Hydraulic Conductance and Xylem Anatomy in Fruit Tree Shoots

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Hydraulic conductance is an important index of water flow in plants. We constructed a simple device for measuring the relative hydraulic conductance of fruit tree shoots. The values of vines (kiwifruit and grape) were the highest among 17 species of major temperate fruit trees, followed by deciduous trees (e.g. chestnut, Japanese pear, and peach), evergreen citrus trees (e.g. Kawanonatsudaidai and Satsuma mandarin), and loquat. The diameter and number of vessels and total vessel area in shoots were calculated with image analysis software from photomicrographs of 13 of the species. The diameter of the vessels was largest in vines (kiwifruit and grape), followed by persimmon and chestnut, and smallest in deciduous trees (e.g. apple and Japanese apricot), citrus, and loquat. Relative hydraulic conductance had a higher correlation with the water flow index \((\sum r^4/S \times \text{xylem ratio})\), calculated from the diameter and number of vessels in the xylem according to the Hagen–Poiseuille law, and than with total vessel area per unit of shoot cross-sectional area.

Key Words: Hagen–Poiseuille law, transpiration, vessel diameter, total vessel area, water flow.

Introduction

In vascular plants, water absorbed from roots is transported to leaves through stems. This flow is often compared to an electric current and, as in an electric current, the reciprocal of resistance \((1/R)\), called conductance, is used as an index of flow (Heine, 1971). Tyree and Zimmermann (2002) suggested that water flow through plant vessels could be compared with the flow through smooth-walled capillaries of circular cross-section. Under this assumption, the Hagen–Poiseuille law, which is often used in fluid dynamics, can be applied to plant vessels, showing that, under laminar flow, the flow rate is proportional to the fourth power of the vessel radius (Reiner, 1998). Thus, hydraulic conductance is influenced by the diameter and number of vessels in the xylem.

Several methods for detecting hydraulic conductance have been developed, relying on a pressure chamber (Nakano et al., 2004), a vacuum pump (Ikeda and Suzuki, 1984), or centrifugal pressure (Cochard et al., 2000). The method of detection varies with the purpose of measurement and the species examined.

Hydraulic conductance and the anatomy of the xylem affect tree growth, and thus the response to cold and drought among other environmental influences. Tracheid-bearing evergreen conifers and broadleaved evergreen trees with narrow vessels did not show severe embolism or water deficit under freeze–thaw cycles in winter, but broadleaved evergreen trees with wide vessels showed significantly reduced hydraulic conductance and shoot dieback under those conditions (Taneda and Tateno, 2005). Water stress also causes embolism. Air enters from surrounding air-filled vessels through the membrane pits to form bubbles. This phenomenon is called cavitation (Sperry and Tyree, 1988). Holbrook et al. (2001) demonstrated by magnetic resonance imaging (MRI) that moisture stress breaks the water column in the vessels of grape, that is, causes embolism formation. Jensen et al. (2004) observed xylem structures from the tropics to the tundra, and showed that membranes with vestured pits in the side of vessels are involved in embolism prevention. In another report, plants with large vessels became easily embolized by water stress (Sperry and Tyree, 1988).

There are several reports of hydraulic conductance in fruit trees. Atkinson et al. (2003) showed that the hydraulic conductance of apple on dwarfing rootstock was lower than that on semi-vigorous rootstock. The relationship between tree vigor and hydraulic conductance has been studied in kiwifruit (Clearwater et al., 2004), olive (Nardini et al., 2006), and peach (Nakano...
Moreover, vessel conductance affects fruit quality, since vessels that lead to the fruits become dysfunctional as fruits mature (Bondada et al., 2005; Dichio et al., 2003; Drazeta et al., 2004).

These reports dealt with differences among several stocks with the same scion or with changes of conductance with fruit development, but did not examine differences among fruit species. Hydraulic conductance has been compared mainly among forest trees, thus, we compared hydraulic conductance among major fruit tree species in Japan with a simple device of our construction.

Materials and Methods

Plant materials

We measured the relative hydraulic conductance of 17 species (19 cultivars) of fruit trees (Table 1) planted at the National Agricultural Research Center for the Western Region Zentsuji, Japan. One- or two-year-old twigs were collected from the field from August to September 2006; the end of each sample was cut in water again and then soaked in water for more than an hour. Shoots with a diameter of 7 to 9 mm were cut into 5-cm lengths with a sharp knife in water before measurement.

Hydraulic conductance detection

We based our device on that of Ikeda and Suzaki (1984), and Figure 1 presents a schematic diagram of our device. After removal of the air bubbles in the tube connected to the water supply tank, each end of the excised sample was fitted into a rubber tube, and air was suctioned by a compact air pump (NUP-1, As-One Co. Ltd., Japan). When the vacuum pressure reached ~0.07 MPa, the two-way stopcock at the base of the pipette was closed. The amount of water collected in the pipette was measured, and hydraulic conductance was calculated as explained below. After each measurement, the water level in the tank was reset.

