Seasonal variations of gas exchange and water relations in deciduous and evergreen trees in monsoonal dry forests of Thailand

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Summary This study compared leaf gas exchange, leaf hydraulic conductance, twig hydraulic conductivity and leaf osmotic potential at full turgor between two drought-deciduous trees, *Vitex peduncularis* Wall. and *Xylia xylocarpa* (Roxb.) W. Theob., and two evergreen trees, *Hopea fereia* Lanessan and *Syzygium cumini* (L.) Skeels, at the uppermost canopies in tropical dry forests in Thailand. The aims were to examine (i) whether leaf and twig hydraulic properties differ in relation to leaf phenology and (ii) whether xylem cavitation is a determinant of leaf shedding during the dry season. The variations in almost all hydraulic traits were more dependent on species than on leaf phenology. Evergreen *Hopea* exhibited the lowest leaf-area-specific twig hydraulic conductivity (leaf-area-specific $K_{\text{twig}}$), lamina hydraulic conductance ($K_{\text{lamina}}$) and leaf osmotic potential at full turgor ($\Psi_o$) among species, whereas evergreen *Syzygium* exhibited the highest leaf-area-specific $K_{\text{twig}}$, $K_{\text{lamina}}$ and $\Psi_o$. Deciduous *Xylia* had the highest sapwood-area-specific $K_{\text{twig}}$, along with the lowest Huber value (sapwood area/leaf area). More negative osmotic $\Psi_o$ and leaf osmotic adjustment during the dry season were found in deciduous *Vitex* and evergreen *Hopea*, accompanied by low sapwood-area-specific $K_{\text{twig}}$. Regarding seasonal changes in hydraulics, no remarkable decrease in $K_{\text{lamina}}$ and $K_{\text{twig}}$ was found during the dry season in any species. Results suggest that leaf shedding during the dry season is not always associated with extensive xylem cavitation.

Keywords: cryo-SEM, drought, embolism, leaf abscission, phenology, water relations.

Introduction

The tropical dry forests provide an interesting system for studying the integration of carbon, nitrogen and water use with respect to leaf lifespan because of a large range of leaf phenological behaviours exhibited by the co-occurring deciduous and evergreen trees (Mooney and Miller 1985, Holbrook et al. 1995, Eamus 1999, Eamus et al. 1999). Several studies on water relations have focused on leaf osmotic potential (Sobrado 1986), leaf hydraulic conductance (Brodribb and Holbrook 2003, 2005) and stem hydraulic conductivity (Sobrado 1993, Machado and Tyree 1994, Brodribb et al. 2002, Choat et al. 2005) in tropical forest trees with contrasting leaf phenologies. Goldstein et al. (1989) and Sobrado (1993) showed that, in neotropical dry forests, drought-deciduous trees maximize carbon productivity and water loss for a short period in the wet season with a more efficient vascular system, whereas evergreens have lower maximum hydraulic efficiency, but greater safety from xylem embolism. Choat et al. (2005) showed that, in a northeastern Australian forest, drought-deciduous trees had wider xylem vessels, lower wood density and higher sapwood-area-specific hydraulic conductivity than evergreen trees. On the other hand, large overlaps in the values of stem hydraulic conductivity (Brodribb et al. 2002) and leaf hydraulic conductance (Brodribb and Holbrook 2005) were reported between deciduous and evergreen trees in Costa Rica. In Mediterranean woody plants, no differences in hydraulic traits were found between evergreen and deciduous trees (Nardini and Salleo 2000).

Leaf bud break generally occurs during the late dry season, the most severe drought period of the year in Thailand.
A high water potential because of rehydration from water stored within the plant body or subsoil is necessary for the subsequent leaf bud break and expansion (Reich and Borchert 1984, Borchert 1994a, 1994b). A decrease in the transport capacity of the xylem caused by drought-induced cavitation has been hypothesized to play an important role in dry season leaf shedding in tropical dry forest trees (Sobrado 1986, Borchert 1994b, Eamus 1999). Recent studies have shown that a decrease in stem conductivity during the dry season occurs in a neotropical dry forest, but not in all deciduous trees (Brodribb et al. 2002, Brodribb and Holbrook 2003). Because leaf expansion and cell enlargement require water, a substantial portion of the xylem function or a refilling capacity should be retained over the dry season even in drought-deciduous trees. Although a decrease in stem and leaf hydraulics before or after leaf shedding was generally found in winter-deciduous trees (Sperry et al. 1988, Sperry 1993, Salleo et al. 2002), the role of xylem cavitation in the phenological behaviour of the leaf is less clearly understood in tropical dry forest trees (Gutiérrez-Soto et al. 2008).

The relationships between transpiration rates and leaf water potential are determined by soil-to-leaf hydraulic conductance. Recent studies have shown that lamina hydraulic resistance is an important component, representing 30–80% of the total hydraulic resistance within a plant body in a given species (Becker et al. 1999, Nardini and Salleo 2000, Brodribb et al. 2002, Sack and Holbrook 2006). Brodribb et al. (2002) showed a positive correlation between lamina hydraulic conductance and photosynthetic capacity during seasonal changes. Hydraulic properties in leaves and stems during the dry season can thus become the main constraint on carbon gain in canopy trees and may determine a resource-use strategy based on the differences in leaf phenology.

