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The Characteristics of Longitudinal Permeability and Hydraulic Resistance in Stem of *Acer mono*[1]*

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고로쇠나무 줄기의 通水性과 通水抵抗의 特性[1]*

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ABSTRACT

This study was carried out to investigate the characteristics of longitudinal permeability and hydraulic resistance, and to compare the longitudinal permeability (K_E) calculated by the Hagen-Poiseuille's law (Siau, 1971) and the longitudinal permeability (K) measured in sapwood of *Acer mono* stem.

The volume flow rate (Q) in a vessel was 0.80×10^{-4} cm^3/sec and the hydraulic resistance (R_S) to viscous flow through a vessel was, on average, 1.37×10^{10} dyn · sec · cm^{-3} · cm^{-2}. The average value of volume flow rate (Q_N) through the cross section of sapwood was 0.32 cm^3 · sec^{-1} · cm^{-2}, and the average resistance (R_{SN}) was 3.59×10^6 dyn · sec · cm^{-3} · cm^{-2}. The values of K decreased as the diameter of stem increases, which was attributable to variations in the number of vessel per unit area rather than in vessel diameter, and to different resistances in the conducting tissues of each part of the stem. The average value of K measured at breast height was 31% of average value of K_E. The K/K_E ratios were 100% in 4 to 6 year-old stems and more than 90% in 7 to 27 year-old stems. The K/K_E ratio decreased as the age of stems increases, and was not more than 20% in near-ground parts of stem.

Key words : longitudinal permeability, hydraulic resistance, relative conductivity

要　　約

이 연구는 고로쇠나무에 대하여 줄기 邊材部의 導管直徑 (㎛)과 單位面積當 導管數 (No./cm^2)를 實測하고 이를 기초로 Hagen-Poiseuille의 법칙에 따른 이론식 (Siau, 1971)을 적용하여 單一 導管 및 邊材 斷面積 당 通水速度와 通水抵抗의 特性을 밝히고, 줄기의 直徑別, 年齡別 通水性 (longitudinal permeability)의 實測値 (K)와 理論値 (K_E)를 구하여 그 관계를 밝히기 위한 것이다.

單一 導管에 대한 通水速度 (Q)는 平均 0.80×10^{-4} cm^3/sec이고, 通水抵抗 (R_S)은 1.37×10^{10} dyn · sec · cm^{-3} · cm^{-2}로 나타났으며, 邊材 斷面積에 대한 通水速度 (Q_N)는 平均 0.32 cm^3 · sec^{-1} · cm^{-2}이고, 通水抵抗 (R_{SN})은 平均 3.31×10^6 dyn · sec · cm^{-3} · cm^{-2}로 나타났다. 줄기 直徑別 通水性은 導管直徑보다 單位面積 당 導管數의 영향으로 줄기 직경이 커짐에 따라 감소하는 경향을 나타냈다. 胸高部에 있어서 通水性의 실측치 K는 理論値 K_E의 평균 31%로 나타났다. 그러나 4~6년생 어린 줄기의 K/K_E 비율은 100%이고, 27년생 이하에서는 90% 이상으로 나타났다. 줄기 각 부위의 K값은 하부로 갈수록 직경과 연령이 증가함에 따라 현저하게 감소하였으며, 특히 根元部의 K값은 K_E값의 20% 이하로 나타났다.

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INTRODUCTION

The water flow in trees occurs through the functional tissues such as vessels or tracheids of sapwood. The diameter and number of conducting elements have closely connected with the longitudinal permeability (hereafter permeability) and hydraulic resistance of sapwood, because of the important physical characteristics in determining the rate of water movement (Ewers, 1985; Ellmore and Ewers, 1985; Tyree and Ewers, 1991; Schultz and Matthews, 1993), and predicting the water status of trees (Jarvis, 1975; Ito *et al.*, 1995). The permeability can be affected by the sapwood area, age, and presence of embolism (Tyree and Sperry, 1989). Moreover, it is considerable ecophysiological relevance influencing sapwood area and leaf area development in stands (Whitehead *et al.*, 1984). However, it is necessary to facilitate the understanding of mechanism of water flow in trees as related to growth that grasp information pertaining to permeability and hydraulic resistance of sapwood in stem.

