, B177: 197- 205.

Sperry, J.S. and J.E.M. Sullivan 1992. Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous, and conifer species. Plant Physiol. 100: 605-613.

Sperry, J.S. and M.T. Tyree 1990. Water-stress induced embolism in three species of conifers. Plant Cell Environ. 13: 427-436.

St. Aubin, G., M.G. Canny and M.E. McCully 1986. Living vessel elements in the late metaxylem of sheated maize roots. Ann. Bot. 58: 577-588.

Streeter, V.L. and E.B. Wylie 1985. Fluid mechanics. 8th ed. McGraw-Hill, New York.

Tyree, M.T. and A.J. Karamanos 1981. Water stress as an ecological factor. *In*: Plants and their atmospheric environment. Eds J. Grace, E.D. Ford and P.G. Jarvis. Blacjwell Scientific, Oxford. pp. 237-261.

Tyree, M.T. and M.H. Zimmermann 1971. Theory and practice of measuring coefficients and sap flow in the xylem of red maple stems (*Acer rubrum*). J. Exp. Bot. 22: 1-18.

Tyree, M.T., S.D. Davis and H. Cochard 1994. Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? I.A.W.A J. 15: 35-360.

Wang, X.L., M.J. Canny and M.E. McCully 1991. The water status of the roots of soil-grown maize in relation to the maturity of their xylem. Physiol. Plant 82: 157-162.

Wenzel, C.L., M.E. McCully and M.J. Canny 1989. Development of water conducting capacity in the root systems of young plants of corn and some other C4 grasses. Plant Physiol. 89: 1094-1101.

Wilcox, H. 1955. Primary organization of active and dormant roots of noble fir, *Abies procera*. Am. J. Bot. 41: 812-821.

Wilcox, H. 1962. Growth studies of the root incense cedar Libocedrus decurrens. I. The origin and development of primary tissues. Am. J. Bot. 49: 221-236.

Wilcox, H. 1964. Xylem in roots of *Pinus resinosa* Ait. in relation to heterorhizy and growth activity. *In*: M.H. Zimmermann (ed.). The Formation of Wood in Forest Trees. Academic Press, New York. pp. 459-478.

Woodhouse, R.M. and P.S. Nobel 1982. Stipe anatomy, water potentials, and xylem conductances in seven species of fern. Can. J. Bot. 69: 135-140.

Zimmermann, M.H. 1978. Hydraulic architecture of some diffuse-porous trees. Can. J. Bot. 56: 2286-2295.

Zimmmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin.

CHAPTER - IV

HYDRAULIC CONDUCTIVITY OF *PINUS TAEDA* SEEDLING ROOTS

SUMMARY

Roots are the site of resistance to water flow to the shoot. Water flow can be adjusted or even regulated by variable hydraulic conductivity depending on the root system architecture and root hydraulic properties. *Pinus taeda* roots are comprised of three anatomically different zones: white, condensed tannin (CT) and cork (McKenzie and Peterson, 1995). Each zone is thought to have different hydraulic properties. The white is thought to be the most conductive for water uptake while the cork should be the least conductive. On the other hand, the capacity fro axial transport increases from the white to the cork zone. The primary goal of this study was to determine the developmental changes of first-year *Pinus taeda* seedlings in root (L_p), radial (L_r) and axial (K_h) hydraulic conductivity of the three zones. The second goal was to use measured K_h and L_r and morphological parameters to investigate distribution of water uptake among root zones and types. L_p and L_r decreased from the white to the cork zone. The conductivity of the tap root (TAPR) and the first-order (FOLRs) and second-order

(SOLRs) lateral roots evolved differently during this study. TAPR L_p decreased while FOLR L_p remained constant and SOLR L_p increased. K_h showed huge increase in the TAPR from the white to the cork zone and from June to November and barely changed in FOLRs and SOLRs. TAPR K_h was as much as several hundred times greater than FOLR and SOLR K_h late in the year. The measured K_h was always smaller by a factor of about two compared to K_h predicted with the Hagen-Poiseuille equation. L_p calculated with the finite-element model was comparable to values found in the literature. The root system conductive capacity was at its peak in July and decreased until November. According to the model, most of the water was absorbed by the CT and cork zones. The presence of mycorrhizae increased the root system ability to absorb water toward the end of the year.

INTRODUCTION

Roots are the main site of resistance to water flow to the shoot (Kramer and Boyer, 1995). They control the amount of soil water available to the plant; therefore, roots are a determining factor in the soil-plant-atmosphere continuum. Research has been made on root systems (growth, spatial distribution, and anatomy) but hydraulic properties that characterize uptake and movement of water and nutrients in the root are not well understood.

Water uptake depends on soil water content, root distribution in the soil, and hydraulic properties of the roots (Passioura, 1988). Water movement from the soil to plant encounters several resistances arranged in series: soil, soil-root interface and root surface (Passioura, 1988; Nobel and Cui, 1992). Under conditions of high water availability, the root system offers the greatest resistance to water uptake (Weatherley, 1982; Sperry *et al.*, 1998). Water flow can be adjusted or even regulated by variable hydraulic conductivity (inverse of the root hydraulic resistance) depending on root system structure and hydraulic properties. This root variability is well documented (Weatherley, 1982; Steudle *et al.*, 1987; Steudle, 1994; Steudle and Peterson, 1998; Henzler *et al.*, 1999). It depends on factors such as water availability, salinity, demand for water from the transpiring shoot, nutrient deficiency, anoxia, temperature and heavy metals. Water uptake (F, $m^3\ s^{-1}$) is proportional to the unit pressure (osmotic or hydrostatic, ΔP, MPa) driving the flow from the soil solution to the root xylem through a root surface area (A, m^2). Root hydraulic conductivity (L_p, m^3 m^{-2} s^{-1} MPa^{-1}) can be expressed as followed (Nobel, 1983, 1991):

$$F = Lp * \frac{\Delta P}{A}$$

The roots of *Pinus taeda* L. can be divided into three zones: white, condensed tannin (CT) and cork (McKenzie and Peterson, 1995a, b; Peterson *et al.*, 1999). The white zone, with its living cortex and not yet fully developed endodermis, was thought to have the largest potential for radial water uptake due to a large plasmalemma surface in contact with the soil solution and abundant passage cells. The development of the suberin lamellae in the endodermis, the progressive death and sloughing of the cortical cells in the CT zone resulted in a decrease in absorbing surface area in this zone. This may lead to an increase of the resistance to radial water uptake. The presence of the cork layer and the totally suberized endodermis in the cork zone should further increase the radial resistance to water flow. This increasing resistance to radial water transport occurs while the longitudinal transport capacity is greatly increasing due to an increasing number of conductive tracheids resulting from secondary growth. Tracheids can significantly affect water movement by imposing conductivity constraints (Tyree and Ewers, 1991). The Hagen-Poiseuille equation has been widely used to predict conductances and flows in the xylem (Zimmermann, 1971, 1983; Milburn, 1979; Nobel, 1983). The capability of roots to absorb water may evolve in space and time because of the development of resistance to water transport at the soil-root interface (Herkellrath *et al.*, 1977; Passioura, 1988, Nobel and Cui, 1992), or heterogeneity (morphology, anatomy) of the root system (Sanderson, 1983; Varney and Canny, 1993), and ontogenetic gradients existing along the root (Cruz *et al.*, 1992; Clarkson *et al.*, 1968; Frensch *et al.*, 1996; Steudle and Peterson, 1998).

I determined root hydraulic conductivity (L_p, $m^3\ m^{-2}\ s^{-1}\ MPa^{-1}$), axial hydraulic conductivity (K_h, $m^4\ s^{-1}\ MPa^{-1}$) and radial hydraulic conductivity (L_r, $m^3\ m^{-2}\ s^{-1}\ MPa^{-1}$) for each of the root zones in loblolly pine seedlings to learn how root function relates to structure. Seedlings were growing in a nursery and studied over six months of their first year of growth. The finite element model (Alm *et al.*, 1992) was used to predict root system L_p from its component parts and learn the relative contribution of the different root zones to total water flux.

MATERIALS AND METHODS

Plant material

Seedlings were obtained from a single open-pollinated Oklahoma family of genetically improved *P. taeda*. Seeds were sown at the Oklahoma State Forest Regeneration Center near Washington, Oklahoma in the first week of May 2002. They germinated in 10 – 15 days. The major cultural operations were fertilization, watering and pesticide application when needed. Lateral root pruning and undercutting were done in early October.

Seedlings were harvested every month from June through November. They were harvested from three replicates. PVC pipes were used to take cores of soil containing five to six trees with the whole taproot (TAPR) and its laterals. Four pipes per replication were collected. Root systems were carefully separated from the soil using water and brought to the laboratory in containers filled with water for measurements. From the four pipes within each bed, ten individual root systems were separated and root segments were selected in the white, condensed tannin and cork zones along the TAPR. First-order lateral roots (FOLRs) were severed from the TAPR and the wound sealed with fast setting dental impression material. L_p, K_h and L_r were determined for each segment. L_p, K_h and L_r were measured on the FOLR and second-order lateral root (SOLR) segments. All manipulations of the roots were made under water to avoid any shrinkage and entry of air into the roots.

Measurement of L_p

Root segments, 30-40 mm long, were carefully cut under water. The basal end of a root segment was inserted tightly into silicone tubing attached to a 305-mm-long glass capillary (internal diameter of 0.64 mm) half filled with water. The connection was sealed with fast setting dental impression material so that the only possible water flow was through the root (Fig. 1). For measurements on segments with two open ends, the distal part was dried and sealed with silicone. The root segments were then suspended in aerated distilled water. A partial vacuum (negative pressure) was applied to the open end of the capillary and the pressure difference (∆P, MPa) between the external solution and the capillary induced water flow through the root segment (Fig. 2). The progress of the meniscus in the capillary was measured along a micrometer with a microscope. The steady (after 15 minutes) volumetric flow rate (F, $m^3\ s^{-1}$) was recorded for three different ∆P (0.018, 0.025 and 0.032 MPa). The volume flow density (F/A, $m^3\ m^{-2}\ s^{-1}$) was calculated as the volume flux per unit of root area and plotted against ΔP. The slope of the relationship between F/A and ΔP was defined as the hydraulic conductivity of the root segment (L_p, $m^3\ m^{-2}\ s^{-1}\ MPa^{-1}$):

$$L_p = \frac{(F/A)}{\Delta P}$$

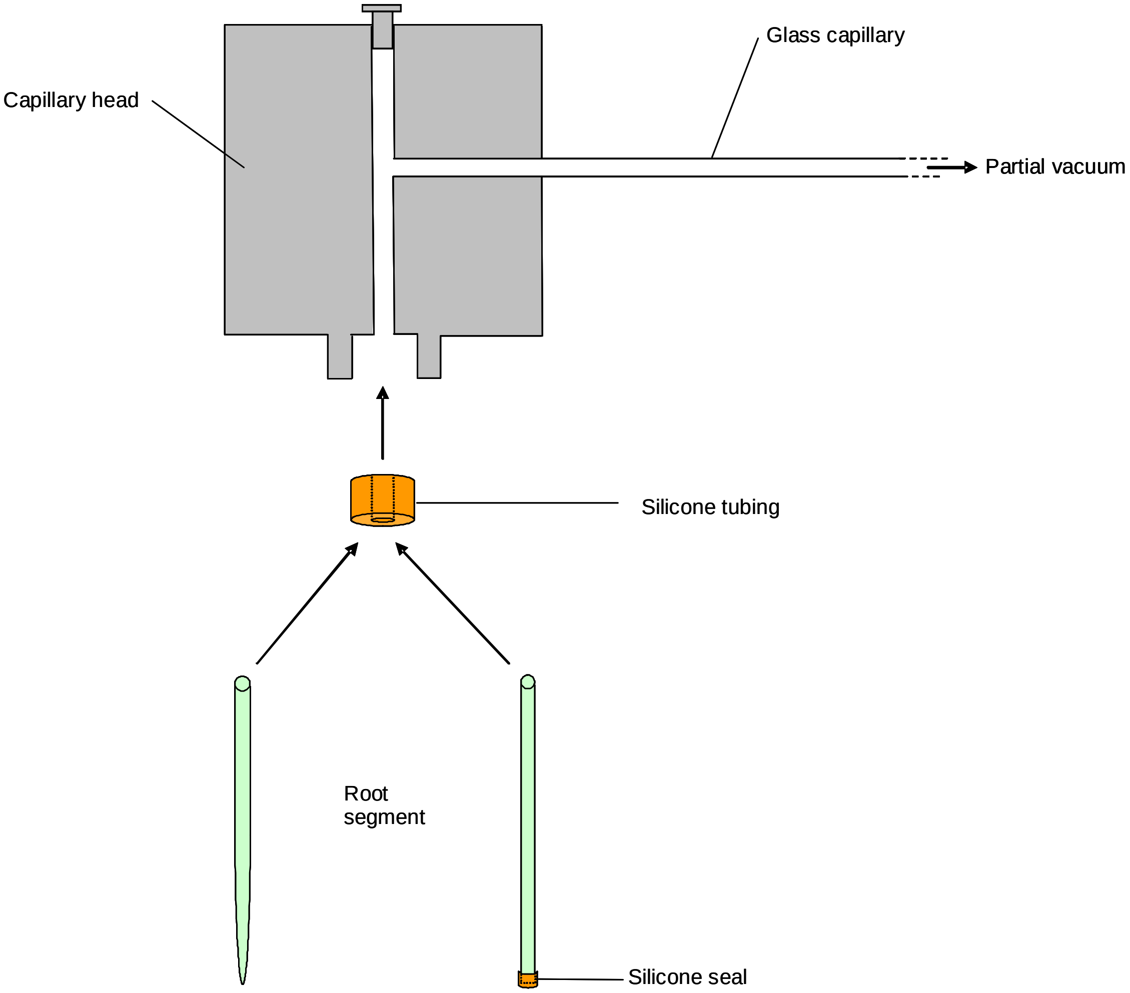


Fig. 1. Diagram showing the connection of the root to the capillary head.