Microscopic observation

Thirteen of the species were examined microscopically. A cross-section of each specimen was sliced with a razor blade. Each sample was dyed with 0.5% safranin (Sigma, USA), and then observed through an optical microscope (Eclipse E200, Nikon, Japan) connected to an LCD-TV (LT17M24CU, Samsung, South Korea). Fifteen to seventeen photographs were taken using a CCD camera (Coolpix 5400, Nikon) mounted on the microscope. We then used image analysis software (Image-Pro Plus, Media Cybernetics, USA) to calculate the diameter of vessels, the number of vessels per mm² xylem area, and the vessel area ratio from the image data.

Calculation of hydraulic indices

1. Hydraulic conductance

The flow rate per unit time (dV/dt) through a capillary is proportional to the applied pressure gradient per unit length (dP/dl) and the hydraulic conductance (K_capillary):

\[ \frac{dV}{dt} = -K_{\text{capillary}} \frac{dP}{dl} \]

If the sample length (l) and applied pressure (P) are constant, the liquid volume (V) per unit time (t) which flows through a stem can be used as an index of hydraulic conductance.

2. Water flow and calculated vessel area indices

Hagen and Poiseuille published the following formula in 1839 and 1840, respectively:

\[ K_{\text{capillary}} = \frac{r^4 \pi}{8 \eta} \]

where r is the radius of the capillary tube and η is the

<table>
<thead>
<tr>
<th>Fruit tree name</th>
<th>Botanical name</th>
<th>Cultivar name</th>
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<tbody>
<tr>
<td>Grape</td>
<td>Vitis vinifera L. × V. labrusca L.</td>
<td>'Kyohou'</td>
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<tr>
<td>Kiwifruit</td>
<td>Actinidia chinensis Planch.</td>
<td>'Kou-ryoku'</td>
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<tr>
<td>Japanese chestnut</td>
<td>Castanea crenata Siebold &amp; Zucc.</td>
<td>'Tsukuba'</td>
</tr>
<tr>
<td>Japanese persimmon</td>
<td>Diospyros kaki Siebold &amp; Zucc.</td>
<td>'Fuyu'</td>
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<tr>
<td>Apple</td>
<td>Malus domestica Borkh.</td>
<td>'Fuji'</td>
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<tr>
<td>Japanese pear</td>
<td>Pyrus pyrifolia Nakai</td>
<td>'Kousui'</td>
</tr>
<tr>
<td>Peach</td>
<td>Prunus persica (L.) Batsch</td>
<td>'Kawanakajima hakutou'</td>
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<tr>
<td>Japanese apricot</td>
<td>Prunus mume Siebold &amp; Zucc.</td>
<td>'Nankou'</td>
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<td>Pomelo</td>
<td>Citrus grandis (L.) Osbeck</td>
<td>'Chandler', 'Tosa'</td>
</tr>
<tr>
<td>Lemon</td>
<td>Citrus limon (L.) Burm. f.</td>
<td>'Lisbon'</td>
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<tr>
<td>Natsudaidai</td>
<td>Citrus natsudaidai Hayata</td>
<td>'Kawano Natsudaidai'</td>
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<td>Iyo</td>
<td>Citrus iyo hort. ex Tanaka</td>
<td>'Miyauchi'</td>
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<td>Navel orange</td>
<td>Citrus chinensis Osbeck var. brasiliensis Tanaka</td>
<td>'Murakami'</td>
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<tr>
<td>Sastuma mandarin</td>
<td>Citrus unshiu Marcow.</td>
<td>'Mihowas'</td>
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<tr>
<td>Ponkan</td>
<td>Citrus reticulata Blanco</td>
<td>'Kousyun'</td>
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<tr>
<td>Marumi kumquat</td>
<td>Fortunella japonica (Thunb.) Swingle</td>
<td>'Puchimaru'</td>
</tr>
<tr>
<td>Loquat</td>
<td>Eriobotrya japonica (Thunb.) Lindl.</td>
<td>'Nagasakiwase', 'Tanaka'</td>
</tr>
</tbody>
</table>
dynamic viscosity of the liquid (Tyree and Zimmermann, 2002). We passed water of almost constant temperature through the sample; therefore, \( \eta \) should be constant. Thus, we derived the following water flow index:

\[
\text{Water flow index} = \sum_i \frac{r_i}{S} \times (\text{xylem ratio})
\]

where \( r \) is the radius of each vessel element and \( S \) is the xylem area on microscope images. The radius of each vessel element was calculated from microscopic image. The xylem ratio was calculated as:

\[
\text{Xylem ratio} = \frac{\text{xylem area}}{\text{stem section area}}
\]

which was measured from the image taken with the CCD camera using the image analysis software described above, respectively. The calculated vessel area index was defined as total vessel area per mm² cross-section area of the sample.

**Results**

The value of relative hydraulic conductance varied with species (Fig. 2). Vines (kiwifruit and grape) showed the highest values, followed by deciduous trees (e.g. chestnut, Japanese pear, and peach), evergreen citrus (e.g. Kawanonatsudaizai and Satsuma mandarin), and loquat. The highest value for grape was 60 times the lowest value for loquat.