In this study, we measured the diameter of vessels (㎛) and the number of vessels per unit cross-sectional area (No./cm^2) of sapwood in *Acer mono*. Using these measured parameters, we calculated the volume flow rate, permeability and hydraulic resistance of sapwood by the Hagen-Poiseuille's law (Siau, 1971). And we discussed relationship between the measured permeability (K) and the calculated permeability (K_E) in terms of diameter and height of stem.

MATERIALS AND METHODS

1. Plant materials

The sample trees were 11 maple trees (*Acer mono* Max.) established naturally in Experiment Forest, College of Forest Science, Kangwon National University in Chunchon. The sample trees were selected to have similar diameters at breast height (1.3 m). Table 1 presents the characteristics of sample trees, including age, height, DBH, cross-sectional area, and flow area. Note that we cannot obtained the measurement of cross-sectional area and the measurement of flow area in No. 11 tree was impossible because of branching at breast height. The permeability and hydraulic resistance were measured at breast height for all sample trees. The permeability and hydraulic resistance of diameter and age in various portions of a stem were measured only for No. 1, 10, and 11 sample trees.

Table 1. The characteristics of sample trees.

Tree No.	Age (year)	Height (m)	DBH (cm)	Cross-sectional area of xylem at breast height (cm^2)	Cross-sectional area of flow at breast height (cm^2)
1	37	11.5	9.4	69.36	53.96
2	36	8.7	9.1	51.50	37.55
3	36	11.1	10.3	83.28	63.73
4	39	11.3	11.3	100.24	57.58
5	28	10.4	9.8	75.39	60.82
6	27	11.7	10.5	86.55	66.24
7	33	8.4	11.8	109.30	63.58
8	28	7.3	9.1	62.18	48.19
9	34	10.9	11.9	111.16	69.03
10	42	9.8	10.9	93.27	37.29
11	41	11.8	9.8	–	–
Mean	34±5	10.3±1.5	10.4±1.0	84.22±19.87	55.80±11.42

※ ± : standard deviation

2. Sample collection

The sample trees were cut early in the morning to prevent cavitation at the end of cut. The trees were cut at 0.2 m above ground, and we collected the sample stems at breast height and at each of 2 m intervals above the breast height. And each sample was recut in about 30 cm long, immediately submersed in water to prevent cavitation, and then carried to the laboratory. Especially for the No. 1, 10, and 11 trees, the sample was recut at 0.2 m, 1.3 m, 3.3 m, 5.3 m, and 7.3 m above ground. The moisture content and age of trees were measured in the stem disks.

3. Anatomical observation

Cylindrical specimens were taken from the sapwood of stem segments with their long axes parallel to the grain. The specimens were immersed in solution of distilled water and glycerol (3 : 1) and were softened by heating mantle. Transverse surfaces of each softened specimen were planed smooth using a microtome, and transverse sections of 15～20 ㎛ thick were cut from each specimen. The each section was dyed by the solution of 1% safranine, dehydrated by alcohol series (50, 70, 90, 99.9%), and deposited in solution of 100% alcohol and 100% xylene (1 : 1) and in solution of 100% xylene. The permanent präparats were made. The diameters of vessels (㎛) were measured at a magnification of ×400, and also the number of vessels in cross-sectional area of 1 cm^2 was counted at a magnification of ×100 using an optical microscope.

4. Calculated equations of the volume flow rate and hydraulic resistance

1) Volume flow rate (Q) and hydraulic resistance (R_S) per a vessel

Assuming that a vessel of hardwood is the open vessel of a cylindrical capillary, the rate of volume flow (Q, cm^3/sec) through a vessel, which has the length of L cm and the radius of R cm, was obtained using Hagen-Poiseuille's equation (Siau, 1971), the equation (1).

$$Q = \frac{\pi R^4 \Delta P}{8 \eta L} \tag{1}$$

where, R is the radius of vessel (cm), ΔP is the pressure differential (dyn/cm^2), η is the viscosity of fluid (dyn · sec/cm^2), L is the length of vessel tube (cm).

