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Pits Role in Embolism Repair of *Populus tomentiglandulosa* T. Lee[1]

Su Kyoung Chun[2†] and Sheikh Ali Ahmed[2]

ABSTRACT

This report explains the intervessel pit dimension of *Populus tomentiglandulosa* and its role in embolism repair according to proposed mechanism by Zwieniecki and Holbrook, 2000. It was found that mean contact angle ( ) of water droplets on the inner surface of vessels was 56°. Openings into the bordered pits were typically elliptical. The angle of the bordered pit chamber (2α) was found 142.17°. From the capillary equation $Pmax = Gcos\ (\quad +\alpha)$, it was found that mathematically the maximum pressure 0.08MPa created by pits, can be employed to force the air within the embolized vessel into solution.

Key words: Embolism, Pit dimension, Liquid flow, Contact angle, Pit chamber.

INTRODUCTION

Different techniques and methods have been developed so far to obtain quantitative and qualitative information about liquid penetration (Rudman 1965; Stone 1956; Stamm 1953). Besides, the amount of liquid penetration is not the same for sapwood and heartwood because the solution uptake by cells is affected by wettablility of the surface of the cell lumen (Iida et al., 2002). Factors of prime consideration governing the flow are the amount of pressure, fluid viscosity, solvent contact angle, wood pore radius and wood capillary length (Usta and Guray 2001). Transport of water through vessels may disrupted by the breakage of water columns under high levels of tension or freezing temperatures (Tyree and Sperry 1989). Because the gas-filled vessels cannot transmit tensions, embolized vessels are permanently lost water conduction capability unless a mechanism exists to reconnect the water column (Holbrook et al. 2001). The idea that embolized vessels can regain their functional state is not new, but it has generally been thought to be limited to situations in which the entire vascular system could be pressurized due to active solute transport by the roots (Cochard et al., 1994; Fisher et al., 1997). Recent studies suggest that cavitated vessels can be repaired even when the water in neighboring conduits is under tension (Salleo et al. 1996; McCully et al. 1998; Zwieniecki and Holbrook 1998). Embolism removal is thought to require positive pressures to force the gas into solution (Holbrook and Zwieniecki 1999).

It has been long recognized that the transport of water under negative pressures in plant potentially vulnerable to cavitation which causes an abrupt phase change from liquid to vapour

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1) This Study was supported by Korea Forest Service.

2) Department of Wood Science and Technology, College of Forest Sciences, Kangwon National University, Chunchon 200-701, Republic of Korea.

† Corresponding author: Su Kyoung Chun (Email: chun@kangwon.ac.kr).

(Sperry et al. 1994). The idea that embolized vessels could be re-filled without pressurization of the entire xylem which suggests that xylem hydraulic conductivity is more dynamic and embolized vessels are refilled while adjacent vessels remain under tension (Zwieniecki and Holbrook 2000).

The major difficulty with the idea of embolized conduits can be refilled despite the existence of tension in the vessel is the absence of a comprehensive mechanism to explain how this could occur. The description of repairing mechanism must explain: 1) how water is forced into a gas-filled conduit against an apparent gradient in chemical potential; 2) how the positive pressures needed for gas dissolution despite the existence of tension in adjacent conduits; and, 3) how a refilled vessel makes a stable transition from positive to negative pressures (Holbrook and Zwieniecki 1999).

This paper explains about the calculation of the maximum pressure that contains within a refilling conduit according to proposed mechanism by Zwieniecki and Holbrook, 2000. This experiment was conducted to understand safranine flow in vessel and wood fiber of *P. tomentiglandulosa*. As safranine is a colored solution, it is easy to observe the flow depth. Although flow depth of liquid is depend upon the surface tension of liquid to be permeated (Chun and Ahmed 2006), this research work was conducted to observe the vessel and fiber role in the non steady state of safranine flow.