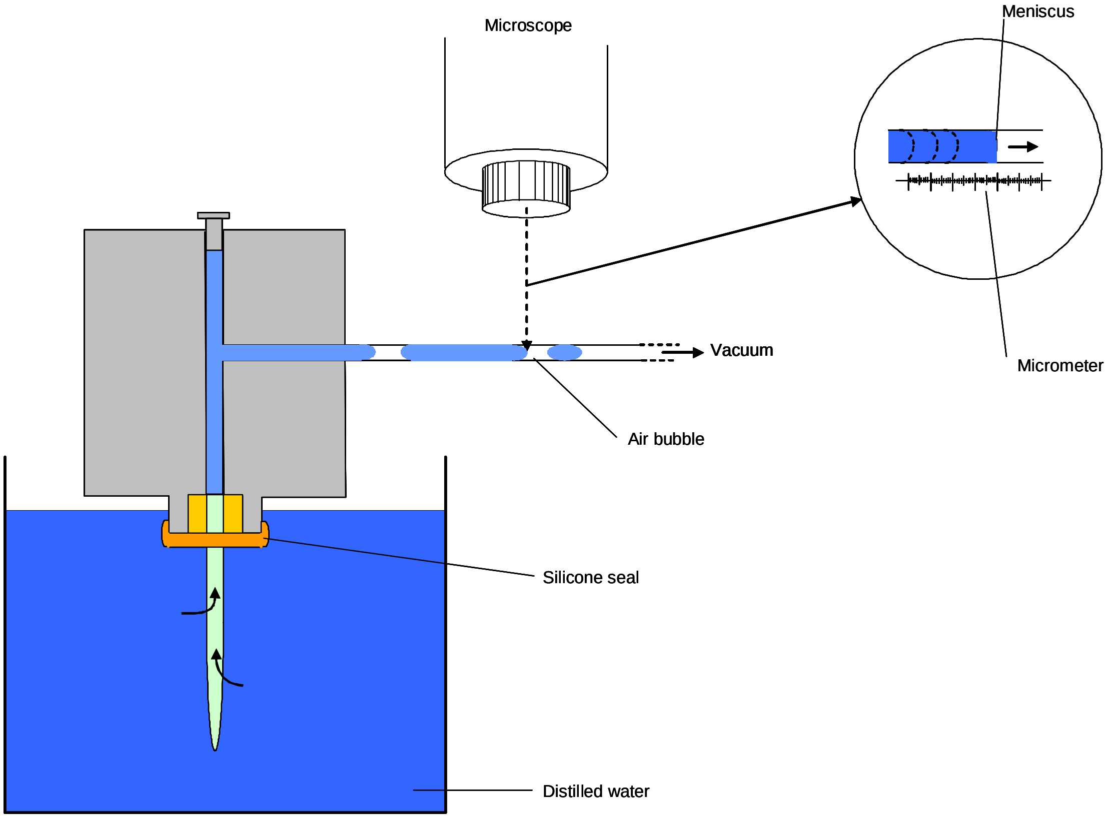


Fig. 2. Apparatus used to measure root hydraulic conductivity.

Regression analysis was used to calculate L_p and values with a $r^2<0.9$ were discarded. We considered that osmotic water flow was negligible compared to flow induced by the hydrostatic gradient. Root surface area (A, m^2) was calculated from the root length and mean diameter. The tip was known to be hydraulically isolated, so the distal 5 mm was not included in the length.

Measurement of K_h

To measure axial conductivity, root segments used for L_p measurement were trimmed under water right at the seal. Radial water flow was negligible, as the remaining segment was entirely surrounded by the seal. The segment inside the seal was 1.5 cm long. The open end was immersed in 100 mM potassium chloride (Sperry, 1986). F was measured after 5 minutes at ΔP of 0.032 MPa. The axial conductivity (K_h, $m^4\ s^{-1}\ MPa^{-1}$) was then calculated as follows

$$K_h = \frac{F}{\Delta P} * L$$

Where L (m) was the length of the root segment in the capillary.

In order to check that there was no leak in the seal, the root segment end was immersed in 0.01% crystal violet at the end of the conductivity measurements. A vacuum of 0.032 MPa was applied for a maximum of 15 minutes and stopped as soon as violet color appeared in the capillary. If the violet color moved on the exterior of the segment, this indicated a leak and the measurements were discarded.

Calculation of L_r

The volumetric flux density ($m^3\ m^{-2}\ s^{-1}$) of water at the root surface divided by the difference in water potential (MPa) from the root surface to the root xylem is equal to the radial hydraulic conductivity, L_r ($m\ s^{-1}\ MPa^{-1}$). The flux density is calculated from measured values of L_p and K_h together with the length l and the radius (r_{root}, m) of the root segment (Landsberg and Fowkes, 1978):

$$Lr = \frac{Lp * \alpha * L}{\tanh\left(\alpha * L\right)}$$

Where α equals $(2\pi\ r_{root}\ L_r / K_h)^{1/2}$. The equation is solved by iteration, for which L_r is initially set equal to L_p and gradually increased.

Predicted K_h

All root segments were stained with violet-blue following axial conductivity measurements (Fig. 3). Cross-sections were cut and observed under light microscope. Stained tracheids were counted and measured for diameter and

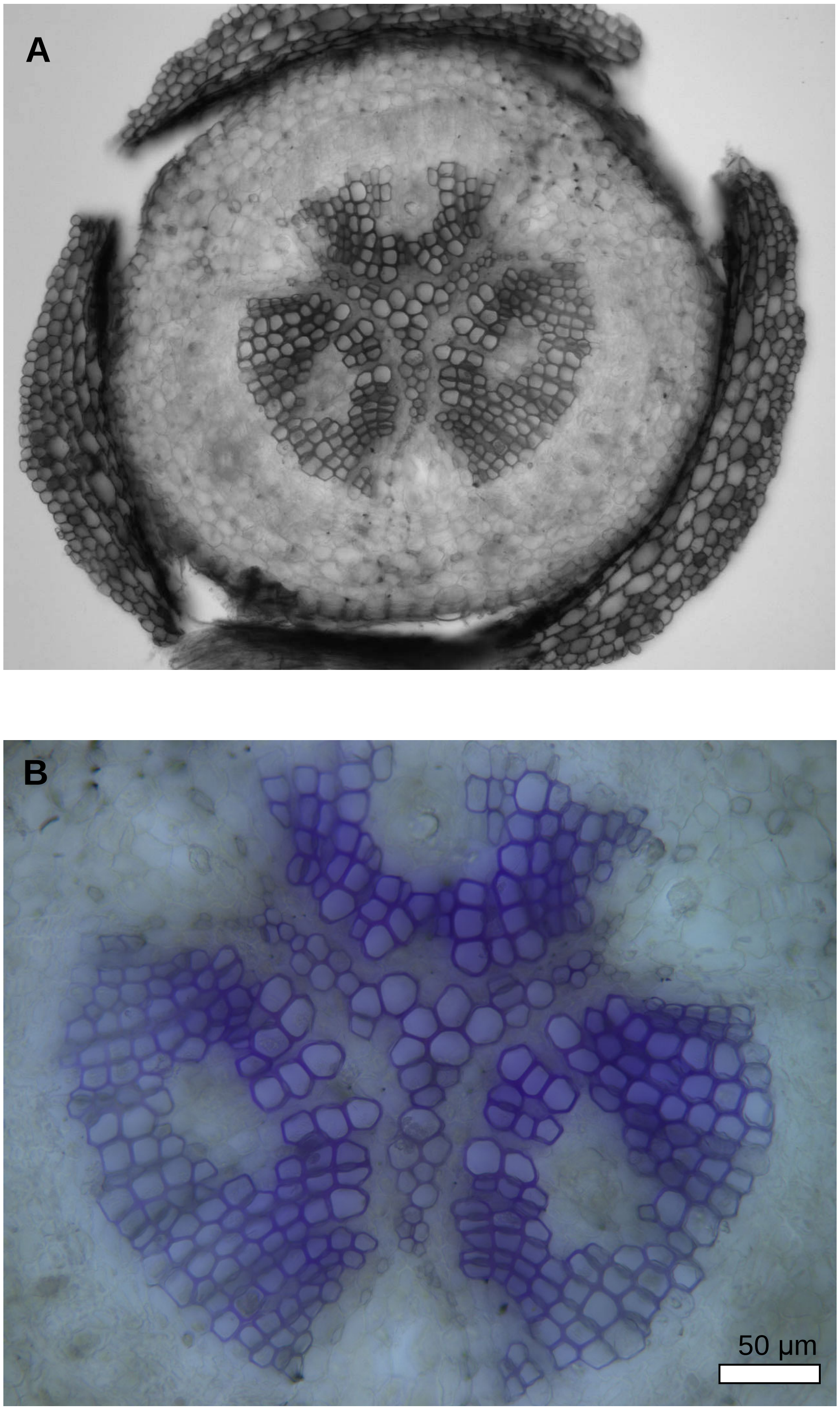


Fig. 3. Cross section of a typical pine root in the CT zone. (A) The root with partially sloughed cortex (100X). (B) A closer view of the xylem stained with 0.01% crystal violet (200X).

surface area using ImagePro Plus software. The predicted K_h was then calculated using the Poiseuille's equation:

$$K_h = \frac{\pi * r^4}{8 * \eta}$$

Where r is the radius (m) of the tracheid, η is the viscosity of water at 25°C ($9.7*10^{-10}$ MPa s^{-1}). The predicted K_h was then compared to K_h obtained experimentally.

Model development

A finite-element model of root water uptake was developed by Alm *et al.* (1992) to represent an intact root as a network of segments, each with its own axial (K_h) and radial (L_r) conductivities (Fig. 4A). I used their model to integrate the root zones (white, CT and cork) and types to calculate L_p for the root system (Fig. 4B).

I was able to provide all the data necessary for predicting L_p with the finite-element model from my own measurements except the mycorrhizae (Chapter II and this Chapter). I did not include these in my measurements because the techniques I used did not allow to measure conductivity of a 2 to 4 mm long mycorrhizal tip. The mycorrhizal contribution to L_p was estimated by using anatomical and morphological data from another study conducted at the same