From the photomicrographs, we calculated the diameter and number of vessels and total vessel area of 13 species (Figs. 3 and 4). The diameter also varied among species: the highest average diameter was 6 times the lowest. The average diameter was highest in vines, moderate in persimmon and chestnut and lowest in citrus, deciduous, and loquat trees.

Total vessel area was highest in vines, followed by deciduous rosaceous trees, and low in persimmon, chestnut, and evergreen trees (Fig. 4). The number of
Fig. 3. Vessel diameter distribution among 13 species of fruit trees. Each sample was dyed with 0.5% safranin, and then observed through an optical microscope connected to an LCD-TV. Fifteen to seventeen photographs were taken by a CCD camera mounted on the microscope. We then used image analysis software to calculate the diameter of vessels.
vessels per xylem area was highest in pome fruit and loquat, moderate in stone fruit, and lowest in citrus, vines, chestnut, and persimmon.

Hydraulic conductance was plotted against the calculated vessel area index and water flow index (Fig. 5). The latter relationship had a higher correlation coefficient.

Discussion

Ikeda and Suzaki (1984) made a device for measuring relative hydraulic conductance, in which the water level in the water supply tank was kept constant via a pipe. We simplified the device by omitting the pipe, and topped up the water to the same level before each run. Also, they used an auto-thermometer to control the water temperature, since the viscosity of a liquid changes with temperature. We did not control the water temperature, and instead conducted our measurement at room temperature, which fluctuated between 20 and 25°C. The consequent fluctuation in water viscosity thus had only a minor effect on the measurement.

The functions of stems of standing trees are mechanical support and the transport of water from roots to leaves, whereas those of vines are mainly water transport; thus, vines can more efficiently transport water (Taneda and Tateno, 2004). This explains the very high hydraulic conductance of kiwifruit and grape in our measurements (Fig. 2).

Broadleaved trees that grow in warm areas without freeze–thaw cycles can grow large vessels, enabling vigorous growth (Davis et al., 1999; Taneda and Tateno, 2005). Thus, we expected that evergreen fruit trees that grow mainly in southwest Japan would have larger vessels than the deciduous trees that grow primarily in northern Japan. However, the hydraulic conductance of evergreen trees was lower than that of deciduous trees (Fig. 2). To explain this disagreement and to understand the relationship between climate and water use efficiency, we need to compare the transpiration rate of each tree species. In addition, we need to measure the hydraulic conductance of tropical fruit trees, since the only evergreen trees that we measured were citrus and loquat.

Grape is well known for its drought tolerance, but kiwifruit is drought-sensitive, even though both have high hydraulic conductance (Fig. 2). Thus, we cannot simply explain the degree of drought tolerance by the value of hydraulic conductance. The difference between the two species is explained by differences in their roots:

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**Fig. 4.** Percentage of total vessel area (A) and number of vessels per mm² xylem area (B). Horizontal bars indicate SE.

**Fig. 5.** Relationships between relative hydraulic conductance and calculated vessel area index (total vessel area per mm² cross-section area) (A) or water flow index ($\sum r^4/S \times$ xylem ratio) (B). ** and NS indicate significant at 1% level and not significant ($n=13$) by t-test, respectively.
those of kiwifruit are shallow, while those of grape are deep (Sale, 1983). In oak (Quercus spp.), wide vessels are laid down in the spring and function as a low-resistance pathway early in the growing season, when ample water is available. As the soil dries out during the summer, these wide vessels cease functioning, leaving narrower vessels produced during the stress period to carry the transpiration stream (Locy, 2006). As shown in Figure 3, grape vessels vary from wide to narrow, whereas those of kiwifruit vary little. Grape may be able to survive in dry conditions by carrying the transpiration stream in its narrower vessels.

We defined the calculated vessel area index as vessel area per mm² cross-section area of the sample, expecting that this could be used as an uncomplicated water flow index since this index is easier to calculate than the water flow index which needs to measure the radius of each vessel element. However, hydraulic conductance was plotted against the calculated vessel area index (Fig. 5), and the relationship had an insignificant correlation coefficient. Thus, the vessel area index is unsuitable for expressing water flow in plants.

In contrast, the coefficient of correlation between the water flow index, calculated from the Hagen–Poiseuille law, and the relative hydraulic conductance was significantly high (Fig. 5). It was higher than expected because vessels can lose their conductance even when immersed in water before measurement (Sperry et al., 1988). Our results show that our device is suitable for measuring hydraulic conductance. The measurement of water flow velocity in fruit tree branches will provide information on water uptake in fruit trees.

As we used 1- or 2-year-old twigs with a diameter of 7 to 9 mm, we did not conclude that we could measure the hydraulics of whole trees. Several methods are used to detect hydraulic parameters to measure whole trees, including hydraulic architecture (Zimmermann, 1978) and the Huber value (Grier and Waring, 1974). Moreover, the relationships among hydraulic conductivity, sap flow, and transpiration rate must be investigated to explain the hydraulics of fruit trees comprehensively. Also, the effects of pruning and training on trees must be taken into careful consideration, since fruit trees, unlike forest trees, are pruned and trained annually.

**Literature Cited**


