Stem water transport of *Lithocarpus edulis*, an evergreen oak with radial-porous wood

**SHIGEKI HIROSE,** **ATSUSHI KUME,** **SHINICHI TAKEUCHI,** **YASUHIRO UTSUMI,** **KOICHI OTSUKI** and **SHIGERU OGAWA**

1 Department of Forest and Forest Products Sciences, Faculty of Agriculture, Kyushu University, Fukuoka 811-2415, Japan
2 Department of Environmental Biology and Chemistry, Faculty of Science, Toyama University, Toyama 930-8555, Japan
3 Corresponding author (akume@attglobal.net)
4 Department of Regional Environment Engineering, Faculty of Engineering, Kyushu-kyouritsu University, Kita-kyushu 807-8585, Japan

Received December 30, 2003; accepted June 30, 2004; published online December 1, 2004

**Summary** The stem water conducting system of an evergreen broad-leaved oak, *Lithocarpus edulis* (Mak.) Nakai, was investigated. Evergreen broad-leaved oaks (*Lithocarpus*, *Castanopsis*, *Cyclobalanopsis*, *Quercus*) belonging to the Quercoideae are a major component of Asian monsoon forests, and are characterized by the possession of radial-porous wood. A characteristic of radial-porous wood is the development of aggregate rays between radially oriented files of vessels. We measured the distribution of vessel lumen diameters in a stem cross section and calculated the theoretical water conductivity of the wood. The radial profile of the heat pulse velocity (HPV) was measured for an intact whole tree under field conditions and compared with the theoretical distribution of water conductivity. Soft X-ray photographs of frozen stem sections indicated that most of the vessel lumina were filled with water, including those of vessels more than 20 years old. Even when vessels were relatively wide (lumen diameters > 100 µm), cavitation was negligible. The rate of water uptake from the cut stem base correlated closely with HPV ($r = 0.96$), and HPV closely reflected the mean volume flow per stem sectional area (SFVs) around the sensor probes. However, the ray tissue sharply inhibited heat transfer, and the positioning of the probes strongly affected the absolute value of HPV. It was also found that HPVs more closely reflected the mean sap flow velocity in the vessels than did SFVs.

**Keywords:** cavitation, heat pulse, sap flow, tree cutting.

**Introduction**

The various *Lithocarpus* species across monsoon Asia are important components of evergreen broad-leaved forests (Aiba and Kitayama 1999, Tang and Ohsawa 2002, Cannon and Manos 2003). Evergreen broad-leaved oaks (*Lithocarpus*, *Castanopsis*, *Cyclobalanopsis*, *Quercus*) belonging to Quercoideae are a major component of most Asian monsoon forests (Hotta 1974). These species have two types of vessel arrangement. Most deciduous members of the Quercoideae have ring-porous wood and their vessel diameter differs conspicuously between early- and latewood; i.e., vessels of different cross-sectional area are distributed concentrically. However, most evergreen species of Quercoideae have radial-porous wood whose vessels appear in stem cross sections in radial files (see Wheeler et al. 1989). Between these radially aligned vessels, aggregate rays develop. The radial files of vessels have comparatively uniform diameters, regardless of their distance from the stem center.

To evaluate the function of stems in water transport, many studies have been conducted in different parts of the world on coniferous trees, ring-porous trees, diffuse-porous trees and lianas (Tyree and Zimmermann 2002). However, the relationship between the xylem structure and water transport in the radial-porous wood of evergreen oaks has not been evaluated.

Since the stem of a tree transports water continuously from the roots to the canopy, the stem provides a site for estimating transpiration (Swanson 1994, Smith and Allen 1996). It is especially important to estimate transpiration from the forest canopy (e.g., Granier 1987, Granier and Bréda 1996, Schäfer et al. 2002). Various methods to estimate sap flux have been proposed, including the heat pulse method (Huber and Schmidt 1937, Closs 1958, Swanson and Whitfield 1981), the thermal heat balance method (Čermák et al. 1973, Sakuratani 1981), and the heat dissipation method (Granier 1985, Granier 1987, Granier et al. 1994). The arrangement of vessels in sapwood, i.e., the distribution of vessel lumen diameters and the degree to which the vessels aggregate, considerably affects the water conductivity of a stem (Tyree and Zimmermann 2002, James et al. 2003). Several papers have pointed out the importance of radial variation in sap flow in various tree species (Hatton et al. 1990, Jiménez et al. 2000, Nadezhidina et al. 2002, Ford et al. 2004); therefore, it is still difficult to estimate sap flux of a stem accurately without calibrating the effects of physical properties of heat transfer in sapwood (Smith and
Allen 1996, Čermák and Nadezhdina 1998, Clearwater et al. 1999). To use such methods for estimating sap flux of a stem properly, it is important to evaluate the effects of vessel characteristics on the sap flow distribution.