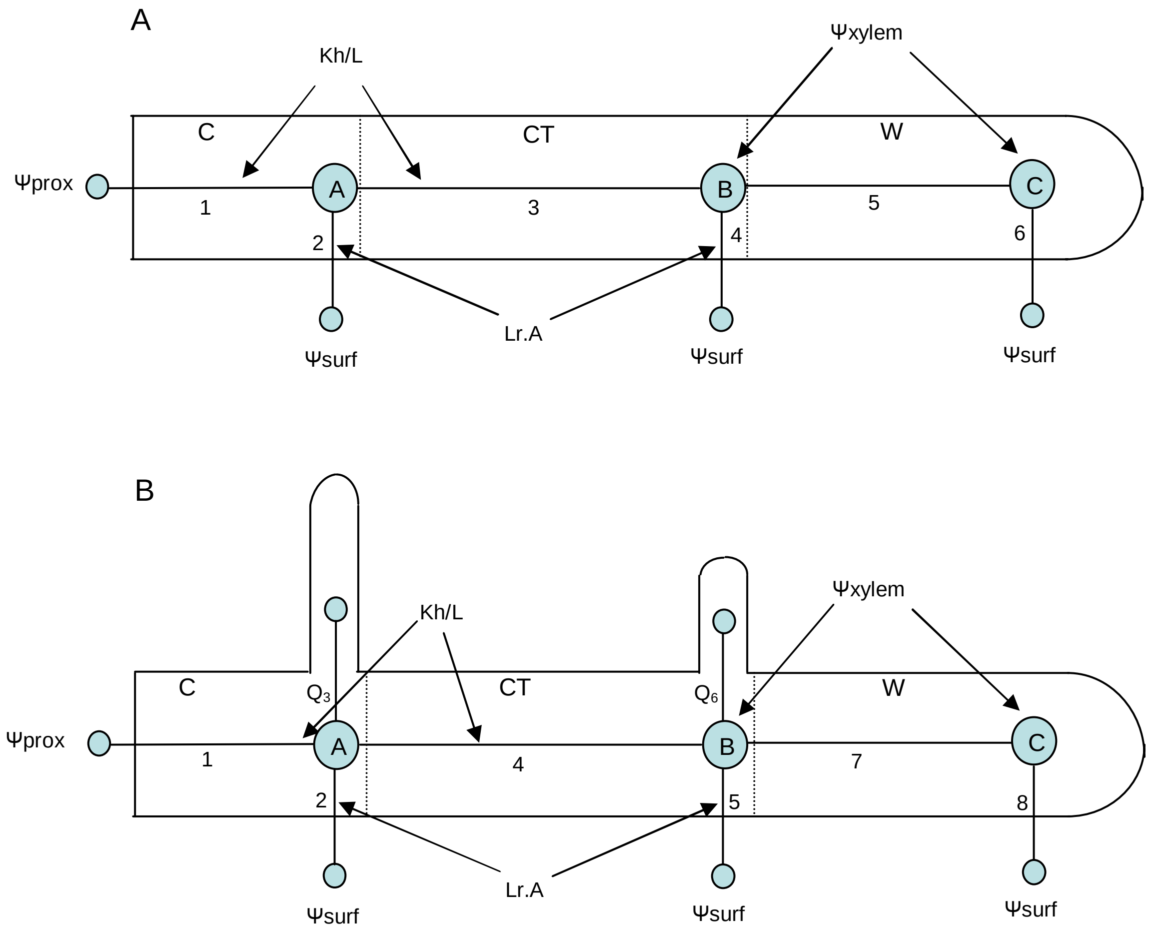
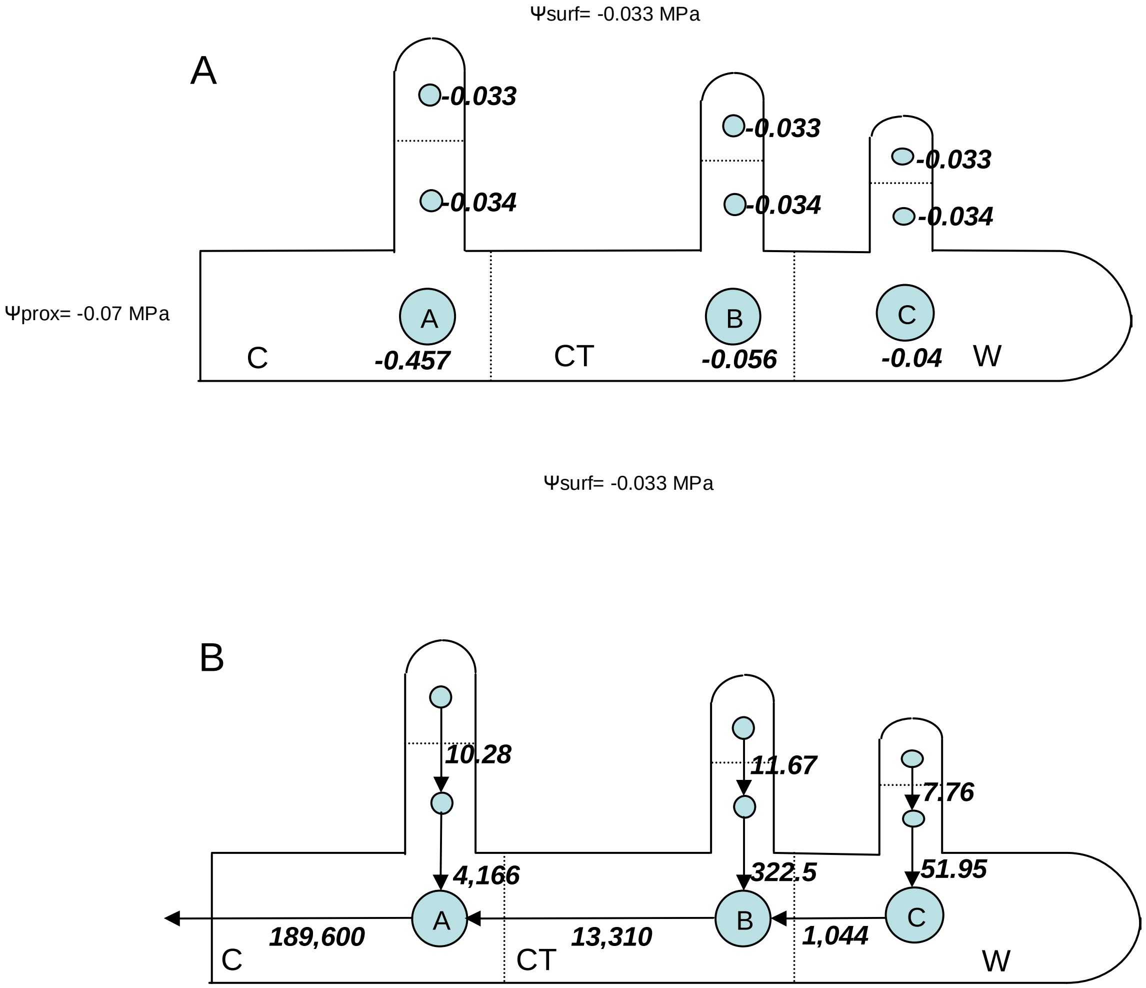


Fig. 4. Diagram of unbranched (A) and branched (B) root divided in three segments representing the white, CT and cork zones. (Adapted from Alm *et al.*, 1992).

time on *P. taeda* in the same nursery (Kumar, 2003). The L_r and K_h for mycorrhizae were considered to be the same as SORL white zone. This was the best estimate available, because the mycorrhizae were produced on SORL and had similar ages and diameters to SORL. Mycorrhizae have been considered to be essentially white zone in other studies (Taylor and Peterson 2000, Kumar 2003). The mycorrhizal tip was white zone with fungal hyphae penetrating the intercellular spaces of the cortex and surrounded by the fungal mantle. The extramatrical hyphae may transport ions (Melin and Nilsson 1958, Finlay et al. 1988) directly to the cortical cell membranes, but the hyphal mantle presented a barrier that has not been characterized (Ashford *et al.*, 1989, Behrmann and Heyser, 1992).

As in Alm *et al.* (1992), each root of the loblolly pine root system was divided into small segments (zones), the center of which were nodes of the simulated root system, with a specified surface area and length. Each segment was connected to its neighbors (same root or branch roots) by an oriented link which was the axial conductivity between the two segments. Likewise, each root node was connected to a soil node by an oriented link (radial conductivity). Segments were numbered serially, starting from the base of the TAPR. The nodes corresponding to the soil and radial conductivity were then numbered followed by the branch roots (axial conductivity). The equations were written in matrix notation as $\Omega\Psi=Q$, where Ψ was the vector of water potentials along the root, Q was the vector of flows (volumetric flux density times area; $m^3\ s^{-1}$) at the root surface and Ω was the conductance matrix. The individual net Q was zero at each xylem node (Kirchoff's law) and unknown at the surface nodes. The xylem water potentials (Ψ_{xyl}) at the root nodes were unknown, whereas the water potentials at the root surface (Ψ_s) were given a uniform value of -0.033 MPa, which corresponds to the soil water potential at field capacity. At the base of the TAPR, water potential (Ψ_{prox}) was given a value of -0.7 MPa which represented the midday xylem water potential at the root collar. The model was first used to calculate Ψ_{xyl} of each TAPR node (Fig. 5). The resulting values were then applied as Ψ_{prox} for the FOLRs to calculate their own Ψ_{xyl}.

A system of linear equations was first solved for individual SOLR and their basal water flows (Q_1) were calculated. SOLRs Q_1 were then integrated into the calculation of the basal water flow of individual FOLRs bearing SOLRs, which, in turn, were applied to calculate Q_1 of the TAPR. Finally the resulting Q_1 was integrated into the calculation of the root system L_p. In August, ectomycorrhizae were considered as SOLR with the L_r and K_h of white zone SOLR from October. When mycorrhizae were found on SOLR in October and November, they were regarded as 3rd order lateral roots with the hydraulic conductivities of white zone SOLR from October.



C

W	1	0.5%
CT	18	8.5%
C	189	91.0%
TOTAL	208	100.0%

Fig. 5. (A) Diagram representing the distribution of xylem water potential (MPa) in the July root system calculated with the model. (B) Water flux density (10^{-14} m^{3} s^{-1}) predicted for the three zones of the TAPR and FOLRs. (C) Total flux density by root zone and the total flux density of the root system (10^{-11} m^{3} s^{-1}).

RESULTS

Root hydraulic conductivity

Root hydraulic conductivity was generally higher in the TAPR than FOLRs and SOLRs in all root zones (Fig. 6 to 8 and Tables 1 to 3). There was a definite trend of decreasing L_p from the white to CT to cork zones and the trend was most marked in TAPR. L_p decreased by a factor of 2 to 3 from the white to cork zone in the TAPR, 2 to 4 in FOLRs and not all in SOLRs. There was a trend of decreasing L_p from June to November for all three root zones for the TAPR. The largest decrease was by a factor of 16 for the white zone and smaller declines occurred for the CT and cork zones. There was no similar seasonal trends for FOLRs and L_p tended to increase from September to November in SOLRs. The FOLRs had the lowest L_p in August and September when it was nearly three orders of magnitude lower than any other time. SOLRs also had very low L_p in September.

Axial hydraulic conductivity

Axial hydraulic conductivity was always much greater in the TAPR than FOLRs and SOLRs in all root zones (Fig. 9 to 11 and Tables 1 to 3). The K_h for the TAPR was as little as 2 times greater than K_h for FOLRs in June to as much as

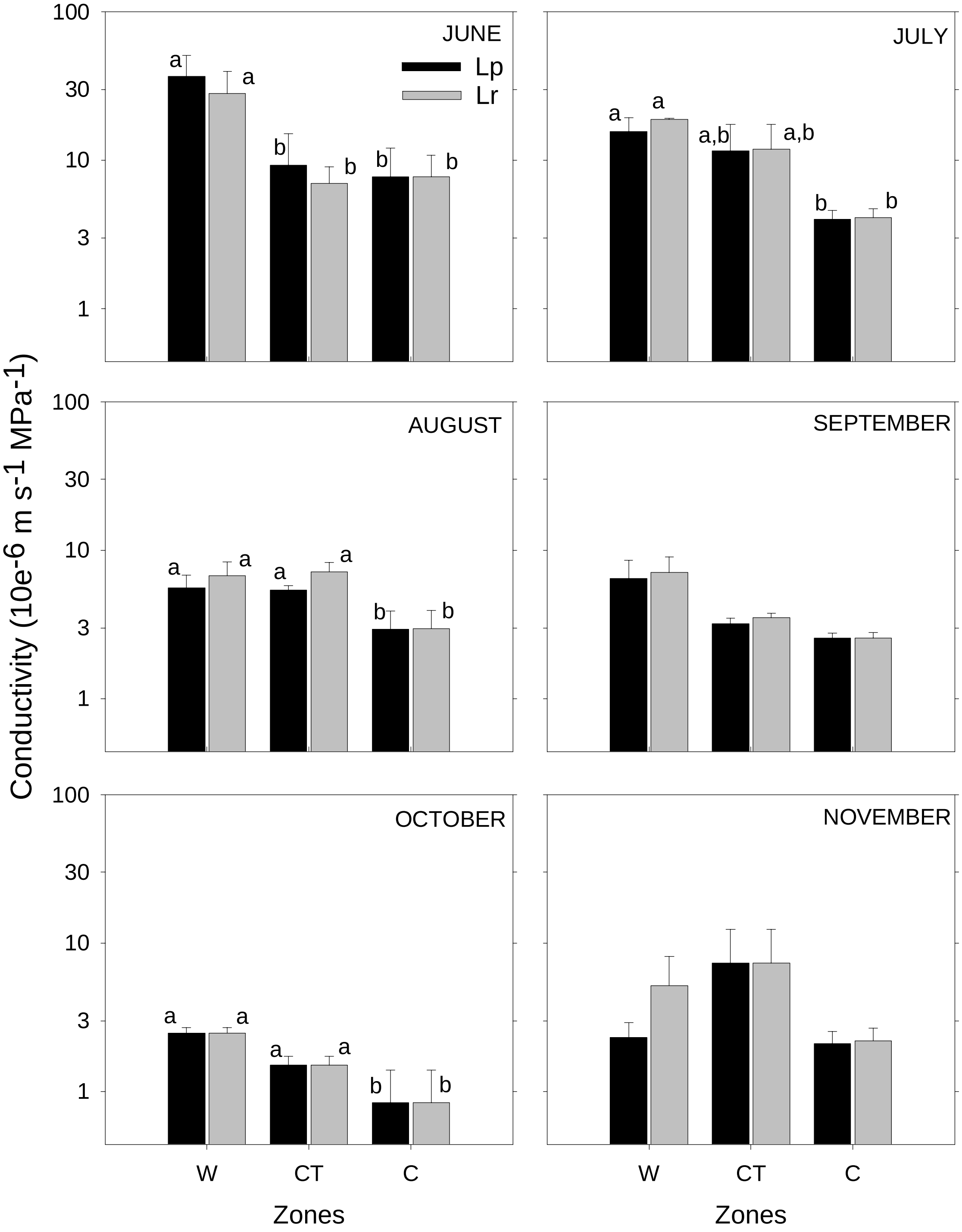


Fig. 6. Root conductivity (Lp) and radial conductivity (Lr) of the TAPR in the three zones: white, condensed tannin and cork. (Mean ± standard error). Letters indicate significant differences, $p \leq 0.05$, n=3.