MATERIALS AND METHODS

Contact angle measurement

Contact angle was measured on freshly collected *Populus tomentiglandulosa* T. Lee. A thick (approximately 0.5 cm) cross section was viewed by camscope (*i*-camscope SV32). Water droplet was placed on the inner surface of vessel using a fine (a tip diameter of 10 μm) glass microcapillary. Droplets angle on the in inner surface of vessel were measured by the advancing of the captive drop method when steady state condition. In this stage, droplet was neither expanding nor receding. Contact angle was determined by measuring the angle between the tangent to the air-water interface and vessel wall by *i*-solution software.

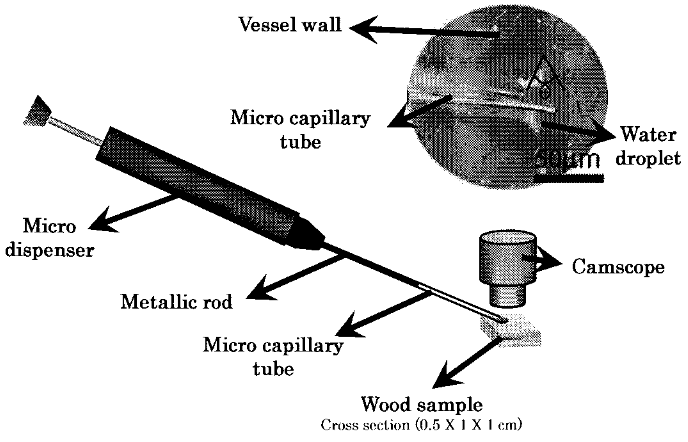

Fig.1. Diagram of experimental setup for measuring the contact angle of water droplet inside the vessel wall.

Intervessel pit dimension measurement

Pit aperture diameter and pit membrane were measured by FE-SEM in tangential sections. Tangential surfaces were finished with a microtome and the clean-cut surface was (3mm x 2mm) cut with 1mm thickness. Samples were mounted on FE-SEM specimen stubs using an electrically conducting paste. Samples were dried under vacuum condition and coated with platinum and palladium by using an ion sputter apparatus. At different resolutions and magnifications, samples were examined at 15kv in a Field Emission Scanning Electron Microscope (FE-SEM).

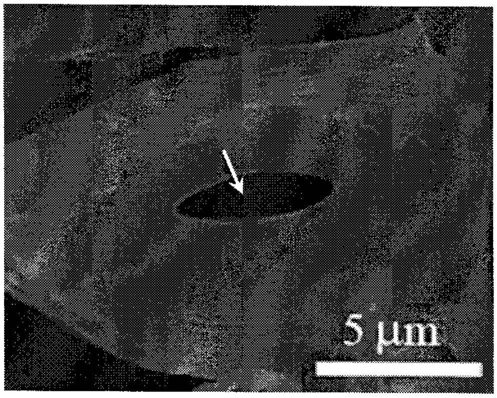

Fig.2. Intervessel bordered pit. Arrow showing an ellipse shape of pit aperture.

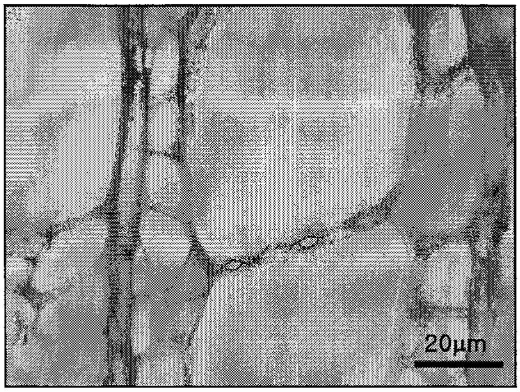

Fig.3. Measurement of pit chamber cell wall angle.

Permanent slides were prepared using sliding microtome and were observed under optical microscope to find out the angles of bordered pit chambers wall. The Angle of the flared opening into the pit chamber was determined by drawing the tangent to the wall surface on both sides of the pit channel.