Evergreen broad-leaved oaks are widely distributed from Southeast Asia to Japan. In southwestern Japan, most secondary forests are covered with evergreen oaks with radial-porous wood. Recently, the effectiveness of these evergreen oak forests in recharging water resources has been widely disputed in Japan. It is therefore important to understand the relationship between forest hydrology and the characteristics of water conductivity of the stem in radial-porous wood, and to develop an appropriate technique to estimate sap flow velocity so that the total water use of a tree can be estimated.

The objective of this study was to investigate the relationships between the anatomical properties of sapwood and the distribution of sap flow velocity in an evergreen broad-leaved oak, *Lithocarpus edulis* (Mak.) Nakai (syn. *Pasania edulis* Makino), having typical radial-porous wood. We measured the distribution of vessel lumen diameters in a cross section of the stem precisely, and then calculated the wood’s theoretical water conductivity. The distribution of water in the vessels was verified by soft X-ray photography of frozen stem sections. The radial profile of heat pulse velocity (HPV) was measured for an intact whole tree under field conditions and was compared with the distribution of the wood’s theoretical specific water conductivity.

**Materials and methods**

**Species**

*Lithocarpus edulis* is an evergreen broad-leaved tree that is widely planted in the Kyushu area of Japan. New leaves expand in May and the mean individual leaf area is about 20 cm$^2$. The mean longevity of the leaves is about 1.5 years.

**Study site**

The study was conducted on a stand of 22-year-old, 11-m-tall *L. edulis* at the Research Institute of Kyushu University Forest (33°38′N, 130°31′E, elevation 50 m). In the forest stand, a scaffold was constructed to access the tree crowns. The annual mean temperature of this site is about 16 °C. The monthly mean of the daily maximum temperature in August is about 34 °C, and the monthly mean of the daily minimum temperature in February is about –3.5 °C. Annual total precipitation is about 1800 mm (120 mm in August).

**Radial profile of heat pulse velocity**

Heat pulse velocity was measured with three sets of HPV sensors (HP-3, Hayashi Denko, Tokyo). The HPV sensors consisted of two thermistor probes and one heater probe (stainless steel, 2 mm in diameter and 60 mm in length). Data were collected with a data logger (CR10X, Campbell Scientific, Logan, UT). The thermistor probes were installed 6 mm below (upstream) and 9 mm above (downstream) the heater probe. Heat pulse velocity was estimated as (Closs 1958, Swanson 1994):

$$\text{HPV} = \frac{x_1 + x_2}{2t_0}$$

where $x_1$ is the distance between the upstream sensor and the heater probe, $x_2$ is the distance between the downstream sensor and the heater probe and $t_0$ is the time when the difference in temperature between the sensors returns to 0 following the heat pulse.

The HPV probe sets were implanted in the stem in 2-mm-diameter holes at three radial positions (Figure 1), 0.8 m above ground on September 4, 2000. A drill guide ensured that the probes were spaced at the correct intervals and in vertical alignment. The data logger was programmed to provide a 45 °C, 2-s heat pulse every 15 min. The probes of the two HPV sets were fixed to a depth of 10 mm (F1 and F2; Figure 1), and the depth of the other set was changed from 10 to 60 mm (S1; 15, 25, 35, 40, 45, 50, 55, 60 and 65 mm from the center of the stem; Figures 1 and 2). At each measured depth, HPV was measured four times in an hour, and then the probes were inserted at the next depth. In order to compare HPV among the different depths, we calculated the relative heat pulse velocity (RHPV):

![Figure 1. Upper image: cross-sectional diagram showing the position of sensor probes implanted in the stem. Two of the probe sets were fixed to a depth of 10 mm (F1 and F2) and the rest ranged in depth from 10 to 60 mm (S1). Lower image: magnified stem section around S1. The rectangle shows the wood section that was analyzed (see Figure 2). The scale is the radius of the stem.](image-url)
RHPV = \frac{HPV_S}{HPV_F} \tag{2}

where HPV_S is HPV at a certain depth and time; HPV_F is HPV at 1-cm depth (F_1), measured at the same time as HPV_S.