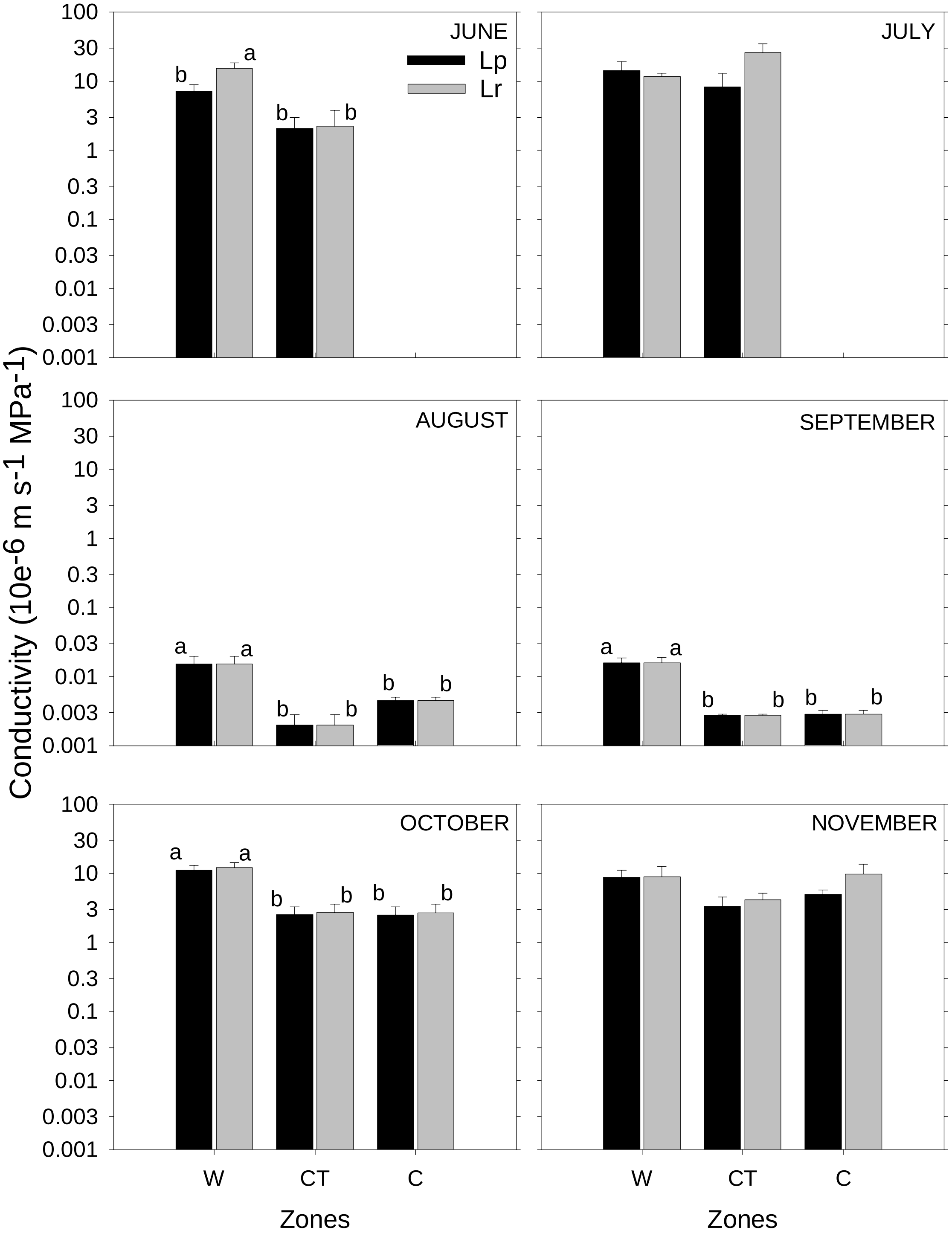


Fig. 7. Root conductivity (L_p) and radial conductivity (L_r) of a FOLR in the three zones: white, condensed tannin and cork. No cork zone was present in June and July. (Mean ± standard error). Letters indicate significant differences, $p \leq 0.05$, n=3.

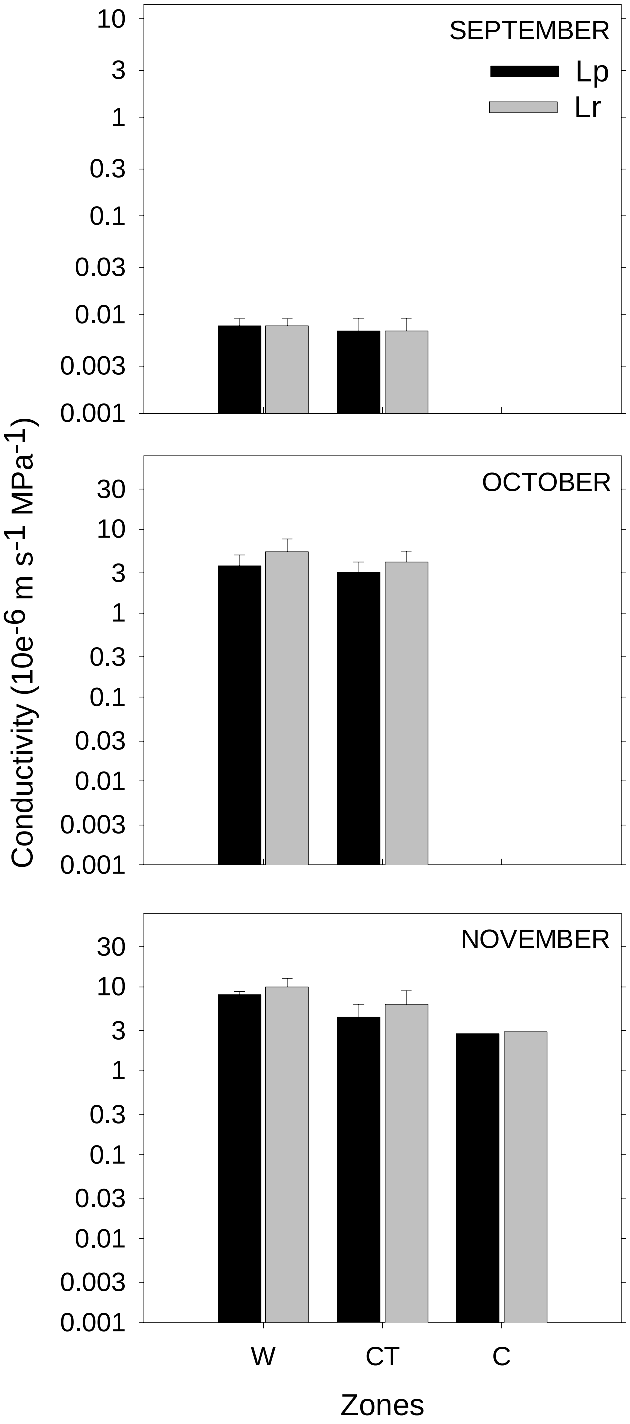


Fig. 8. Root conductivity (Lp) and radial conductivity (Lr) of a SOLR in the three zones: white, condensed tannin and cork. No cork was present in September and October (Mean ± standard error).

Table 1. TAPR root hydraulic conductivity (L_p, 10^{-6} m s^{-1} MPa^{-1}), radial hydraulic conductivity (L_r, 10^{-6} m s^{-1} MPa^{-1}) and axial hydraulic conductivity (K_h, 10^{-11} m^4 s^{-1} MPa^{-1}) of the white zone, CT zone and C zone from June until November. Mean and (standard error).

Root type	N	L_p	L_r	K_h
White zone				
Jun	3	36.60 (14)^{a}	28.50 (11)^{a}	1.15 (0.3)^{b}
Jul	3	15.60 (3.7)^{a}	18.90 (0.3)^{a}	0.46 (0.07)^{b}
Aug	2	5.59 (1.2)^{b}	6.74 (1.6)^{b}	1.78 (1.3)^{b}
Sep	3	6.47 (2.0)^{b}	7.11 (1.9)^{b}	1.10 (0.04)^{b}
Oct	3	2.47 (0.2)^{b}	2.47 (0.2)^{b}	343 (169)^{a}
Nov	3	2.31 (0.6)^{b}	5.17 (2.9)^{b}	2.35 (0.1)^{b}
CT zone				
Jun	3	9.26 (5.8)^{a}	6.95 (2.1)^{b}	1.58 (0.4)^{b}
Jul	3	11.60 (5.8)^{a}	11.90 (5.6)^{a}	1.29 (0.2)^{b}
Aug	2	5.39 (0.4)^{a}	7.18 (1.1)^{b}	66.10 (15.4)^{b}
Sep	2	3.20 (0.3)^{a}	3.52 (0.2)^{b}	22.8 (21.7)^{b}
Oct	3	1.50 (0.2)^{b}	1.50 (0.2)^{b}	929 (169)^{a}
Nov	3	7.32 (5.0)^{a}	7.37 (5.0)^{b}	357 (166)^{b}
Cork zone				
Jun	3	7.72 (4.3)	7.73 (3.1)^{a}	4.97 (2.9)^{a}
Jul	3	4.01 (0.5)	4.11 (0.6)^{a,b}	111 (25)^{a}
Aug	3	2.94 (0.9)	2.95 (0.9)^{a,b}	249 (61)^{a}
Sep	3	2.56 (0.2)	2.56 (0.2)^{b}	540 (110)^{b}
Oct	2	0.84 (0.5)	0.84 (0.5)^{b}	1008 (98)^{c}
Nov	3	2.10 (0.4)	2.20 (0.4)^{b}	594 (131)^{b}

Note: monthly means followed by different letters were significantly different ($LSD_{0.05}$)

Table 2. FOLR root hydraulic conductivity (L_p, 10^{-6} m s^{-1} MPa^{-1}), radial hydraulic conductivity (L_r, 10^{-6} m s^{-1} MPa^{-1}) and axial hydraulic conductivity (K_h, 10^{-11} m^4 s-1 MPa^{-1}) of the white zone, CT zone and C zone from June until November. Mean and (standart error)

Root type	N	L_p	L_r	K_h
White zone				
Jun	3	7.18 (1.7)^{a,b}	15.40 (3.0)	0.514 (0.1)^{a,b}
Jul	3	14.30 (4.6)^{a}	11.70 (1.2)	0.0133 (0.002)^{b}
Aug	3	0.0152 (0.004)^{b}	0.0152 (0.004)	0.332 (0.05)^{a,b}
Sep	3	0.0157 (0.003)^{b}	0.0157 (0.003)	0.147 (0.05)^{a,b}
Oct	3	11.10 (1.8)^{a}	16.80 (2.2)	0.409 (0.1)^{a,b}
Nov	3	8.79 (2.2)^{a}	8.96 (3.5)	1.29 (0.8)^{a}
CT zone				
Jun	3	2.07 (0.9)^{a,b}	2.21 (1.5)^{b}	0.273 (0.1)^{b}
Jul	3	8.18 (4.5)^{a}	26.0 (8.9)^{a}	0.0249 (0.001)^{b}
Aug	3	0.001 (0.0008)^{b}	0.001 (0.0008)^{b}	0.829 (0.1)^{b}
Sep	3	0.002 (0.0001)^{b}	0.002 (0.0001)^{b}	0.696 (0.2)^{b}
Oct	3	2.48 (0.7)^{a,b}	2.68 (0.8)^{b}	3.07 (0.8)^{a}
Nov	3	3.35 (1.2)^{a,b}	4.11 (1.0)^{b}	3.17 (1.0)^{a}
Cork zone				
Jun				
Jul				
Aug	3	0.0045 (0.0005)^{c}	0.004 (0.0005)^{b}	3.22 (0.5)^{a,b}
Sep	3	0.00287 (0.0003)^{c}	0.00287 (0.0003)^{b}	1.83 (0.1)^{b}
Oct	3	2.48 (0.7)^{b}	2.68 (0.8)^{b}	3.07 (0.8)^{a,b}
Nov	3	4.94 (0.7)^{a}	9.69 (3.8)^{a}	4.09 (0.5)^{a}

Note: monthly means followed by different letters were significantly different ($LSD_{0.05}$)

Table 3. SOLR root hydraulic conductivity (L_p, 10^{-6} m s^{-1} MPa^{-1}), radial hydraulic conductivity (L_r, 10^{-6} m s^{-1} MPa^{-1}) and axial hydraulic conductivity (K_h, 10^{-11} m^4 s^{-1} MPa^{-1}) of the white zone, CT zone and C zone from June until November. Mean and (standart error)

Root type	N	L_p	L_r	K_h
White zone				
Jun				
Jul				
Aug				
Sep	3	0.00773 (0.001)^{c}	0.00773 (0.001)^{c}	0.283 (0.08)^{b}
Oct	3	3.68 (1.4)^{b}	5.37 (2.3)^{a,b}	0.90 (0.2)^{a}
Nov	3	8.08 (0.7)^{a}	6.16 (0.2)^{a}	0.391 (0.07)^{b}
CT zone				
Jun				
Jul				
Aug				
Sep	3	0.00679 (0.002)^{c}	0.0068 (0.002)	0.445 (0.02)
Oct	3	3.07 (0.9)^{a,b}	4.10 (1.3)	1.27 (0.5)
Nov	3	4.39 (1.8)^{a}	6.16 (2.7)	0.87 (0.2)
Cork zone				
Jun				
Jul				
Aug				
Sep				
Oct				
Nov	1	2.75	2.90	3.77

Note: monthly means followed by different letters were significantly different ($LSD_{0.05}$)

300 times greater late in the year. K_h for FOLRs and SOLRs were comparable. There was a marked trend of increasing K_h from white to CT to cork zone for the TAPR and FOLRs. The TAPR showed the greatest increase ranging from a factor of 4 in June to nearly 500 later in the year. The largest increase for FOLRs was by a factor of 12 and change in K_h could not be detected in SOLRs. There was a clear pattern of K_h increasing from June to November in the TAPR and FOLRs. The highest values for TAPR were observed in October and when they were 300 to 600 times greater in June.

Radial hydraulic conductivity

Radial hydraulic conductivity was calculated from L_p and K_h (Landsberg and Fowkes, 1978). L_r was never different from L_p (Fig. 6 to 8 and tables 1 to 3).

Predicted and measured K_h

K_h predicted by the Hagen-Poiseuille equation was always much larger than the measured K_h (tables 4 to 6). Measured K_h averaged near 50% of the predicted K_h for all root zones and types across the 6 months of the study.