When the sap flow through a cylindrical vessel, the hydraulic resistance necessarily occur (Hinckley *et al.*, 1978; Running, 1980). The hydraulic resistance can be expressed as equation (2), because it is equal to a reciprocal equation (1). Thus, the hydraulic resistance (R_S, dyn · sec · cm^{-3} · cm^{-2}) of a vessel can be calculated from equation (2).

$$R_S = \frac{\Delta P}{Q} = \frac{8 \eta L}{\pi R^4} \tag{2}$$

2) Volume flow rate (Q_N) and hydraulic resistance (R_{SN}) per cross-sectional area in sapwood

The rate of volume flow (Q_N, cm^3/sec) through the N functional vessels, which have the radius of R (cm) per cm^2 of cross-sectional area in sapwood was obtained in using equation (3) (Siau, 1971).

$$Q_N = \frac{N \pi R^4 \Delta P}{8 \eta L} \tag{3}$$

where, N is number of vessels per cm^2 of cross-sectional area (No./cm^2).

Assuming that the sum of vessels in functional sapwood is N, the hydraulic resistance (R_{SN}, dyn · sec · cm^{-3} · cm^{-2}) per cm^2 of cross-sectional area can be calculated from equation (4).

$$\frac{1}{Q_N} = R_{SN} = \frac{8 \eta L}{N \pi R^4 \Delta P} \tag{4}$$

5. Experimental measurement and calculation of permeability

In general, the value of hydraulic conductivity is expressed as the quantity of water per unit cross-sectional area of sapwood passing through a specific length of a stem per unit time and pressure, and it is called the permeability or relative conductivity, K (Heine, 1971; Petty, 1978; Ikeda and Suzaki, 1984).

In this study, the values of permeability were expressed as measured permeability, K and calculated permeability, K_E, that were obtained from Hagen-Poiseuille's equation.

1) Measured permeability, K

For measuring the value of permeability, the actual water flow rate (Q, m^3/sec) was obtained using an apparatus as Fig. 1.

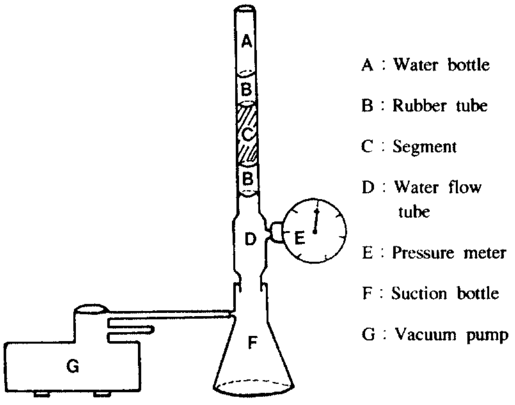

Fig. 1. An apparatus for measuring the permeability.

Each segment, which was measured, was cut in 10 cm length. And, it was fitted at its upper end with a water container, and the other end with a suction bottle that was connected to vacuum pump (ADC, UT). Then, the Q value passing through a segment per unit time was measured under a specific pressure (71596 N/m^2).

To remove air bubbles that can occur at surfaces of the cut, the segment was cut both ends as it submerse, and the actual Q was measured after constant flow rate.

After measuring Q, the segments were perfused with the solution of 1.0% acid fuchsine to demarcate the area of conducting sapwood. And then, we observed the dyed sapwood area of each segment in the intervals of 3 cm.