RESULTS AND DISCUSSION

The primary root of water movement in hardwood is xylem which becomes thick at maturity, lignified secondary cell walls and lack all cytoplasmic content (Esau 1977; Zimmermann 1983). It forms a capillar structure. To understand the capillary structure, the anatomical features of P. tomentiglandulosa is described else where (Lu et al. 2006). Based on capillary phenomenon (Chun and Ahmed 2006), liquid can penetrate in wood. But in living tree, generating positive pressures within an embolized conduit, it must be hydraulically compartmentalized to allow generation of local positive pressures. Thus, pits are important which are in contact with adjacent conduits. The thick and heavily lignified vessel walls contain numerous pores or pits that enable living cells to access the fluid, as well as pits that interconnect adjacent xylem conduits (intervessel pits). At the center of this chamber there is pit membrane. The geometry of these intervessel pits provides a structural view to understand the hydraulic compartmentation necessary for refilling without subsequently impeding water flow once the vessel has been refilled (Zwieniecki and Holbrook 2000). The ellipse opening into the pit chamber could allow the pit for the formation of a convex meniscus. The actual curvature of this meniscus depends on the surface energy between water and the interior surface of the vessel, as well as the geometry of the pit chamber. The very small pores in the pit membrane are thought to prevent the spread of air embolisms between vessels (Zimmermann 1983; Tyree and Sperry 1989). An embolized vessel requires positive pressure to force the gas into the surrounding liquid phase (Pickard 1981; Yang and Tyree 1992). To exert pressure, the perimeter of the vessel must be effective and be sealed. This pressure will dissolve the trapped gas in liquid and gas trapped in bordered pits.

Mean contact angle (θ) of water droplets on the inner surface of vessels was 56° (SD= 4.554, range 51.30-60.63°). Openings into the bordered pits were typically elliptical and major axis 3.43 μm (SD= 0.729, range 2.13-4.97 μm) and the minor axis 1.74 μm (SD= 0.275, range 1.22-2.4 μm). Pit membranes were found typically circular in shape and average diameter was 8.34 μm (SD= 1.26, range 6.43-11.76 μm). The angle of the bordered pit chamber (2α) was found 142.17° (SD= 6.278, range 130.07-1149.23° μm). One-half angle across the flared opening of the pit chamber (α) ranged from 65° to 75°. Specifically, as water enters into the straight- walled channel of the bordered pit, the gas-water interface will be concave (as $\theta < 90°$). In this condition both the water hydrostatic pressure and the surface tension force act in the same direction which pulls water into the border pit. For the convex shape, the force due to surface tension will oppose the hydrostatic pressure exerted by the water in the lumen. The maximum pressure difference ($\Delta Pmax$) between gas in the refilling vessel and the gas trapped in the border pit that can be counterbalanced by a meniscus within the bordered pit can be calculated from the capillary equation (Nobel 1983; Denny 1993):

$$\Delta Pmax = \gamma G\cos(\theta + \alpha)$$

Where γ is the surface tension of water (0.0728 Nm-1 at 20°C) and G is the ratio of the perimeter to cross-sectional area of the pit channel opening (per meter). Measurements of both contact angle and pit chamber geometry of P. tomentiglandulosa, the estimated positive pressures that can be balanced by the forces arising from surface tension of this curved interface to be 0.08MPa. This value sets the maximum pressure that can be employed to force the air within the embolized vessel into solution. As xylem conduits are interconnected in many places (Zimmermann 1983), the hydraulic contact should be established at all of the pits simultaneously to prevent the vessel from re-cavitating. Thus, refilling will be stable only if there is a mechanism which can synchronize the reconnection through pits. For such synchronization to occur, a mechanism must exist to delay or somehow coordinate the pressure transmission through pit membranes.

CONCLUSIONS

Because gas filled vessels cannot transmit tensions, embolized vessels are permanently lost from water transport system unless a mechanism exists to reconnect the water column. This study was conducted followed by the model given by Zwieniecki and Holbrook, 2000. According to the result, cavitated vessel can be repaired even when the water in neighboring conduits under tension. Estimated maximum pressure difference that can exist between gas in the refilling vessel and gas trapped in the bordered pit chamber without the expansion of the water in to the bordered pit chamber was 0.08MPa which can be stabilized by the curvature of interface formed in bordered pit. While impregnating of solution into the woodchip, pressure application can create force the cavitated vessel to dissolve the trapped air in solution. Ultimately, it will increase the solution reservoir area for the impregnation of solution into the cell lumen.

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