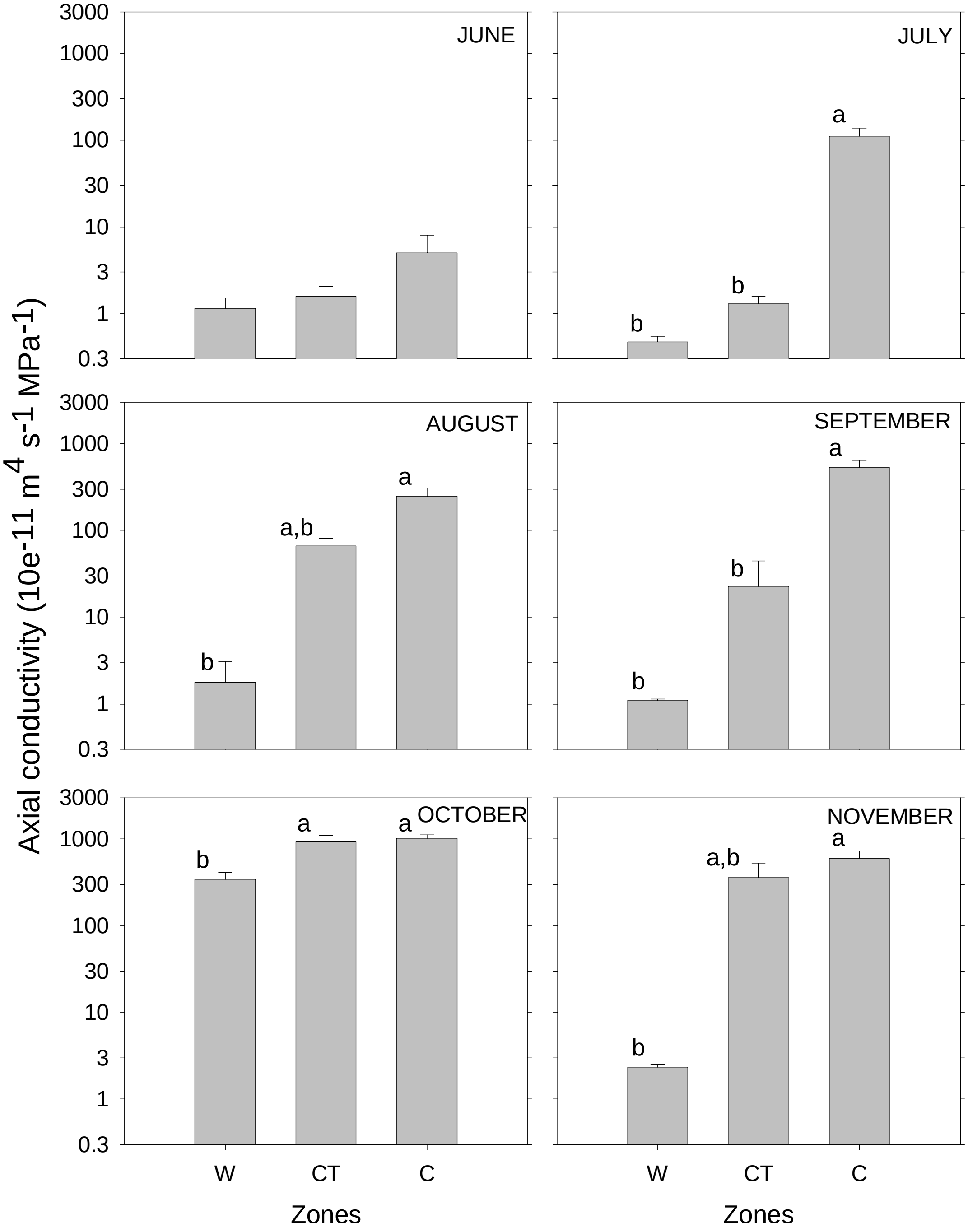


Fig. 9. Axial conductivity (K_h) of the TAPR in the three zones: white, condensed tannin and cork. (Mean ± standard error). Letters indicate significant differences, $p \leq 0.05$, n=3.

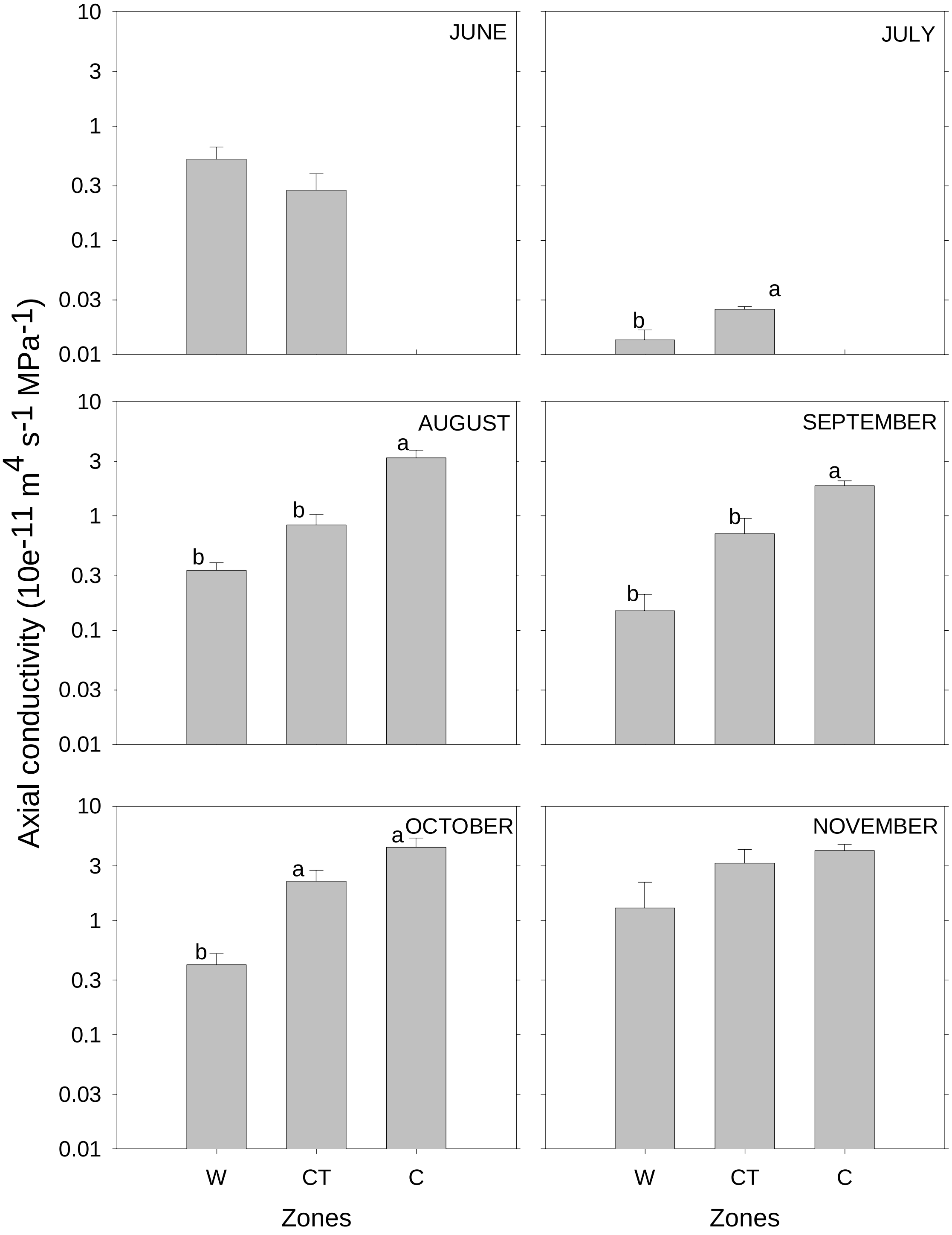


Fig. 10. Axial conductivity (Kh) of a FOLR in the three zones: white, condensed tannin and cork. (Mean ± standard error). Letters indicate significant differences, $p \leq 0.05$, n=3.

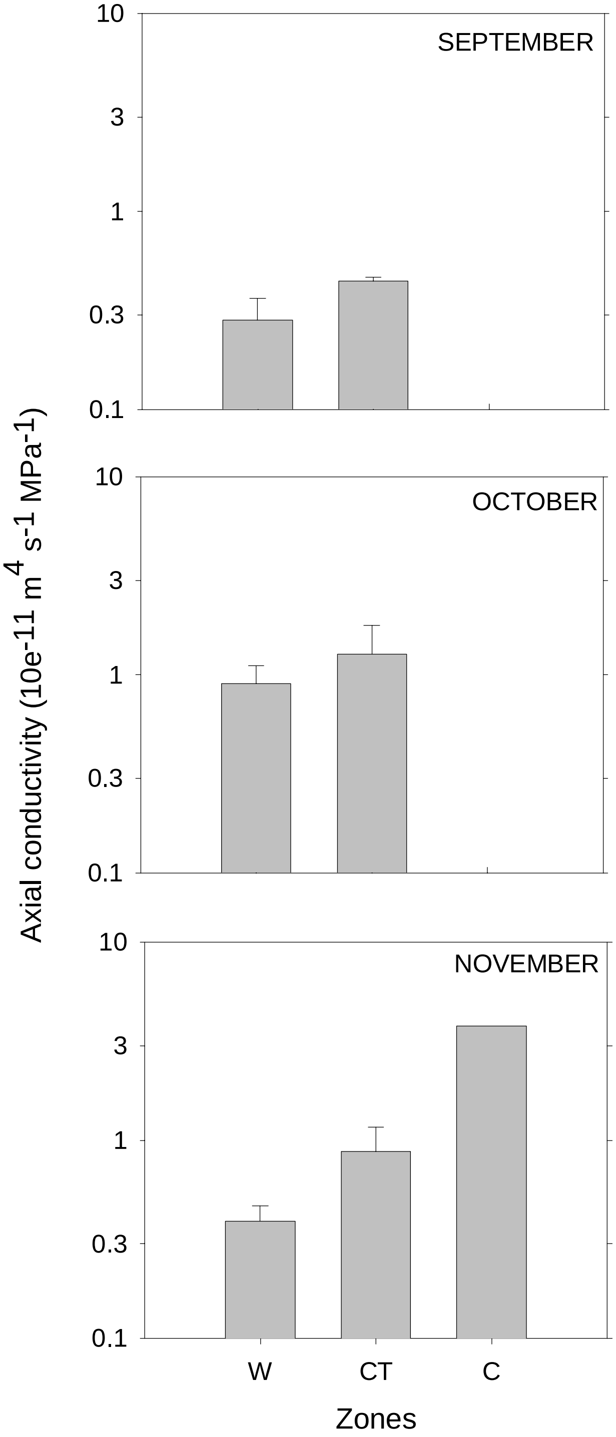


Fig. 11. Axial conductivity (Kh) of a SOLR in the three zones: white, condensed tannin and cork. No cork was present in September and October. (Mean ± standard error).

Table 4. Comparison of the axial hydraulic conductivity of the TAPR in the different zones calculated by the Hagen-Poiseuille equation to the values measured by induced water-flow experiments from June to November (Mean +/- standard error). Significant differences ($p \leq 0.05$) between monthly means for a given zone are indicated by different letters.

Root type	N	Poiseuille	Measured	% of the poiseuille
		($*10^{-11}$ m^{4} s^{-1} MPa^{-1})		
White zone				
Jun	3	2.57 (0.19)^{b}	1.15 (0.365)^{b}	45
Jul	3	0.518 (0.04)^{b}	0.181 (0.045)^{b}	35
Aug	2	4.04 (0.97)^{b}	1.78 (1.32)^{b}	44
Sep[1]				
Oct	3	965 (485)^{a}	343 (67.7)^{a}	36
Nov	3	5.76 (0.44)^{b}	2.66 (0.179)^{b}	46
CT zone				
Jun	3	6.03 (0.69)^{c}	3.24 (1.96)^{b}	54
Jul	3	3.08 (5.15)^{c}	1.29 (0.294)^{b}	42
Aug	2	101 (34.4)^{c}	66.1 (15.3)^{b}	65
Sep	1	154^{c}	87.5^{b}	57
Oct	3	1750 (199)^{a}	814 (283)^{a}	47
Nov	3	763 (40.5)^{*,b}	357 (166)^{a,b}	47
C zone				
Jun	3	7.84 (0.51)^{*,d}	4.49 (2.49)^{d}	57
Jul	3	312 (10.6)^{*,d}	111 (25)^{d}	36
Aug	3	596 (17.5)^{*,c}	240 (66.2)^{c,d}	40
Sep	3	1010 (87.4)^{b}	540 (110)^{b,c}	53
Oct	1	2180^{a}	1010^{a}	46
Nov	3	979 (33.9)^{*,b}	594 (131)^{b}	61

* Poiseuille value is significantly higher than the measured one

[1] No data

Table 5. Comparison of the axial hydraulic conductivity of the FOLR in the different zones calculated by the Hagen-Poiseuille equation to the values measured by induced water-flow experiments from June to November (Mean +/- standard error). Significant differences ($p \leq 0.05$) between monthly means for a given zone are indicated by different letters.

Root type	N	Poiseuille	Measured	% of the Poiseuille
		(*10^{12} m^4 s^{-1} MPa^{-1})		
White zone				
Jun	3	8.93 (3.92)^{a}	5.14 (1.44)^{a}	58
Jul	3	0.251 (0.009)^{b}	0.13 (0.0294)^{c}	52
Aug	3	9.42 (1.45)^{a,b}	3.32 (0.586)^{a,b}	35
Sep	3	3.23 (1.34)^{a,b}	1.53 (0.537)^{b,c}	47
Oct	3	7.46 (3.08)^{a,b}	4.09 (1.05)^{a,b}	55
Nov^{1}				
CT zone				
Jun	3	11.3 (0.86)*^{,c}	2.73 (1.07)^{b}	45
Jul	3	0.533 (0.008)*^{,c}	0.246 (0.013)^{b}	46
Aug	3	16.2 (3.69)^{b,c}	8.29 (1.96)^{b}	51
Sep	3	19.3 (0.80)*^{,b,c}	7.16 (2.59)^{b}	37
Oct	3	41.6 (12.8)*^{,a,b}	30.7 (8.64)^{a}	74
Nov	3	56.8 (14.7)^{a,b}	29.1 (12.5)^{a}	51
C zone				
Jun^{2}				
Jul^{2}				
Aug	3	51.2 (1.81)*	32.2 (5.62)^{a,b}	63
Sep	3	41.7 (5.48)*	18 (1.94)^{b}	43
Oct^{1}				
Nov	3	108 (34.3)*	43.1 (7.19)^{a}	40

* Poiseuille value is significantly higher than the measured one

[1] No data

[2] The zone was absent or too small for measurements

Table 6. Comparison of the axial hydraulic conductivity of the SOLR in the different zones calculated by the Hagen-Poiseuille equation to the values measured by induced water-flow experiments from June to November (Mean +/- standard error). Significant differences ($p \leq 0.05$) between monthly means for a given zone are indicated by different letters.

