Distribution of Hydraulic Resistance within Shoots of Pasania edulis Makino Grown in Sunny and Shaded Crown

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Distribution of Hydraulic Resistance within Shoots of *Pasania edulis* Makino Grown in Sunny and Shaded Crown*

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Abstract

Hydraulic resistance of main stems and petiols of *Pasania edulis* Makino was measured by pressure chamber to clarify the distribution of hydraulic resistance in sun shoots at the top of crown (sunny conditions) and shade shoots at the bottom of crown (shaded conditions).

Hydraulic conductance was higher in sun shoots than in shade shoots. A clear relationship was obtained between the hydraulic conductance of the main stem and cumulative leaf area. This relationship confirmed the pipe model theory from the view point of water conduction. Leaf specific resistance per unit stem length, derived from the relationship between leaf specific resistance and conductive distance of the main stem, was constant in several sun shoots.

Conversely, the effect of conductive distance on leaf specific resistance in shade shoots can be ignored. Leaf specific resistance of petiols was greater than that of main stems in all shoots. In particular, the percentage of leaf specific resistance of petiols in the total shoot resistance was about 90% in sun shoots. This result suggests that petiolar resistance is a limiting factor, analogous to a bottle neck in the movement of water in shoots. The strong regulation of water movement at petiols in the sun shoots was thought to help avoid catastrophic water loss of total shoots under high transpirational demand.

Key words：hydraulic resistance；petiols；the pipe model theory；shade shoots；sun shoots.

1. Introduction

Distribution of hydraulic resistance is an important factor in predicting water status in trees. There are many studies on water use by a single leaf which analyzed CO_2 and

vapor exchange characteristics of leaves (e.g., Cowan, 1982). In deducing these ideas for trees that have complex branching, it is necessary to look at trees structurally, for example, as a tree system consisting of branches described by Tyree and Sperry (1988). This paper focuses on the distribution of hydraulic resistance within a shoot system consisting of sun and shade leaves with different characteristics of gas exchange and water relations.

Ito and Suzaki (1990) suggested that hydraulic resistance in petiols plays an important role as a limiting factor in water movement in a tree by measuring the hydraulic resistance of branches and sprouts of *Eucalyptus grobulus*. We also measured the large proportion of petiolar resistance in *Pasania edulis* Makino (Ito *et al.*, 1995). This paper aims to clarify the distributional pattern of hydraulic resistance within shoots by separating resistance of main stems and petiols.

2. Materials and methods

2.1. Plant materials

The species examined in this paper was *Pasania edulis* Makino (matebashii), which is common in warm‑temperate evergreen hardwood forests in southwestern Japan. Materials were taken from an adult tree (8m in height) grown in the nursery of Kyushu University, Fukuoka, southwestern Japan. Current shoots in the sunny crown (the top of the canopy : sun shoots) and shade crown (the lowest layer of the closed canopy : shade shoots) of this tree were collected and cut under tap water before sunrise in August 1992. After being returned to the laboratory, the shoots were recut under distilled water just before measurement to have a stem of 15cm.

2.2. Measurement of hydraulic conductance in the main stem

Fig. 1 shows the measurement procedure schematically. The samples were settled into a plastic bag filled with distilled water in a pressure chamber. The main stem was cut just below each leaf junction from the shoot apex, and air pressure in the chamber was maintained at 0.2 MPa. Sap flow from the cut end of the main stem was collected for 30 seconds with a plastic tube filled with tissue paper. Sap flow was determined as the difference in tube weight before and after measurement. Three samples of both sun and shade shoots were measured. Hydraulic conductance (the reciprocal value of resistance) was calculated by the following equation :

$$C = V \quad \Delta P^{-1} \quad t^{-1} \qquad \text{(Eq.1)},$$

where C is hydraulic conductance which includes the effect of conductive distance from the shoot base to the cut end. V (kg), ΔP (Pa) and t (sec) are sap flow, air pressure in the chamber and time for the measurement, respectively. Area of detuched leaves (m²) was measured to calculate leaf specific conductance (Zimmermann, 1983).
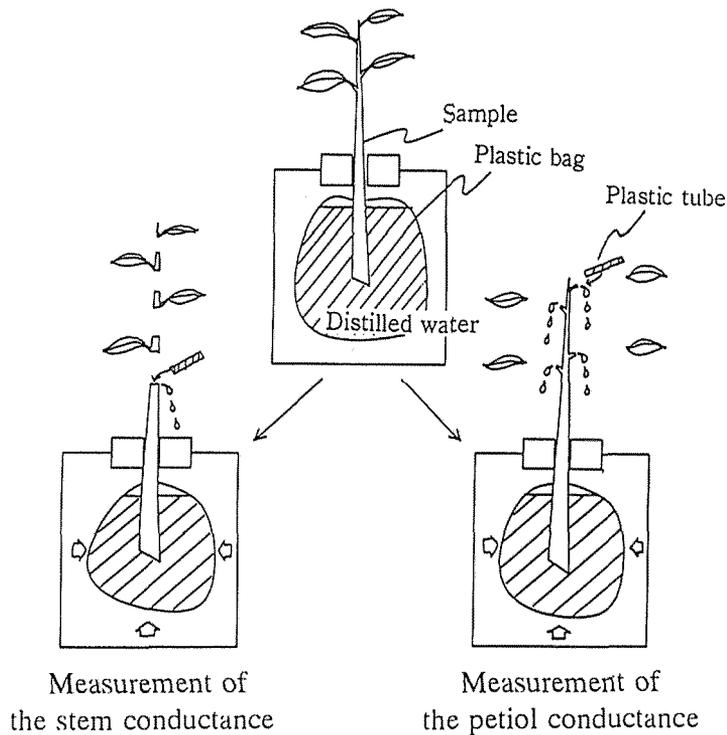
Fig. 1　Schematic illustration of measuring procedure.