The value of K was obtained from equation (5) using Q and A (Heine, 1971).

$$K = \frac{QL\eta}{t \cdot \Delta PA} \qquad (5)$$

where, K is measured relative conductivity or permeability (m^2), Q is the volume of solution obtained by suction (m^3), L is the length of the cut segment (m), η is the viscosity of the solution ($N \cdot s/m^2$), t is the time during measurement (sec), ΔP is the suction force (N/m^2), and A is the cross-sectional area of sapwood (m^2) (Hein, 1971; Jarvis, 1975; Petty, 1978; Pothier *et al.*, 1989).

2) Calculated permeability, K_E

The calculated permeability, K_E can be expressed as the equation (6) from Hagen-Poiseuille's equation (equation 3). The value of K_E was calculated by equation (6) with observed values of the average vessel radius and the number of vessels per unit area (Siau, 1984; Pothier *et al.*, 1989).

$$K_E = \frac{N\pi R^4}{8A} \qquad (6)$$

where, K_E is the calculated permeability (m^2), N/A is the number of vessels per unit cross-section area (No./m^2), and R is the average radius of vessel (m).

RESULTS AND DISCUSSION

1. Volume flow rate and hydraulic resistance per a vessel

The volume flow rate, Q and hydraulic resistance, R_S to viscous flow through a vessel of sapwood at breast height were shown in Table 2 (obtained from equation 1, 2).

The average diameter of vessels was 42.94 ㎛ at breast height. The average Q in single vessel

Table 2. The volume flow rate (Q) and hydraulic resistance (R_S) to viscous flow through a vessel at breast height in *Acer mono.*

Sample number	Mean vessel diameter (μm)	Q (cm^3/sec)	R_S (dyn · sec · cm^{-3} · cm^{-2})
		$\times 10^{-4}$	$\times 10^{10}$
1	38.22±0.53	0.48	2.10
2	38.01±0.47	0.62	1.65
3	43.16±0.62	0.81	1.25
4	41.32±0.75	0.58	1.76
5	43.18±0.55	0.85	1.20
6	48.08±0.56	1.21	0.84
7	45.62±0.73	0.83	1.23
8	39.72±0.73	0.64	1.59
9	45.92±0.90	0.88	1.15
10	46.18±0.73	1.13	1.08
Mean	42.94±1.12	0.80±0.07	1.37±0.13

※ ± : standard errors

was 0.80×10^{-4} cm^3/sec, and the average R_S was 1.37×10^{10} dyn · sec · cm^{-3} · cm^{-2}. Han and Kim (1999) reported that the average Q in single vessel was 1.55×10^{-4} cm^3/sec in diffuse-porous species, and 1.81×10^{-2} cm^3/sec in ring-porous species. In addition, they found that the average R_S was 0.78×10^{10} dyn · sec · cm^{-3} · cm^{-2} in diffuse-porous species, and 0.79×10^{6} dyn · sec · cm^{-3} · cm^{-2} in ring-porous species.

2. Volume flow rate and hydraulic resistance per cross-sectional area in sapwood

The volume flow rate, Q_N and hydraulic resistance, R_{SN} to viscous flow through the vessels per cm^2 of sapwood cross-sectional area at the breast height were shown in Table 3 (obtained from equation 3, 4).

The number of vessels per unit sapwood area was 3937 No./cm^2. The average Q_N through the cross-section of sapwood was 0.32 cm^3 · sec^{-1} · cm^{-2}, which was obtained from equation 3, and the average R_{SN} was 3.31×10^{6} dyn · sec · cm^{-3} · cm^{-2}, which was obtained from equation 4. Han and Kim (1999) found that the average Q_N through the cross-section of sapwood was 0.91 cm^3/sec in diffuse-porous species, and 7.43 cm^3/sec in ring-porous species. Also, the study showed that the average R_{SN} was 1.30×10^{6} dyn · sec · cm^{-3} · cm^{-2} in diffuse-porous species, and 0.20×10^{6} dyn · sec · cm^{-3} · cm^{-2} in ring-porous species.

3. Comparison of K and K_E values

As shown in Table 4, the values of K were considerably less than the values of K_E in stem.