Root type	N	Poiseuille ($*10^{12}$ m^4 s^{-1} MPa^{-1})	Measured ($*10^{12}$ m^4 s^{-1} MPa^{-1})	% of the Poiseuille
White zone				
Jun[2]				
Jul[2]				
Aug[2]				
Sep	3	4.26 (0.327)	2.83 (0.807)	66
Oct	3	15.7 (8.97)	7.14 (2.13)	45
Nov	3	6.7 (0.182)	3.95 (0.716)	59
CT zone				
Jun[2]				
Jul[2]				
Aug[2]				
Sep	3	5.72 (0.965)*,[c]	4.45 (0.2)	78
Oct	3	27.0 (2.48)[b]	12.7 (5.03)	47
Nov	3	15.6 (1.53)*,[a]	8.45 (2.7)	54
C zone				
Jun[2]				
Jul[2]				
Aug[2]				
Sep[2]				
Oct[2]				
Nov	1	13*	5.62	43

* Poiseuille value is significantly higher than the measured one

[2] The zone was absent or too small for measurements

Modelled root system L_p

Root system L_p predicted by the finite element model tended to decrease from June to November (Fig. 12). An exception was the root system L_p predicted for October which followed root pruning and undercutting and was at least 10 times greater than at any other time. The mycorrhizae which were first observed in another study in August did not make a large contribution to root system L_p until November (Fig. 12).

Modelled water volume flux density by root zone

The finite element model predicted water flux density was almost always greatest for the cork zone (23 to 91%) and least for the white zone (0.5 to 23%; Table 7). This was somewhat consistent with surface area allocation to cork zone (14 to 60%) and white zone (7 to 51%). Mycorrhizae did not affect the allocation of predicted water flux density by zone.

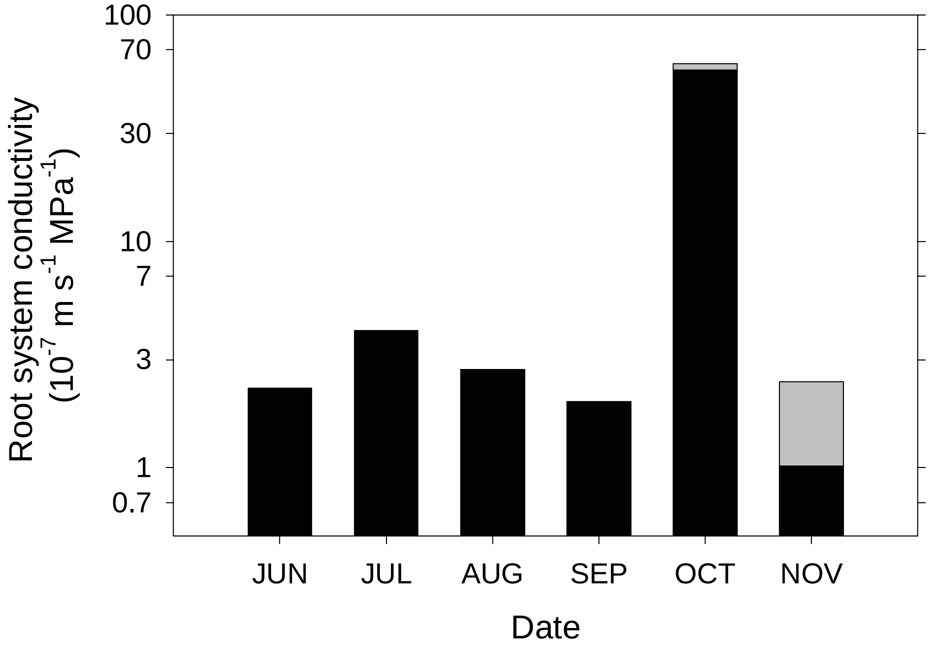


Fig. 12. Comparison of root conductivity of the entire root system without (■) and with mycorrhizae (▨) as predicted by the FEM. Mycorrhizae were present August to November.

Table 7. Root surface area and water flow by zone as a percentage of the total surface area and total water flow predicted by the model.

Harvest	No myco SA %	 Flow %	Myco SA %	 Flow %
Jun				
W	51	22	51	22
CT	26	12	26	12
C	23	66	23	66
Jul				
W	30	0.5	30	0.5
CT	56	8.5	56	8.5
C	14	91	14	91
Aug				
W	7	4	7	4
CT	33	18	33	18
C	60	78	60	78
Sep				
W	11	4.5	11	4.5
CT	40	7.5	40	7.5
C	49	88	49	88
Oct				
W	23	23	23	23
CT	58	54	58	54
C	19	23	19	23
Nov				
W	11	5	11.5	5
CT	43	20	43	18
C	46	75	45.5	78

DISCUSSION

The results clearly showed major changes in root hydraulic properties including L_p, L_r, and K_h across root orders, root zones and seasons. These results confirm numerous earlier studies showing variation in uptake according to degree of root suberization and age (Rosene, 1937; Brouwer, 1954; Sanderson, 1983; Haussling *et al.*, 1988; Frensch and Steudle, 1989; North and Nobel, 1991; Melchior and Steudle, 1993). The results significantly extend knowledge because they link function (hydraulic properties) to structure (anatomy and morphology) of easily identifiable root zones (McKenzie and Peterson 1995a, b). *P. taeda* L_p decreased 3 fold from tip to base of the TAPR and 2 to 4 fold for FOLRs. An earlier study showed non-suberized roots had an L_p 2.6 fold higher than suberized roots of *P. taeda* (Sands et al., 1982). They called white roots “non-suberized” and brown roots “suberized” which is a classification system shown to be inaccurate (McKenzie and Peterson 1995a, b). Other studies have reported a decrease in conductivity from young to old roots (McCully and Canny, 1988; Steudle and Frensch, 1989; and Frensch and Hsiao, 1996). I believe it is much more accurate and useful to classify the roots by zone as white, CT and cork, because these zones have recognizable anatomical differences that can be associated with hydraulic properties.

The TAPR was the first root produced by the seedling and in the early period it was the main provider of water and nutrients. Later the seedling produced laterals of higher and higher order that in turn came to dominate uptake. At first the TAPR had the highest L_p for all root zones compared to FOLRs and by November there were no differences (Fig. 6 to 8, Table 1 to 3). In contrast, K_h was similar among zones and between the TAPR and FOLRs early and later differences became very large. The K_h of the TAPR CT and cork zone came to be the largest for the entire seedling reflecting the large amount of secondary xylem in the TAPR and the importance of the TAPR for upward transport of water absorbed by laterals.

The three root zones: white, CT and cork zone documented in jack pine by McKenzie and Peterson (1995a, b) have also been described in loblolly pine roots (Peterson *et al,* 1999). The anatomical differences were thought to have a significant role in the absorption of water and ions. Indeed my results revealed that changes in root hydraulic conductivity (L_p) were consistent with anatomical changes during root development. The white zone showed the highest water conductivity. Its cortical cells were alive and its endodermis contained abumdant non-suberized passage cells (State II, Peterson and Enstone, 1996). The diminishing number of passage cells in the endodermis increased the resistance to water flow in older regions of the white zone and in the CT zone by reducing the available path for water to enter the stele. In addition, the cortical cells died progressively and were partly abraded resulting in a smaller water transport capacity for the CT zone due to the elimination of the symplastic pathway (Enstone *et al.*, 2001). On the other hand, the reduced and dead cortical cells would present a low resistance apoplastic pathway up to to the endodermal passage cells. The ability to transport water further decreased with the development of an impermeable cork layer under the suberized endodermis. However, this cork layer was not impervious to water as some water may have penetrated through lenticels, lateral root bypasses and wounds (Addoms, 1946) as L_p was not equal to zero.

The axial hydraulic conductivity (K_h) increased 4 to about 500 times from the tip of the TAPR to its base and 2 to 12 times for FOLRs (Tables 1 to 3, Fig. 9 to 11). This was also consistent with the observations made in onion (Melchior and Steudle, 1993), *Agave deserti* (North and Nobel, 1991) and Barley (Sanderson, 1983). Changes in axial hydraulic conductivity were consistent with anatomical changes during root development. K_h increased from the white to the cork zone, as the number and diameter of conductive tracheids increased due to the secondary xylem growth. In the white zone, a few millimeters of the tip was hydraulically isolated as it possessed only living xylem elements (Enstone *et al.*, 2001). A few millimeters farther from the tip, just a few tracheids were able to conduct water. As the root developed, more tracheids were available for water conduction. The production of secondary xylem in the TAPR increased greatly the conductive capacity of the root.

L_r was not different from L_p, signifying that L_r was the primary limiter of root water uptake (Steudle and Jeschke, 1983; Frensch and Steudle, 1989; North and

Nobel, 1992; Fig. 6 to 8). The white zone, with few conductive tracheids, possessed a K_h high enough to conduct the radially absorbed water. However K_h was the limiting factor in the hydraulically isolated tip region of the white zone (Frensch and Steudle, 1989).

Seasonal changes

TAPR L_p decreased for all zones from June to November (Table 1). An increase in the suberization of the endodermis could be at the origin of this decrease. McCrady and Comerford (1998) reported that suberization was an internal cellular process and may result from several conditions (high temperature, low temperature, drought). Wilcox (1954, 1968) showed that suberization of the endodermis was occurring closer to the tip as conditions became adverse, reducing the amount of symplastic flow. Increased suberization would result in a smaller number of passage cells closer to the tip. In the white zone with a high absorptive capacity due to the living cortical cells and numerous passage cells, such phenomena would greatly reduce the radial paths available for water. Indeed white zone L_p decreased the most from June to November compared to CT and cork. With the death and sloughing of the cortical cells in the CT zone, the only path for water to penetrate the root was through the passage cells present in the endodermis (Peterson *et al.*, 1999). As the CT endodermis had only a few passage cells in June, an increase in the suberization would result in a small decrease of L_p from June to November.

The TAPR cork zone is characterized by the hydrophobic layer of cork with no passage cells surrounding the stele. Therefore L_p was not affected by an increase of the suberization. However, the production of lateral roots could be the reason for the high L_p in June and July. They originated below the endodermis and their growth through it is thought to allow the passage of water into a stele otherwise isolated from the soil solution (Karas and McCully, 1973; Peterson and Lefcourt, 1990; Peterson and Moon, 1993). From August to November, L_p remained constant although few new lateral roots were produced. This indicates that the cork layer was not as impermeable to water as thought. Several studies concluded that the old suberized roots were also the site of water uptake (Addoms, 1946; Kramer and Bullock, 1966). The drop of L_p in October was probably due to the undercutting made two weeks before the harvest. Only the old cork zone close to the shoot remained, which may be more impermeable than younger parts of the zone.

The constant K_h in the TAPR white zone from June to November, except October, resulted from a relatively low and constant number of conductive tracheids over the season, implying that the white zone didn't vary in its axial structure (Table 1). October showed a peak in K_h caused by the undercutting of the TAPR. It resulted in the growth of new roots from the cut stump. These new roots possessed a higher number of tracheids (Chapter II). The increase of K_h in the CT was due to the increased number of conductive tracheids (Chapter II).

The increase in the cork zone from June to November was mostly due to the secondary growth of the xylem that produced an increasing number of tracheid in these zones.

The FOLR's white, CT and cork zones showed L_p to be fairly constant over the season, with a drop in August and September (Table 2). The constancy of white and CT L_p could be explained by a relatively constant number of passage cells in the endodermis over the season which would be different from the TAPR. Cork L_p didn't change because the relative impermeability of the cork layer didn't change throughout the season. The very low values of FOLR L_p in August and September coincided with the slow growing period of the root system occurring in the hot dry summer months (Dougherty *et al*, 1994; Sword, 1998; Livonen *et al.*, 2001). During this period, FOLR growth slowed and the endodermis in the white and CT zones may have become more suberized, reducing the passage of water. The cork zone could also have reinforced its natural impermeability by sealing potential apoplastic bypasses (Addoms, 1946; Dumbroff and Peirson, 1971; Peterson *et al.*, 1981) or changing its chemical composition. Drier soil surface may have affected the FOLRs growing mostly in the top soil layer without affecting the deeper TAPR. During the strong growing periods in October and November, new white and CT tissues with passage cells were formed, leading to a higher L_p comparable to the beginning of the season. Moreover, the production of SOLRs may have created leaks in the endodermis of the CT and cork zones.

White zone K_h in FOLRs remained relatively constant from June to November with the exception of July (Table 2). This agreed with the constant number of conductive tracheids in the stele (Chapter II). The CT zone also showed a fairly uniform K_h except in October and November when the production of new roots with more tracheids lead to a higher K_h.