2.3.　Measurement of hydraulic conductance in petiols

The samples were settled same as the measurement of the hydraulic resistance of the main stem (Fig. 1). All leaves were detached from the base of the leaf blade, and air pressure in the chamber maintained at 0.2MPa. Sap flow from all cut ends of petiols were measured for 60 seconds, as in the measurement of the main stem. Measurement was carried out of three samples for both sun and shade shoot. Hydraulic conductance from the shoot base to the cut end of petiols was calculated using Eq.1.

3.　Results

3.1.　Hydraulic conductance in the main stem

The results were analyzed in relation to the following two factors which may affect the distribution of hydraulic conductance of the main stem; conductive distance and leaf area supported by conductive organs.

Fig. 2 shows the relationship between shoot length and hydraulic conductance of the main stem. In all samples, short shoots had high hydraulic conductance. Sun shoots had higher conductance than shade shoots of the same length. The degree of change in conductance along the shoot length was also higher in sun shoots. However, the
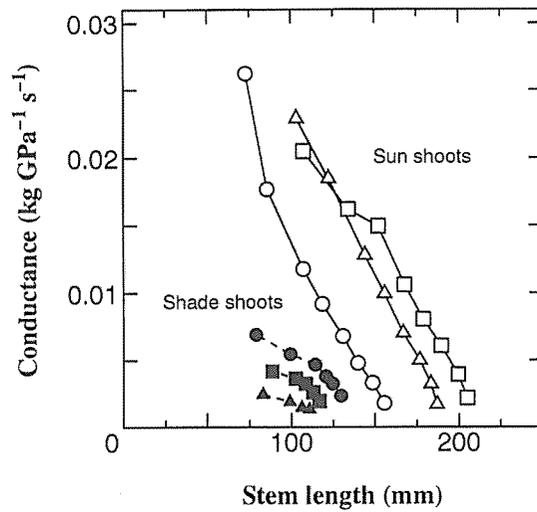
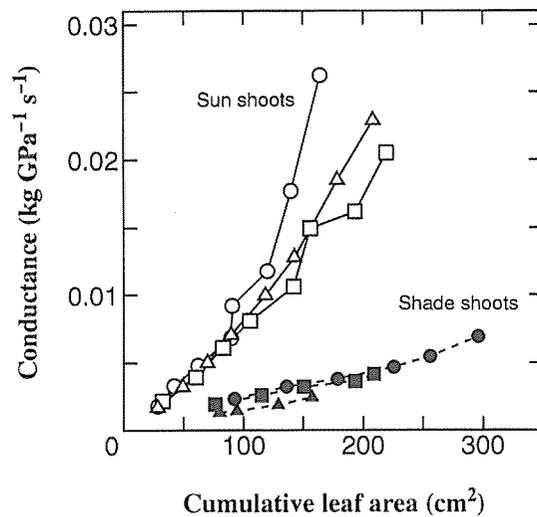Fig. 2 Relationship between length and hydraulic conductance of main stems.

Fig. 3 Relationship between cumulative detached leaf area and hydraulic conductance of main stems.

relationship could not be expressed by a function because of large variations within each shoot category.