If the all vessels are open, the K_E reached approximately 100%. But the results indicate that the values of K range from 8% to 70% of the

Table 3. The volume flow rate(Q_N) and hydraulic resistance(R_{SN}) to viscous flow through the vessels per cm^2 of sapwood cross-sectional area at breast height in *Acer mono.*

Sample number	Mean vessel diameter (μm)	Mean vessel number (No./cm^2)	Q_N (cm^3/sec)	R_{SN} (dyn·sec·cm^{-3}·cm^{-2})
				$\times 10^{6}$
1	38.22±0.53	3616±60	0.17	5.32
2	38.01±0.47	3861±57	0.24	5.09
3	43.16±0.62	3610±48	0.29	3.27
4	41.32±0.75	3354±46	0.19	4.19
5	43.18±0.55	4383±60	0.37	2.69
6	48.08±0.56	4377±51	0.53	1.75
7	45.62±0.73	4019±48	0.33	2.36
8	39.72±0.73	4375±73	0.28	3.77
9	45.92±0.90	3870±70	0.34	2.38
10	46.18±0.73	3914±63	0.44	2.30
Mean	42.94±0.66	3937±58	0.32±0.03	3.31±0.39

※ ± : standard errors

Table 4. The measured permeability, K and calculated permeability, K_E of sapwood at breast height in *Acer mono*.

Sample number	Mean vessel diameter (μm)	Mean vessel number (No./cm^2)	K ($\times 10^{-12}$ m^2)	K_E ($\times 10^{-12}$ m^2)	K/K_E (%)
1	38.22±0.53	3616±60	1.02±0.02	1.89	53.87
2	38.01±0.47	3861±57	1.38±0.05	1.98	69.95
3	43.16±0.62	3610±48	0.51±0.02	3.07	16.64
4	41.32±0.75	3354±46	0.67±0.07	2.40	28.08
5	43.18±0.55	4383±60	0.39±0.01	3.74	10.54
6	48.08±0.56	4377±51	1.04±0.06	5.74	18.14
7	45.62±0.73	4019±48	0.36±0.01	4.27	8.38
8	39.72±0.73	4375±73	1.61±0.07	2.67	60.46
9	45.92±0.90	3870±70	0.81±0.03	4.22	19.17
10	46.18±0.73	3914±63	1.25±0.04	4.36	28.58
Mean	42.94±0.66	3937±58	1.04±0.20	3.43±0.39	31.38±6.96

※ ± : standard errors

values of K_E, and the K value was, on average, 31% of the values of K_E. These results imply the influences of the resistance to water flow and the existence of non-conducting tissues (Petty, 1978). Pothier *et al.* (1989) reported that the measured values of permeability in jack pine sapwood were never more than 60% of the values calculated by Hagen-Poiseuille's law and were generally less than 40%. Vines have the vessels that behave just like ideal capillaries so that the resistance to flow through them is not noticeably different from capillaries, and then have 100% of K/K_E ratio. The K/K_E ratio in rootwood of oak, a ring- (*i.e.* large-) porous tree ranged from 35 to 84%, and stem wood is probably a bit lower (Zimmermann, 1971).

The variations of K and K_E value across different ages were shown in Fig. 2. The K and K_E values decreased as the stem diameter and age increase. The K/K_E ratios were 100% in 4~6 year-old stems, and more than 90% in 7~27 year-old stems, indicating that the relatively young sapwood can conduct fluid, but over 27-year-old stems cannot. The K/K_E ratio remarkably decreased as the age of stem increases, and the K values in near-ground parts of stem were not more than 20%