**Distribution of vessel lumen diameter**

To evaluate the effects of vessel characteristics on RHPV distribution, we collected a stem section adjacent to the location of heat pulse measurement (S_1; Figure 1). The excised wood section was embedded with Hotmelt (HB-40S-BK, Taiyo Electric, Hiroshima), a mixture of ethylene-vinyl acetate resin and hydrocarbon resin. The embedded wood surface was mirror-finished with a water-resistant sandpaper (roughness grade 400–600). The Hotmelt penetrated all vessel lumina, making them clearly visible (Figure 2). The images of the surface of the stem cross section were recorded with a digital camera (Coolpix950, Nikon, Tokyo) through a stereoscopic zoom microscope (SMZ800, Nikon). The number and diameter of vessel lumina recorded in the digital images were determined with the aid of image analysis software, Image J for Windows (Version 1.29, Wayne Rasband, National Institutes of Health, Bethesda, MD; http://rsb.info.nih.gov/ij/). In the analysis of lumen diameter, Image J calculated the lengths of major and minor axes of vessel lumina. We used the geometric means of the results as representative values.

**Tree-cutting experiment**

In order to evaluate the relationship between the water uptake of a whole tree and the heat pulse velocities of the stem, we conducted a tree-cutting experiment. On September 5, 2000, a crane truck and scaffold were placed near the test tree. The tree was roped to the top of the crane and then cut 0.1 m above ground at 0425 h. The lower end of the cut tree was put into a 0.6 m³ tank filled with water and recut under water with a handsaw. The tree was then raised by the crane and fixed to the scaffold. As the tree took up water, the supply was replenished every 15 min, and the amount of water added recorded. The top of the water tank was covered to prevent evaporation. The heat pulse velocity and water uptake of the tree were measured for 3 days. At 0730 h on the last day, the cut stem base was immersed in 0.1% acid fuchsin solution.

**Soft X-ray photography**

In October, the xylem sap was fixed by freezing the stems of an individual from the same stand. A watertight collar made with a plastic funnel was fitted to the sample stem and the collar filled with liquid nitrogen (LN2) before sunrise (Utsumi et al. 1996, 1998). The part of the stem within the collar froze in approximately 10 min. The frozen stem section was excised and placed in an LN2 dewar flask and stored in a cold room at –20 °C. When the sample had equilibrated to –20 °C, it was cut with a handsaw into 2-mm-thick transverse sections. These sections were transferred to an X-ray apparatus (Super Soft, Koizumi X-ray, Tokyo) and mounted over X-ray film (X-ray FR, Fuji Photo Film, Tokyo). The stem sections were irradiated at 20 kV and 5 mA for 120 s from a distance of 1.3 m, following Sano et al. (1995). Because water has a high X-ray absorbency, lumina filled with water appeared dark on the X-ray image. The images were enlarged to allow naked-eye examination of the distribution of water-filled vessels.

**Results and discussion**

**Water distribution in the stem**

In a soft X-ray photograph of a frozen stem transverse section (Figure 3), most of the vessel lumina appeared darker than the background tissue, suggesting that they were filled with water. Consistent with this conclusion, most of the lumina in all of the annual rings of stems immersed in acid fushin were
stained. Thus it appears that most of the vessels of *L. edulis* were filled with water and had, presumably, been transporting water for 20 years or more. We obtained similar results with other radial-porous tree species (*Quercus acuta* Thunb. and *Castanopsis cuspidata* Thunb.). However, our results contrast with many observations of deciduous ring-porous trees, in which the vessels have been observed to fill with tyloses within a few years (Čermák et al. 1992, Saitoh et al. 1992, 1993, Usumi et al. 1996).

**Vessel distribution**

The surface of the stem transverse section adjacent to the sensor probe (10 × 734 mm) (Figure 2) shows aggregate rays between the lines of radially oriented vessels. Such tissue heterogeneity was also observed in cross sections of small branches. Although annual rings were formed, the wood was fairly homogeneous from the center to the outer layer of the stem. It was difficult to distinguish between earlywood and latewood. The volumetric water content of the wood was 0.43 ± 0.02 (m³ m⁻³) and did not differ significantly between the inner and outer sapwood. In the distribution of vessel lumen diameters at 1-mm intervals, the median diameter near the pith was less than 60 µm and gradually increased toward the cambium, reaching a maximum value at about 25 mm from the pith (Figure 4). At the outer sapwood, both the deviation within each segment and the fluctuation among the segments were large, but the pattern of distribution of vessel lumen diameters within each segment was nearly normal. The median or mean lumen diameter was relatively large (about 100 µm), but smaller than the typical earlywood vessel of a deciduous ring-porous tree (200 to 300 µm). As previously noted by Gartner (1995), xylem elements declined in density as the cambial age and diameter of the stem increased (Figure 5A). However, the proportion of vessel lumen area gradually increased with stem diameter (Figure 5B).