Fig. 3 shows the relationship between conductance and cumulative area of detached leaves, i.e., the leaf area supported by the cut end of the main stem. There was a clear relationship between the conductance and the cumulative detached leaf area in each shoot category. Variation within shoot category was also smaller than in the relationship
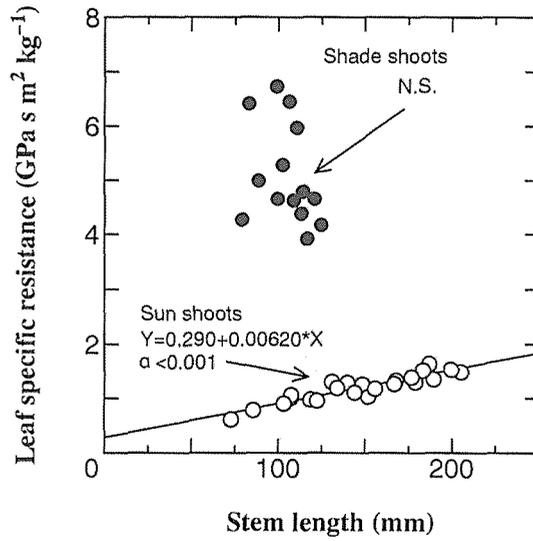
Fig. 4 Relationship between leaf specific resistance and length of main stems.
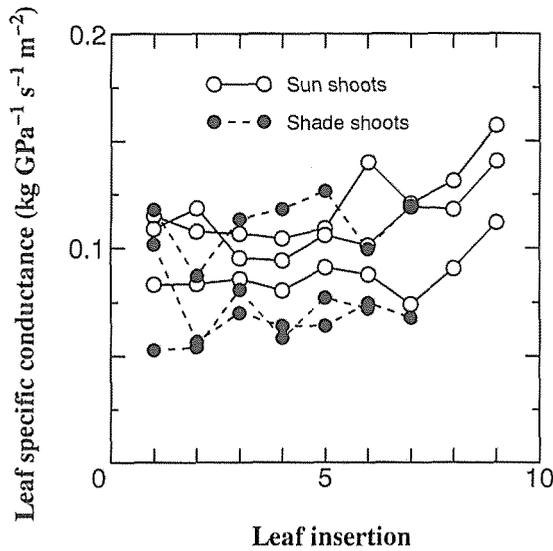

Fig. 5 Distribution of leaf specific conductance from the stem base to the cut end of petiols.

between conductance and distance. This result indicates that the variations in conductance among shoots can be ignored by calibrating conductance as leaf specific values (cf. Zimmermann, 1983 ; Ito and Gyokusen, 1993).

Fig. 4 shows the relationship between leaf specific resistance and stem length. A clear linear relationship was obtained for sun shoots. The slope of the regression line
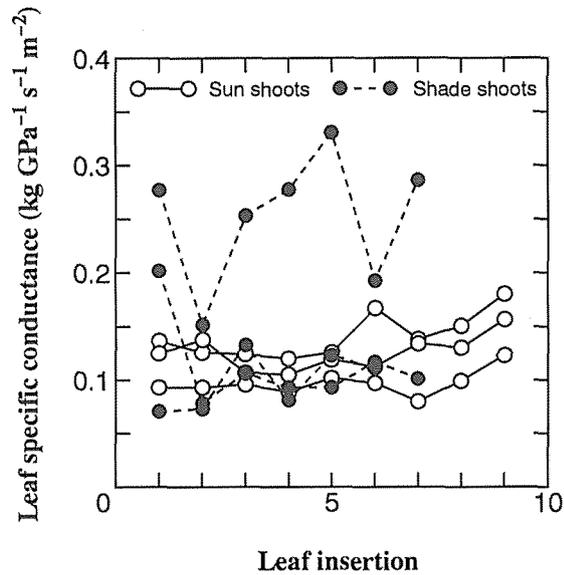
Fig. 6   Distribution of leaf specific conductance of
petiols and their junctions.

(6.20 GPa s m² kg⁻¹) indicates leaf specific resistance per unit length of the main stem.
No significant relationship between leaf specific resistance and stem length was obtained
for shade shoots. This is thought to be due to large variation in leaf specific resistance,
and to the small range in conductive distance due to concentrated leaf distribution at the
shoot apex.

3.2.   Hydraulic resistance in petiols

Fig. 5 shows leaf specific conductance from the shoot base to the cut end of petiols
(Ct) along the leaf insertion. The leaf specific conductance of shade shoots was relatively
lower than for sun shoots. This was partly due to the larger single leaf area of shade
leaves. From the Ct shown in Fig. 5 and leaf specific conductivity of the main stem per
unit stem length (Cs) estimated from the regression in Fig. 4 (the average leaf specific
conductance for shade leaves; 0.205 kg GPa⁻¹ s⁻¹ m⁻²), leaf specific conductance of petiols
and petiolar junctions (Cp) was calculated using the following equation:

$$Cp = 1/(1/Ct - 1/Cs)   \text{(Eq.2)},$$

Fig. 6 shows Cp along the leaf insertion. No tendency was observed in the Cp of
shade shoots due to large fluctuations. On the other hand, Cp of sun shoots tended to
increase near the shoot base, corresponded to the pattern of Ct shown in Fig. 5.

Table 1 shows the mean value of leaf specific resistance of each part. Total leaf
specific resistance (Ct) was greater in shade shoots than in sun shoots. This difference

Table 1. Hydraulic resistance per unit leaf area of each shoot part.