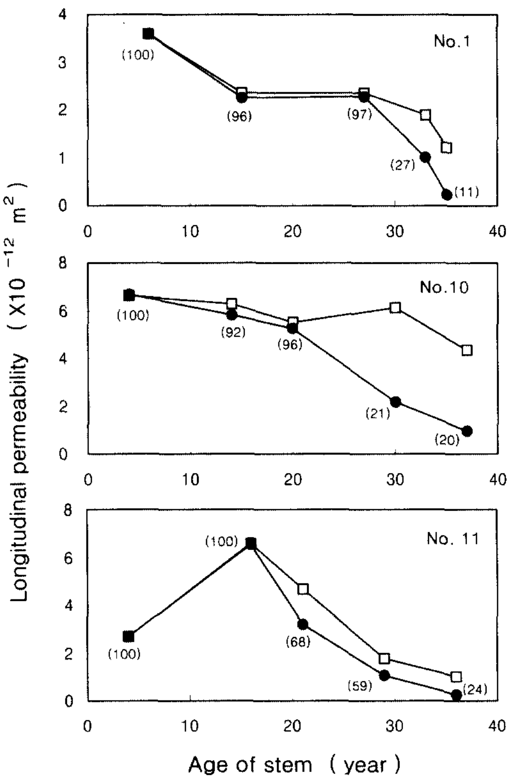

Fig. 2. The the measured permeability, K and calculated permeability, K_E of sapwood as related to stem age in *Acer mono* trees. □-□ : K_E, ●-● : K, ( ) : K/K_E ratio.

of the K_E values (Fig. 2). Pothier *et al.* (1989) reported that permeability, K in jack pine stands decreased with the increase in the age and site quality of stand, and that the relationship of K with the age and site index followed a negative exponential function.

4. Distribution of the permeability and hydraulic resistance in various parts of stems

The distribution of measured permeability (K) and hydraulic resistance (R_{SN}) of sapwood in various parts of stems were shown in Fig. 3. The value of K appeared to be the smallest at near-ground parts of the stems, and increased forward to upper parts of the stem. The largest value of R_{SN} was observed at near-ground parts of the stems, and decreased forward to upper parts of the stem.

There was a reverse relation between K and R_{SN}. Especially the highest R_{SN}, in the lower part of stem suggested that there was the small number of vessels and non-conducting vessels per unit sapwood area in the lower parts of stems (Ikeda and Suzaki, 1984; Tyree and Sperry, 1989; Han *et al.*, 1998; Kozlowski and Pallardy, 1997).

5. K value and structure of conducting tissue

Fig. 4 shown the mean vessel diameter, the number of vessels per unit area, and permeability (K) as related to the size of stem diameter.

The diameter of vessels expressed as similar values was independent of stem diameter as shown in Fig. 4, and the number of vessels per unit area tended to be decreased with the increase in the diameter of stem. The value of K decreased as the