The theoretical water conductivity of a vessel (mg m MPa⁻¹ s⁻¹, *K*ₙ) is known to obey Hagen-Poiseuille’s law (see Tyree and Zimmermann 2002):

\[
K_n = \frac{d^4 \pi \rho}{128 \eta_W}
\]

where *d* is the diameter of a single lumen (m), *ρ* is the density of water at 25 °C (kg m⁻³), and *η*₃₆₀ is the viscosity of water (MPa·s). The mean value of *K*ₙ (Figure 5C) at 1-mm stem diameter intervals was small at the inner sapwood because of the small lumen diameters (Figure 3).

We calculated the water conductivity of each segment, i.e., the specific conductivity of the wood (kg m⁻¹ MPa⁻¹ s⁻¹, *K*ₜₚ), as a sum of *K*ₙ (Figure 5D). In the distribution of *K*ₜₚ at 1-mm intervals, *K*ₜₚ near the pith was less than 5 kg m⁻¹ MPa⁻¹ s⁻¹ and gradually increased toward the cambium, as was the case with the distribution of vessel lumen diameters.

These results suggest that if the same negative pressure is applied over all of the stem cross section, the sap flow velocity of each vessel lumen will be proportional to *K*ₙ and lower at the stem center than in the outer portion of the stem because of the differences in lumen diameter. Nevertheless, the mean sap flow per stem sectional area will be proportional to the value of *K*ₜₚ. If the same negative pressure is applied over the entire stem cross section and if all the vessels are filled with water, it is reasonable to consider *K*ₙ an index of mean sap flow velocity in the vessels (SFVᵥ), and to consider *K*ₜₚ an index of the mean volume flow per stem sectional area (SFVₛ).

**Effects of vessel distribution on heat pulse velocity**

In the tree-cutting experiment, the mean sap flux (SF), i.e., the rate of water uptake, was highly correlated with HPV measured at F₁ (Figure 6, *r* = 0.96). This result indicates that HPV was closely related to stem water transport. However, the relationship is curvilinear with HPV becoming asymptotic as SF increases. A simple heat transfer model can explain this asymptotic relationship. It is thought that two factors determine HPV. One is SFVᵥ, which is affected by the diameter and concentration of vessels, and the other is the heat conductance and distribution of ray tissue. Therefore, HPV can be thought to represent the mean heat transport velocity from the heat source to the thermistor, and can be thought to depend on the heat transport velocity at ray tissue (HPVᵥ) and the heat transport velocity at vessels (HPVₛ). This relationship can be described as follows:

\[
HPV = \frac{HPV_v}{aHPV_v + bHPV_s}
\]

![Figure 3. Soft X-ray photograph of a frozen stem transverse section of *L. edulis*. The water-filled vessels appear darker than the background tissue. The dark lines are files of radially oriented water-filled vessels.](image)
where \( a \) is the constant representing the heat conductance of parenchyma and \( b \) is the constant representing the heat conductance of vessels. If SF increases, i.e., if the rate of water uptake increases, HPV\(_S\) increases linearly with the sap flux velocity but HPV, does not change. Under this assumption, HPV, can be treated as a constant, \( r \).

\[
\text{HPV} = \frac{r_{\text{HPV}_S}}{a_{\text{HPV}_S} + br} 
\]

This relationship is curvilinear with HPV becoming asymptotic as HPV\(_S\) increases. The value of HPV\(_S\) is proportional to SFD, so HPV has an asymptotic relationship with SF.

As shown in Figure 2, the lines of radially oriented vessels were distributed alternately with the aggregate rays in the stem of *L. edulis*. Because an aggregate ray is ineffective in conducting or storing water (Figure 3), the positioning of the sensor probes should greatly affect HPV. In fact, when HPV was measured at different positions but at the same stem depth (Figure 1), it was about twice as large at F\(_1\) than at F\(_2\) (Figure 7). This is because the probes at F\(_1\) were adjacent to the line of vessels, whereas those at F\(_2\) were embedded in the well-developed ray tissue. This result suggests that the ray tissue strongly inhibits heat transfer and affects the absolute value of HPV. However, HPV at F\(_1\) and F\(_2\) highly correlated \((r = 0.96)\) with the rate of water uptake. Therefore, HPV closely reflected the relative water transport velocity in the stem, regardless of the presence of ray tissue. In short, the absolute value of HPV was highly affected by the positioning of the probes, but the relative value of HPV was robust to the positioning of the probes.