	Hydraulic resistance (GPa $\cdot$ s $\cdot$ m$^2\cdot$ kg^{-1})	
	Stem	Petiol and junction
Sun shoot	1.106 (11.4)	8.570 (88.6)
Shade shoot	4.871 (37.7)	8.037 (62.3)

Figures in parentheses indicate the proportion in total shoot resistance.

was mainly caused by differences in resistance of main stem. Leaf specific resistance in petiols and petiolar junctions was larger in sun shoots.

4. Discussion

The clear relationship of hydraulic conductance of the main stem with cumulative leaf area (Fig. 3) suggests that hydraulic conductance was distributed to balance with the leaf area supported by the main stem, rather than conductive distance. This result indicates a functional relationship between conductive organs and transpirational organs, which is independent on conductive distance. This suggests confirmation of 'the pipe model theory', proposed by Shinozaki *et al.* (1964), from the view point of water conduction. However, there was a large difference in leaf specific conductance between sun and shade shoots. Therefore, it is thought that the hydraulic pipe model has different parameters as the specific pipe length according to differences in environmental conditions even within a species.

The difference between sun and shade shoots was observed in leaf specific conductance per unit stem length (Fig. 4). Leaf specific conductance per unit stem length was constant even in several sun shoots. Therefore, the effect of conductive distance on leaf specific conductance is thought to be definite in sun shoots. In contrast, there was no significant relationship between leaf specific conductance and conductive distance in shade shoots (Fig. 4). Thus, the effect of conductive distance on leaf specific conductance in shade shoots can be ignored.

Leaf specific conductance from the shoot base to the cut end of petiols (Ct) could not be expressed as a function of leaf insertion because of large fluctuations within individual shoots and in variations between shoots (Fig. 5). However, in sun shoots, the Ct tended to increase near the shoot base. This tendency was also observed in the distribution of leaf specific conductance of petiols (Cp, Fig. 6). It is therefore concluded that variations in Ct were promoted by variations in Cp in both sun and shade shoots.

As shown in Table 1, the difference in leaf specific resistance between sun and shade shoots originates from the difference in the resistance of the main stem. However, the proportion of petiolar resistance in total shoot resistance was high in both sun and shade

shoots. Therefore, the resistance of petiols is thought to be a limiting factor in water movement analogous to 'the bottle neck' (Zimmermann, 1983) in a shoot.

The higher proportion of petiolar resistance (the leaf specific value) of sun shoots (88.6%) than shade shoots (62.3%) indicates stronger regulation of water movement at petiols in sun shoots. This is thought to be related to physiological characteristics of leaves and environmental conditions. Generally, sun leaves have higher gas exchange rates than shade leaves (Saeki, 1959). Higher transpirational demand such as higher vapor pressure difference is also anticipated in sunny crown than in shade conditions. Therefore, strong regulation of water movement at petiols of sun shoots is thought to help avoid catastrophic water loss of total shoots in such conditions. In conclusion, the distribution of hydraulic resistance of the main stem could be expressed as the hydraulic pipe model in terms of leaf specific resistance. However, in this study, an equation could not be obtained to express the distribution of petiolar resistance which is the most important factor regulating the water movement in shoots. Thus, further measurement and analysis in relation to leaf water relation characteristics are necessary for a more functional interpretation of the distribution of petiolar resistance.

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マテバシイ陽樹冠および陰樹冠における
水分通導抵抗のシュート内分布

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要　　約

　マテバシイの陽樹冠および陰樹冠内の水分通導抵抗の分布を明らかにする目的で，当年生シュートの主軸および葉柄部の水分通導抵抗をプレッシャー・チャンバーを用いて測定した．主軸の水分通導性は陽樹冠で陰樹冠よりも高く，通導距離よりも通導面が支持する葉面積との間で明瞭な関係が認められた．これによって樹形のパイプモデルを水分通導機能面から検証できた．さらに，葉面積ベースでの水分通導抵抗と通導距離との関係から，単位通導距離当たりの葉面積ベースの主軸の水分通導性が陽樹冠のシュート内では一定であり，陰樹冠のシュート内では通導距離の影響がほとんどないことを明らかにした．また，単位葉面積あたりの葉柄の水分通導抵抗は主軸に比較して大きかった．特に陽樹冠のシュートでは全シュートの通導抵抗における葉柄の通導抵抗の割合が約90％を占めており，葉の水分特性やガス交換特性との関連性が示唆された．この結果は，葉柄の抵抗がシュート内での水分通導の規制要因となっていることを示しており，特に蒸散要求度の高い陽樹冠では，シュートの全体の致死的な水分損失を回避する上で重要な役割を果たすと考えられた．
キーワード：水分通導抵抗，葉柄，パイプモデル，陰樹冠，陽樹冠