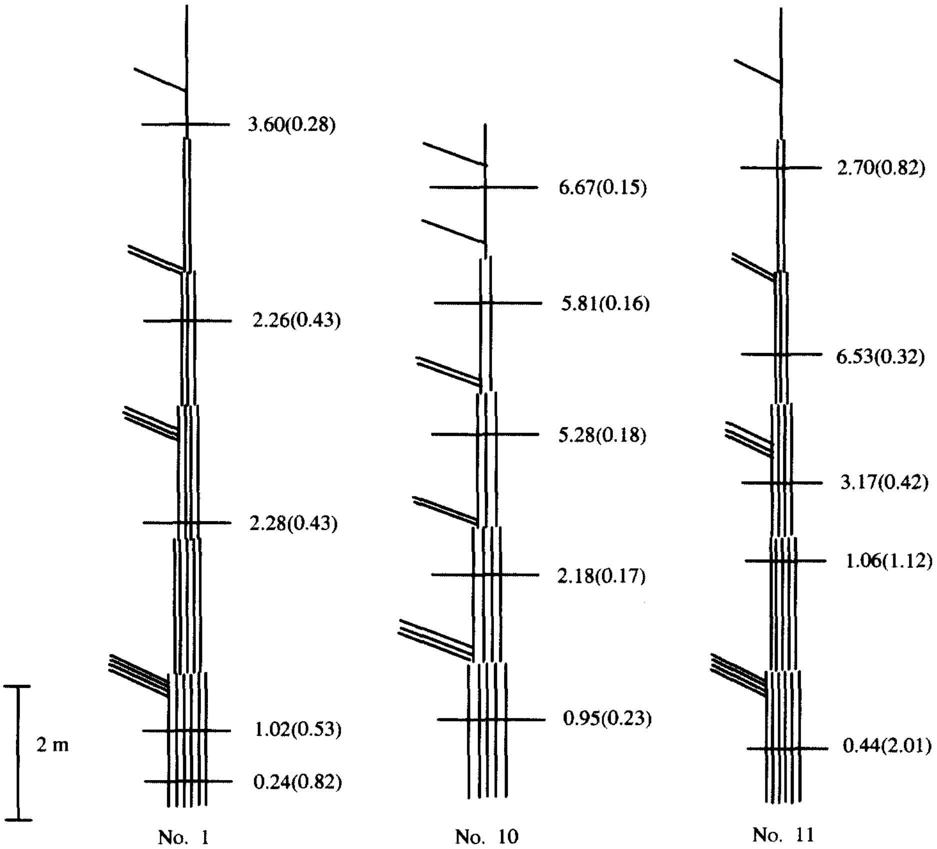

Fig. 3. Distribution of the permeabilities (K, $\times 10^{-12}$ m^2) and hydraulic resistances (parenthesis, R_{SN}, $\times 10^7$ dyn · sec · cm^{-3} · cm^{-2}) of sapwood in various parts of stems.

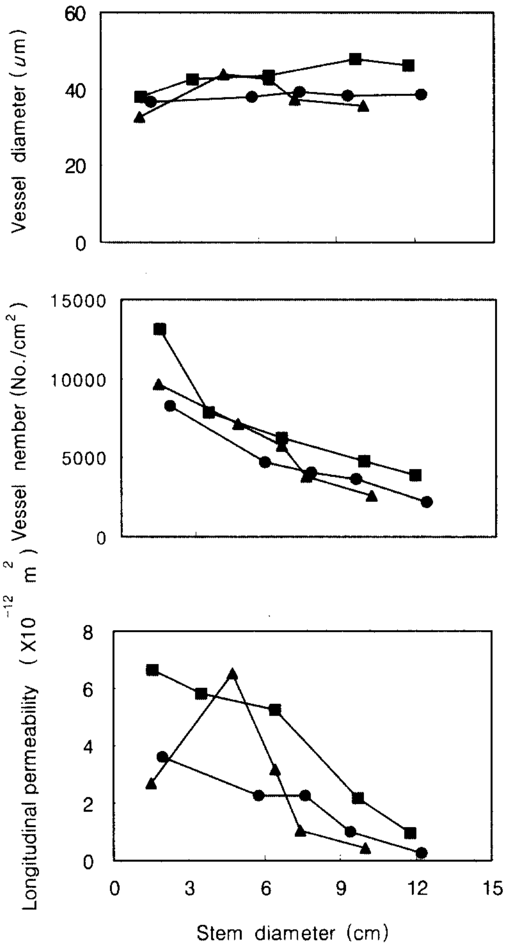

Fig. 4. The mean vessel diameter, the number of vessels per unit area, and permeability (K) as related to the size of stem diameter in *Acer mono* trees. ●-● : No. 1, ■-■ : No. 10, ▲-▲ : No. 11.

diameter of stem increases, which was attributable to variation in the number of vessels per unit area than in vessel diameter. Han and Kim (1999) reported that the factors in determining the K were the diameter and number of vessels in diffuse-porous trees, and the vessel diameter in ring-porous trees, rather than the number of vessels per unit area. The K of xylem is generally determined by the structure and size of the vessels (Schultz and Matthews, 1993; Tyree and Ewers, 1991). While, Pothier *et al.* (1989) reported that the K for jack pine stands was linearly related to the relative water content of sapwood. In this study, the average moisture content of each sample was 66±7% at the time of cut.

Petty (1978) have suggested that the discrepancy between measured and theoretical K arises from the resistance to flow at the perforation plates at the ends of vessel elements in birch (*Betula pubescens* Ehrh.).

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