Predicted water flow

The classical approach for studying water flow in tracheary elements has been to compare measured values of xylemic water flow with the values calculated from lumen diameter of conduits by using the Hagen-Poiseuille equation for ideal capillaries with circular transections (Münch, 1943; Zimmermann and Brown, 1971; Zimmermann, 1983; Gibson *et al.*, 1984). For tracheids these calculations have produced measured values of K_h that were always less than ideal and generally less than half the predicted value. When the Hagen-Poiseuille equation was modified to calculate flow in noncircular tracheid lumens, the differences were even greater. In this study, both the measured and predicted values of K_h changed gradually along the root axis; however, the measured K_h were always roughly 50% of the Hagen-Poiseuille predictions (Tables 4 to 6). This discrepancy was close to values seen for ferns (Woodhouse and Nobel, 1982) and vine (Giordano *et al.*, 1978). Similar results were reported for the woody stems of *Acer rubrum* (Tyree and Zimmermann, 1971) and the root wood of four other angiosperm trees (Riedl, 1937). Münch (1943) found measured K_h

to be 20 to 40% of the predicted values for various trees, including *Abies pectinata*. Sands *et al.* (1982) found that *P. taeda* tracheids conducted water at 55% of idealized Poiseuille flow.

The Hagen-Poiseuille relation was originally developed to describe fluid flow through long ideal capillaries of constant diameter. Conduit number and diameter are the principal determinants of conductance in plants. However, pits and tracheid shape may form local constrictions that lower the actual K_h below this theoretical maximum. Conifers such as *P. taeda* have their xylem composed of short, closed-ended tracheids with large, circular bordered pits with a torus (Esau, 1977). These characteristic are quite different from the long, open-ended vessels without any real barrier found in angiosperms. Although water must move from tracheid to tracheid through pit membranes, it can travel through many vessel elements before meeting an analogous cell wall material of intervessel pits. Nonetheless, no clear evidence has been found to support the idea that tracheids are less effective in conducting water than vessels of similar diameter (Bailey, 1953; Carlquist, 1975). Becker *et al.* (1999) observed no significant differences in conductances between nine evergreen angiosperms and three conifers. The tracheid lumen and the pit characteristics must be determined to model correctly the hydraulic conductance of the xylem. It is necessary to describe the properties of tracheids and bordered pit to quantify the resistance to water flow. In this study, we found that the measured K_h was always around 50% of the predicted K_h for all root types and zones. Analyses of the tracheid properties made in Chapter III revealed that the resistance of the tracheids remained constant during the season and between zones. In addition, the bordered pit structure was the same across root zones and seasons. Bordered pits contributed most of the tracheid resistance. Thus, the fact that their structure was conserved is consistent with the constant difference between measured and predicted K_h.

Model

L_p calculated with the model agreed with the values found in the literature (Chung and Kramer, 1975; Sands *et al.*, 1982; Van Rees and Comerford, 1990; Fig. 12). Sands *et al.* (1982) calculated a L_p of $1.4*10^{-7}$ m s^{-1} MPa^{-1} for an eight-month-old *P.taeda* root system, and Chung and Kramer (1975) measured a L_p equal to $1.18*10^{-6}$ m s^{-1} MPa^{-1} for a one-year-old *P.taeda* root system. Van Rees and Comerford (1990) had a L_p ranging from $1.62*10^{-7}$ to $7.65*10^{-7}$ m s^{-1} MPa^{-1} for *P. elliottii* engelm. In these studies, seedlings were harvested from nurseries and transferred to a nutrient solution to regenerate new roots before conductivity measurements were made. Thus, it appeared that growing in a nutrient solution or in the soil did not significantly affect L_p. The large root system L_p in October resulted from undercutting and lateral pruning. Such treatments have been shown to increase the number of new roots (white zone) with a high uptake potential (Chauhan and Mishra, 1996). The water uptake capacity of the root system was improved by these cultural practices.

My calculations showed that the conductive capacity of the seedling root system reached a peak in July and then decreased until November with the exception of October, despite a continuous growth in length and surface area. This could indicate that the root system was at its maximum uptake capacity in July and that the root tissues and root types formed afterward were not able to maintain the water uptake at this level. This can be explained by the seasonal increase of the amount of CT and cork tissues with a small L_p, while the amount of white zone with a high L_p remained constant. Indeed the model calculations showed that water was mostly absorbed through the cork zone and not through the white and CT zones as usually thought (Table 7). Crider (1933), Nightingale (1935), Head (1967) and Wilson and Atkinson (1978) found that trees had very few growing root tips and were able to absorb water and nutrients, implying that water absorption must occur through woody roots. Kramer and Bullock (1966) found that the suberized roots of a 34-year-old loblolly pine represented 97% of the root system surface area and that these roots were absorbing about 75% of the total water. This is very similar to the values found in this study; the CT and cork zones were 70 to 93% of the root system surface area and they absorbed 67 to 99.5% of the water.

Recently, Van Rees and Comerford (1990) revealed that the water uptake per surface area by *P. elliottii* woody roots were often comparable with the uptake of entire root systems. This supports the idea that the role of the white zone was to principally absorb ions and water was mainly absorbed by the other parts of the root system. Indeed the CT and cork zones represent most of the root system surface area enabling contact with available water over a greater volume of soil. The white zone represented a small portion of the root system and was localized at the tip of the roots. This enabled the roots to prospect the soil for new pools of ions which are not abundant and are attached to the soil particles. These ions are absorbed actively via transporters in the cell membranes. The white zone possessed living cortical cells capable of such absorption (McKenzie and Peterson, 1995a,b; Enstone *et al.,* 2000; Kumar, 2003).

The addition of mycorrhizae increased modeled L_p. Relatively little research has been made about water uptake capacity of mycorrhizal root systems. Sands and Thedorou (1978) reported that L_p of the ectomycorrhizal radiata pine root system was less than that of non-inoculated controls. Sands *et al.* (1982) found no differences between infected and non-infected loblolly pine seedlings. By contrast, Safir *et al.* (1972a, b) studied the endomycorrhizal soybean root system and observed that L_p was greater than that of non-inoculated controls. According to them, this higher L_p resulted from an enhanced nutrient status of the plant. More recently, Muhsin and Zwiazek (2002) found that mycorrhizal *Ulmus americana* root system had a greater L_p than a non-mycorrhizal plant. Fungal hyphae normally penetrate the root central cortex and do not reach the endodermis. Therefore, the large increase in L_p of ectomycorrhizal seedlings provided additional support for the view that the major resistance to root water flow is not in the endodermal layer, but that it is spread over the living tissues of the root (Peterson and Steudle, 1993; Steudle and Peterson, 1998). However, our L_p measurements of the white, CT and cork zones based on the anatomical differences such as the color of the root, the death of the cortex and the suberization of the endodermis revealed that L_p decreased with the increasing suberization. Obviously, more work is needed to determine the exact mechanisms of water flow regulation in mycorrhizal roots. But it is clear that the presence of mycorrhizae plays an important role in the uptake and transport of water to the host plants.

CONCLUSIONS

- The hydraulic properties and anatomy of the TAPR, FOLR and SOLR were consistent with their supposed functions. The TAPR was mostly cork zone with low L_r and a large amount of highly conductive secondary xylem. This structure ensured reduced radial water loss to the soil and efficient transfer of water from the higher order lateral roots to the shoot. The FOLRs and SOLRs were mostly CT and white zone with high L_r and a modest K_h which facilitated rapid water uptake.

- The hydraulic properties and anatomies of the three root zones were consistent with their supposed functions. White zone had relatively high L_r due to live cortex and plentiful passage cells and a low K_h because it never produced a large number of tracheids. CT and cork zones had reduced L_r due to increased suberization and a cork layer and K_h increased progressively due to the production of more large diameter tracheids. Capacity for water uptake decreased and axial transport increased as the root matured.

- FOLR experienced strongly reduced L_r and K_h in mid-summer perhaps due to the warm dry conditions of the surface soil. The deeper TAPR did not show the same declines.

- Measured K_h was always approximately 50% of the ideal Poiseuille K_h regardless of root type, zone and season which was consistent with the finding that bordered pit structure was highly conserved across root zones and seasons.

- The finite-element model predicted a root system L_p consistent with published data for similar species. Predicted L_p was highest in July when the root system was young and declined in the winter. The estimated contribution of mycorrhizae was significant in November. Elimination of older roots by undercutting and pruning in October followed by rapid production of new roots resulted in the highest seedling L_p over the months of the study.

- The finite-element model predicted the cork zone had the greatest contribution to water uptake followed by the CT and white zone, despite the cork zone having a very low Lr compared to the white and CT zones. This was probably due to the model predicting a substantial drop in Ψ that reduced the driving force for water uptake in the white zone to very low levels.

FUTURE RESEARCH

- The degree of suberization of the endodermis was an important parameter modifying the radial conductivity. Its evolution during the growing season and under stressed conditions (high temperature, drought, nutrients) needs to be studied. Also little is known about the cork zone. Is the cork layer the same from the beginning of the zone to the base of the root? According to the model, the cork zone is absorbing much of the water. Is it only due to the presence of lenticels, wounds or lateral root emergence? Is the chemical composition of the cork changing?

- The finite element model showed that most of the water was absorbed by the CT and cork zones, which represented most of the root system surface area. This is consistent with the idea that the white zone would mainly absorb ions while the CT and cork would principally absorb water. Ion absorption in the zones needs to be clarified.

- The role of the mycorrhizae in water uptake was only estimated. The hydraulic properties of mycorrhizae need to be measured and their contribution to total water uptake needs to be verified.

- In the present research, the conductivity was measured during the first year of seedling growth. Large ontogenetic changes may occur in older trees resulting in different hydraulic properties. Further work should be done on older trees in the field.

- The finding that the cork zone is the major zone of water uptake is a radical departure from the general notion that younger CT and white zone have anatomies better suited to water uptake. This finding should be verified by other independent techniques.

REFERENCES

Addoms, R.M. 1946. Entrance of water into suberized roots of trees. Plant Physiol. 21: 109-111.

Alm, D.M., J. Cavalier and P.S. Nobel 1992. A finite element model of radial and axial conductivities for individual roots: developments and validation for two deserts succulents. Ann. Bot. 69 : 87-92.

Ashford, AE, W.G. Allaway, C.A. Peterson and J.W.G. Cairney 1989. Nutrient transfer and the fungus-root interface. Aust. J. Plant Physiol. 16: 85-97.

Bailey, I.W. 1953. Evolution of the tracheary tissue of land plants. Am. J. Bot. 40: 4-8.

Becker, P., S. Patino and M.T. Tyree 1999. Vulnerability to drought-induced embolism of Bornean heath and dipterocarp forest trees. Tree Physiol. 18: 583-588.

Behrmann, P., W. Heyser 1992. Apoplastic transport through the fungal sheath of *Pinus sylvestris suillus-Bovinus* ectomycorrhizae. Botanica Acta, 105 (6): 427-434.

Brouwer, R. 1954. The regulating influence of transpiration and suction tension on the water and salt uptake by the roots of intact Vicia faba plants. Acta Bot. Neerl. 3: 264-312.

Carlquist, S. 1975. Ecological Strategies of Xylem Evolution. University of California Press, Berkeley.

Chauhan, S.K. and V.K. Mishra 1996. Effect of undercutting on the biomass of *Ulmus villosa* seedlings. Indian J. For. 19 (3): 283-284.

Chung, H.H. and P.J. Kramer 1975. Absorption of water and 32P through suberized and unsuberized roots of loblolly pine. Can. J. For. Res. 5: 229-235.

Clarkson, D.T., J. Sanderson and R.S. Russell 1968. Ion uptake and root age. Science 220 : 805-806.

Crider, F.J. 1933. Selective absorption of ions not confined to young roots. Science 78: 169.

Cruz, R.T., W.R. Jordan and M.C. Drew 1992. Structural changes and associated reduction of hydraulic conductance in roots of *Sorghum bicolor* L. following exposure to water deficit. Plant Physiol. 99 : 203-212.

Dougherty, P.M., D. Whitebread and J.M. Vose 1994. Environmental influences on the phenology of pine. Ecol. Bull. 43 : 64-75.

Dumbroff, E.B. and D.R. Peirson 1971. Probable sites for passive movement of ions across the endodermis. Can. J. Bot. 49:35-38.

Enstone, D.E., C.A. Peterson and S.W. Hallgren 2001. Anatomy of seedling tap roots of Loblolly pine (*Pinus tadea* L.). Trees 15 : 98-111.

Esau, K. 1977. Plant anatomy. Second edition. John Wiley & Sons, Inc., New York.

Finlay, R.D., H. Ek, G. Odham and B. Soderstrom 1988. Mycelial uptake, translocation and assimilation of nitrogen from 15N labelled ammonium by *Pinus sylvestris* plants infected with four different ectomycorrhizal fungi. New Phytol. 110: 59 66.

Frensch, J. and E. Steudle 1989. Axial and radial hydraulic resistance to roots of maize (*Zea mays* L.). Plant Physiol. 91: 719-726.

Frensch, J., T. Hsiao and E. Steudle 1996. Water and solute transport along developing maize roots. Planta 198: 348-355.

Gibson, A.C., H.W. Calkin and P.S. Nobel 1984. Xylem anatomy, water flow and hydraulic conductance in the fern *Cyrtomium falcatum*. Am. J. Bot. 71: 564-574.

Giordano, R., A. Salleo, S. Salleo and F. Wanderling 1978. Flow in xylem vessels and Poiseuille's law. Can. J. Bot. 56: 333-338.

Haussling, M., C.A. Jorns, G. Lehmbecker, C. Hecht-Buchholz and H. Marschner 1988. Ion and water uptake in relation to root development in Norway spruce (*Picea abies* (L.) Karst). Plant Physiol. 133: 486-491.