The maximum SFV\(_V\) can be calculated based on the amount of water uptake and the ratio of lumen area per total wood area. That value, 3.6 m h\(^{-1}\), is within the range of the midday peak velocity with roughly 100-µm-diameter vessels as reported by Huber and Schmidt (1937). The maximum SFV\(_S\) was about 14.5 cm h\(^{-1}\), which corresponded well with the approximately 12.5 cm h\(^{-1}\) mean peak HPV at F\(_1\) and F\(_2\), in which the value at F\(_1\) was 16 cm h\(^{-1}\) and at F\(_2\) was 9 cm h\(^{-1}\). It is possible that HPV closely reflects the SFV\(_S\) surrounding the probes, but that the area represented was restricted.

**Representativeness of HPV**

For a stem with a heterogeneous vessel distribution, as in *L. edulis*, we should examine the degree to which temperature fluctuations, as measured by stainless steel probes, reflect water transport through the vessels. We calculated the mean conductivity around the probes from 1 to 15 mm in the radial direction, and compared the resulting values with those obtained for HPV. We applied the HPV values obtained at depths of 10, 15, 20, 30, 35, 40, 50 and 60 mm from the stem surface. The mean vessel conductivity correlated highly with HPV when the area surrounding the probes was larger than 5 mm. It is possible that the inserted stainless probes acted as a physical barrier that prevented sap flow when the area surrounding the probes was smaller than 5 mm. The correlation coefficient was greatest at 9 mm. These results show that the resolution of HPV in the radial direction was larger than 5 mm, and that HPV was affected by the characteristics of a considerable area of stem cross section, i.e., those of the surrounding 100 to 300 mm\(^2\) of stem.

In our preliminary experiments, we installed HPV sensors for about one year in three other stems of *L. edulis* growing in the same stand. The HPV measurements showed significant seasonal changes with canopy transpiration, but showed no significant decreases during the experimental period. This may be explained by the highly compartmentalized organization of radial-porous wood. The effect of wounding the stem by the installation of the probes may be quite restricted compared with the effect in coniferous wood.

**Radial distribution of vessels and RHPV**

In the measurement of HPV, heat is transferred with the flowing sap. When the vessels around the sensor probes are distribu-
uted homogeneously, the relationship between the heat pulse velocity and water transport, i.e., between HPV and SFV_S, showed a high correlation. However, when vessels around the sensor probes are distributed heterogeneously and SFV_S varies widely, as shown in this study, it is unclear whether the high correlation between HPV and SFV_S is consistent. Therefore, we compared the radial profiles of relative HPV (RHPV), K_n and K_S (Figure 8). The profile of RHPV corresponded more closely with that of K_n than with that of K_S. Although RHPV was significantly smaller than K_S at 25 mm, we found that the inhibition of HPV was caused by the overlap of ray tissue. Except for the data at 25 mm from the pith, the correlation coefficient between K_S and RHPV was 0.96. This suggests that RHPV better reflected K_n than K_S. Consequently, RHPV reflected SFV_V more closely than it did SFV_S. When the vessels around the sensor probes are distributed homogeneously, SFV_S is proportional to SFV_V and there should be no difference between them when HPV is estimated from water flow. However, the difference between SFV_S and SFV_V was as much as twofold for the radial-porous wood of L. edulis (Figure 8).

This difference may be dependent on the diameters of the sensor probes: if the probes have small diameters, the possible difference between SFV_S and SFV_V will increase. If the diameters are large, HPV will be closer to the mean and the difference between SFV_S and SFV_V will decrease, but the inhibition of water conduction will become obvious. Nevertheless, precise estimation of water flow with heat sensor probes appears...
wood has vessels that remain functional for more than 20 years, despite the large diameters of these vessels. The water conductivity of a stem was determined by the distribution of vessel diameters. The absolute value of HPV was greatly affected by the positioning of the probes, but the relative value of HPV was robust with respect to the positioning of the probes.

Acknowledgments

We thank the members of the Laboratory of Forest Ecosystem Management at Kyushu University for their assistance with the field experiments, especially Mr. M. Oono and Ms. K. Yasuoka. We also thank Dr. K. Arakawa, Dr. Y. Sano, Dr. R. Funada and Dr. S. Fujikawa of Hokkaido University, for the use of the Soft X-ray imaging system. This study was supported by a Grant-in-Aid for Scientific Research (Nos. 10306009 and 14360088) from the Ministry of Education, Science and Culture of Japan, and by the Joint Research Program of the Institute of Low Temperature Science, Hokkaido University (No. 02-3).

References