Head, G.C. 1967. Effects of seasonal changes in shoot growth on the amount of unsuberized root on apple and plum trees. J. Hort. Sci. 42: 169-180.

Henzler, T., R.N. Waterhouse, A.J. Smyth, D.T. Cooke, A.R. Schäffner, E. Steudle and D.T. Clarkson 1999. Diurnal variations in hydraulic conductivity and root pressure can be correlated with the expression of putative aquaporins in the roots of *Lotus japonicus*. Planta 210: 50-60.

Herkellrath, W.N., E.E. Miller and W.R. Gardner 1977. Water uptake by plants: II. The root contact model. Soil Sci. Soc. Am. J. 41: 1039-1043.

Karas, I. and M.E. McCully 1973. Further studies of the histology of lateral root development in *Zea mays*. Protoplasma 77: 243-269.

Kramer, P.J. 1983. Water relations of plants. Academic Press, Orlando. 489p.

Kramer, P.J. andJ.S. Boyer 1995. Water relations of plants and soil. Academic Press, New York. 495p.

Kramer, P.J. and H.C. Bullock 1966. Seasonal variations in the proportions of suberized and unsuberized roots of trees in relation to the absorption of water. Am. J. Bot. 53: 200-204.

Kumar, P. 2003. Anatomical characteristics of roots of loblolly pine seedlings. Ph.D. thesis, Department of Forestry, Oklahoma State University.

Landsberg, J.J. and N.D. Fowkes 1978. Water movement trough plant roots. Ann. Bot. 42: 493-508.

Livonen, S., R. Rikala and E. Vapaavuori 2001. Seasonal root growth of Scots pine seedlings in relation to shoot phenology, carbohydrate status and nutrient supply. Can. J. For. Res. 31: 1569-1578.

Luxová, M. 1990. Effect of lateral root formation on the vascular pattern of barley roots. Botanica Acta 103: 305-310.

MacFall, J.S., G.A. Jonnson and P.J. Kramer 1990. Observation of a water depletion region surrounding Loblolly pine roots by magnetic resonance imaging. Proc. Natl Acad. Sci. USA 87: 1203-1207.

MacFall, J.S., G.A. Jonnson and P.J. Kramer 1991. Comparative water uptake by roots of different ages in seedlings of Loblolly pine (*Pinus taeda* L.). New Phytol. 119: 551-560.

McCrady, R.L. and N.B. Comerford 1998. Morphological and anatomy relationships of loblolly pine fine roots. Trees, 12: 431-437.

McCully, M. E. and M.J. Canny 1988. Pathways and processes of water and nutrient movement in roots. Plant Soil, 111: 159-170.

McKenzie, B.E., C.A. Peterson 1994a. Root browning in *Pinus Banksiana* Lamb. and *Eucalyptus pilularis* Sm. 1. Anatomy and permeability of the White and Tannin Zones. Botanica Acta 108: 127-137.

McKenzie, B.E., C.A. Peterson 1994b. Root browning in *Pinus Banksiana* Lamb. and *Eucalyptus pilularis* Sm. 2. Anatomy and permeability of the Cork Zone. Botanica Acta 108: 138-143.

Melchior, W. and E. Steudle 1993. Water transport in Onion (*Allium cepa* L.) roots. Changes of axial and radial conductivities during root development. Plant Physiol. 101: 1305-1315.

Melin, E., H. Nilsson and E. Hacskaylo 1958. Translocation of cations to seedlings of *Pinus Virginia* through mycorrhizal mycelium. Bot. Gaz. 119: 243-246.

Mesonet. The Oklahoma Climatological Survey (http://www.ocs.ou.edu)

Muhsin, T.M. and J.J. Zwiazek 2002. Ectomycorrhizas increase apoplastic water transport and root hydraulic conductivity in *Ulmus Americana* seedlings. New Phytol. 153: 153-158.

Münch, E. 1943. Durchlässigkeit der Siebröhren für Druckströmungen. Flora 136:223-262.

Nightingale, G.T. 1935. Effects of temperature on growth, anatomy, and metabolism of apple and peach roots. Bot. Gaz. 96: 581-639.

Nobel, P.S. 1983. Biophysical plant physiology and ecology. W.H. Freeman, San Francisco.

Nobel, P.S. 1991. Physicochemical and environmental plant physiology. Academic Press, San Diego.

Nobel, P.S. and M. Cui 1992. Prediction and measurement of gap water vapor conductance for roots located concentrically and eccentrically in air gaps. Plant Soil 145: 157-166.

North, G.B. and P.S. Nobel 1991a. Drought-induced changes in hydraulic conductivity and structure in roots of *Ferocactus acanthodes* and *Opuntia ficus-indica*. New Phytol. 120: 9-19.

North, G.B. and P.S. Nobel 1991b. Changes in hydraulic conductivity and anatomy caused by drying and rewetting roots of *Agave desertii* (Agavaceae). Am. J. Bot. 78: 906-915.

North, G.B. and P.S. Nobel 1995a. Radial hydraulic conductivity of individual root tissues of *Opuntia ficus-indica* (L.) Miller as soil moisture varies. Ann. Bot. 77: 133-142.

North, G.B. and P.S. Nobel 1995b. Hydraulic conductivity of concentric root tissues of *Agave deserti* Engelm. Under wet and drying conditions. New Phytol. 130: 47-57.

Passioura, J.B. 1988. Water transport in and to roots. Annu. Rev. Plant Physiol. Plant Mol. Biol. 39: 245-265.

Peterson, C.A. and D.E. Enstone 1996. Function of passage cells in th endodermis and exodermis of roots. Physiol. Planta. 97: 592-598.

Peterson, C.A. and B.E.M. Lefcourt 1990. Development of endodermal casparian band and xylem in lateral roots of broad bean. Can. J. Bot. 68: 2729-2735.

Peterson, C.A. and G.J. Moon 1993. Effect of lateral root outgrowrh on the structure and permeability of onion root exodermis. Botanica Acta 106: 411-418.

Peterson, C.A. and E. Steudle 1993. Lateral hydraulic conductivity of early metaxylem vessels in *Zea mays* L. roots. Planta 189: 288-297.

Peterson, C.A., M.E. Emanuel and G.B. Humphreyd 1981. Pathways of movement of apoplastic fluorescent dye tracers through the endodermis at the site of secondary root formation in corn (*Zea mays*) and broad bean (*Vicia faba*). Can. J. Bot. 59: 618-625.

Peterson, C.A., D.E. Enstone and J.F. Taylor 1999. Pine root structure and its potential significance for root function. Plant Soil 217: 205-213.

Riedl, H. 1937. Bau und Leistungen des Wurzelholzes. Jb. Wiss. Bot. 85: 1-72.

Rosene, H.F. 1937. Distribution of the velocities of absorption of water in the onion root. Plant Physiol. 12: 1-19.

Safir, G.R., J.S. Boyer and J.W. Gerdemann 1972a. Mycorrhizal enhancement of water transport in soybean. Science, 172: 581-583.

Safir, G.R., J.S. Boyer and J.W. Gerdemann 1972b. Nutrient status and mycorrhizal enhancement of water transport in soybean. Plant Physiol. 49: 700-703

Sanderson, J. 1983. Water uptake by different region of the barley root. Pathways of radial flow in relation to the development of the endodermis. J. Exp. Bot. 34 (140): 240-253.

Sands, R. and C. Theodorou 1978. Water uptake by mycorrhizal roots of radiate pine seedlings. Aust. J. Plant Physiol. 5: 301-309.

Sands, R., E.L. Fiscus and C.P.P. Reid 1982. Hydraulic properties of pine and bean roots with varying degrees of suberization, vascular differentiation and mycorrhizal infection. Aust. J. Plant Physiol. 9: 559-569.

SAS 1999. The SAS for Windows, Release 8.0. SAS Institute Inc., Cary, NC 27513.

Sperry, J.S. 1986. Relationship of xylem embolism to xylem pressure potential, stomatal closure and shoot morphology in the palm *Rhapis excelsa*. Plant Physiol. 80: 110-116.

Sperry, J.S., F.R. Adler, G.S. Campbell and J.P. Comstock 1998. Limitation of plant water use by rhizosphere and xylem conductance : results from a model. Plant Cell Environ. 21: 347-359.

Steudle, E. 1994a. The regulaton of plant water at the cell, tissue and organ level : role of active processes and of compartimentation. Flux Control in Biological Systems. From enzymes to populations and ecosystems. Ed : E. D. Schulze, Academic Press, Inc, San Diego, 237-299.

Steudle, E. 1994b. Water transport across roots. Plant Soil 67: 79-90.

Steudle, E. and J. Frensch 1989. Osmotic response of maize roots. Water and solute relations. Planta 177: 281-295.

Steudle, E. and W.D. Jeschke 1983. Water transport in barley roots. Measurements of root pressure and hydraulic conductivity of roots in parallel with turgor and hydraulic conductivity of root cells. Planta 158: 237-248.

Steudle, E. and C.A. Peterson 1997. How does water get through roots? J. Exp. Bot. 49: 775-788.

Steudle, E., R. Oren and E.D. Schulze 1987. Water transport in maize roots. Measurement of hydraulic conductivity, solute prmeability and of reflection coefficient of excised roots using the root pressure probe. Plant Physiol. 84: 1220-1232.

Sword, M.A. 1998. Seasonal development of loblolly pine lateral roots in response to stand density and fertilization. Plant Soil 200: 21-25.

Taylor, J.H., C.A. Peterson 2000. Morphometric analysis of *Pinus banksiana* Lamb. root anatomy during a 3-month field study. Trees 14(5): 239-247.

Tyree, M.T. and F.W. Ewers 1991. The hydraulic architecture of trees and other woody plants. New Phytol. 119: 345-360.

Tyree, M.T. and M.H. Zimmermann 1971. Theory and practice of measuring coefficients and sap flow in the xylem of red maple stems (*Acer rubrum*). J. Exp. Bot. 22: 1-18.

Van Rees, J.C. and N.B. Comerford 1990. The role of woody roots of slash pine seedlings in water and potassium absorption. Can. J. For. Res. 20: 1183-1191.

Varney, G.T. and M.J. Canny 1993. Rates of water uptake into the mature root system of maize plants. New Phytol. 123:775-789.

Wang, X.L., M.E. McCully and M.J. Canny 1994. The branch roots of Zea. IV. The maturation and openness of xylem conduits in first-order branches of soil-grown roots. New Phytol. 126:21-29.

Weatherley, P.J. 1982. Uptake and flow in roots. *In*: Physiological Plant Ecology, II: Water relation and carbon asssimilation, 12B : 79-109.

Wilcox, H.G. 1955. Primary organization of active and dormant roots of noble fir, *Abies procera*. Am. J. Bot. 41: 812-821.

Wilcox, H.G. 1968. Morphological studies of the root of red pine, *pinus resinosa*. I. Growth characteristics and patterns of branching. Am. J. Bot. 55(2): 247-254.

Wilson, S.A. and D. Atkinson 1978. Water and mineral uptake by fruit tree roots. *In*: Symposium on root physiology and symbiosis, Sept. 11-15, Nancy. Edited by A. Riedacker and J. Gagnaire-Michard, Proceedings IUFRO, Nancy, France. pp. 372-382.

Woodhouse, R.M. and P.S. Nobel 1982. Stipe anatomy, water potentials, and xylem conductances in seven species of fern. Can. J. Bot. 69: 135-140.

Zimmermann, M.H. 1971. Transport in the xylem. *In*: Trees: Structure and function. Eds M.H.Zimmermann and C.L. Brown. Springer-Verlag, New York. pp. 169-200.

Zimmerman, M.H. 1983. Xylem Structure and the Ascent of Sap. Edited by Timell T.E., Springer Series in Wood Science. Springer, Berlin.

Zimmermann, M.H. and C.L. Brown 1971. Transport in the xylem. *In*: Trees. Structure and Function. Springer Verlag, New York. pp. 169-220.

VITA

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Title of Study: HYDRAULIC PROPERTIES OF ROOTS OF LOBLOLLY PINE SEEDLINGS (*PINUS TAEDA* L.)

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Major Field: Plant Science

Scope and Method of Study: Loblolly pine root system is composed of a vertical taproot (TAPR), horizontal first-order lateral roots (FOLRs) and second-order lateral roots (SOLRs). Each root is composed of anatomically different zones (white, condensed tannin (CT) and cork). Changes occurring in the anatomy and morphology of these roots have a decisive role in the movement of water and ions. The objective was to quantify limitations to water uptake of *P. taeda* root systems, by investigating (1) the changes in the root system morphological parameters during its first year of growth, (2) the seasonal changes in the tracheid traits and the resistance of each tracheid component to the total tracheid resistance, and (3) the changes in hydraulic conductivity during root growth and development. Seedling root systems were harvested monthly in the nursery using PVC pipes. Based on zones and root type, root system morphology was measured, tracheids were studied under bright-field microscope and SEM and hydraulic conductivity was quantified.

Findings and Conclusions: The white zone was not a major component of the root system length or surface area. Its role may be more essential for ion than water uptake. The CT zone was more important, implying a more significant role in water uptake. Lateral roots represented most of the length and surface area of the root system. Tracheids were longer and wider in the CT and cork zones and their number also increased from the white to the cork zone to accommodate increasing water flow. The bordered pit dimensions remained constant between zones and throughout the growing season. Pit resistance represented 82 to 97% of the tracheid resistance. TAPR tracheid resistance was constant over the growing season despite the increase in diameter. Conductivity varied according the zone anatomical characteristics. Tracheid conductivity was the limiting factor to the axial conductivity. Predicted root system conductivity decreased throughout the season. Most of the water was absorbed by the CT and cork zones.

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