The aims of this study are to examine (i) whether leaf and twig hydraulic properties and water relations differ between evergreen and deciduous trees and (ii) whether xylem cavitation in leaves and twigs is an important determinant of leaf shedding. To carry out this study, a parallel observation of the seasonal variations in leaf gas exchange, leaf osmotic potential and water transport efficiency of leaves and twigs at the top canopies of adult deciduous and evergreen trees with con-

![Figure 1. Seasonal variations in microclimate and leaf gas exchange in 2007. Daily mean air temperatures (soil lines) and daily rainfall (vertical bars) at (A) the deciduous forest and (B) the evergreen forest, and (C, D) the maximum water vapour stomatal conductance and (E, F) the maximum net photosynthetic rates in deciduous trees (Vitex and Xyilia) and evergreen trees (Hopea and Syzigium). Arrows show measurement days. Error bars show ±1 SD.](https://academic.oup.com/treephys/article-abstract/30/8/935/1692849)
trasting leaf phenologies was carried out in Thailand. To directly detect xylem cavitation, transverse sections of frozen twigs were observed with cryo-scanning electron microscopy (cryo-SEM).

Materials and methods

Study sites and plant species

This study was conducted in a mixed deciduous forest (MDF) and a dry evergreen forest (DEF) in the lowlands of Thailand. The MDF study site was set at the Mae-Klong Watershed Research Station (14°34′ N, 101°55′ E, 160 m a.s.l.), about 250 km northwest of Bangkok, located on a branch of the Khwae Noi River in Western Thailand. The DEF study site was set at the Sakaerat Environmental Research Station (14°34′ N, 101°55′ E, 563 m a.s.l.), about 180 km northwest of Bangkok, located on a branch of the Mekong River in Northeastern Thailand. Details of the methods of microclimate measurements were previously described by Ishida et al. (2006). In 2007, the mean temperature and the annual rainfall at the MDF were 25.3 °C and 1400 mm, respectively, and those at the DEF were 24.1 °C and 1200 mm, respectively (Figure 1). There was a distinct dry season of ∼4 months, from November to February, during which <1% of annual rainfall occurred.

MDFs consist of many tree species with tall-canopy trees (∼25–30 m high), and almost all woody plants are drought-deciduous trees; however, dipterocarp trees are rare (Marod et al. 1999). MDFs occur on limestone hills from Western to Northern Thailand, the soil is relatively eutrophic and the soil pH is close to neutral (around 6.5) (Rundel and Boonpragob 1999). MDFs are distributed in areas from Eastern to Northeastern Thailand. The soil in these areas is of sandstone origin and acidic (pH of around 4.5) and has relatively poor nutrient content with high porosity (Ishida et al. 2006, Murata et al. 2009). A few dipterocarp tree species, such as Hopea ferrea Lanessan and Shorea henryana Pierre, with tall canopies (∼25–35 m high) are predominant in MDFs (Bunyavejchewin 1999).

Two deciduous trees, *Xyliya xylocarpa* (Roxb.) W. Theob. and *Vitex peduncularis* Wall., in the MDF and two evergreen trees, *Hopea ferrea* Lanessan and *Syzygium cumini* (L.) Skeels, in the DEF were selected. The uppermost canopy heights above the ground were 23–27 m, and the trunk diameters at breast height were 38–75 cm (Table 1). To access the uppermost canopies, a 45-m-high scaffolding tower and a crane car were used in the MDF and DEF, respectively.

Measurements of leaf gas exchange

Five measurement dates were chosen in 2007: February in the late dry, April in the early wet, July in the middle wet, October in the late wet and December in the early dry seasons (Figure 1). An adult tree in each species and five shoots from the top or outer edge of the canopy in each tree were selected. The maximum net assimilation rates (*A* max) and water vapour stomatal conductance (*G* max) in a fully expanded sunlit leaf selected from each shoot were measured for the period from 0900 to 1100 hours to avoid midday depression (Ishida et al. 2006) using an open-flow, portable measurement system (LI-6400; LI-COR, Lincoln, NE). The measurements were conducted under conditions of 380 mmol mol$^{-1}$ CO$_2$ in the inlet gas stream and 2000 mmol m$^{-2}$ s$^{-1}$ photosynthetic photon flux (PPF) using a 6-cm$^2$ chamber with red–blue light-emitting diodes. After the measurements, the leaves were collected and the leaf discs were then cut with a borer. The leaf discs were oven-dried (70 °C, 72 h) and weighed to determine the leaf mass per area (LMA).

Measurements of water relations

After measuring the leaf gas exchange, several branches at the top or from the outer edge of the canopies were collected to examine the leaf and twig water relations. The cut ends of the branches were immediately re-cut under water and then transferred to the laboratory where they were again re-cut under water. On the following day, canopy leaves were collected from seven branches as samples for measuring leaf osmotic potentials at full turgor (*Ψ*$_o$). Each sample was double-wrapped with a thin film of polyvinyl chloride to prevent dehydration, and the samples were transferred into a freezer. Subsequently, with the extract from these samples, the values of *Ψ*$_o$ were determined under constant room temperature (20 °C) using an osmometer (VAPRO 5520; Wescor, UT).

<table>
<thead>
<tr>
<th>Tree species (family)</th>
<th>Tree height (m)</th>
<th>Diameter at breast height (m)</th>
<th>Leaf phenology</th>
<th>Timing of leaf flushing</th>
<th>Wood density (g cm$^{-3}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vitex peduncularis (Verbenaceae)</td>
<td>23</td>
<td>0.64</td>
<td>Deciduous</td>
<td>Late dry season</td>
<td>0.52–0.93</td>
</tr>
<tr>
<td>Xyliya xylocarpa (Leguminosae)</td>
<td>25</td>
<td>0.59</td>
<td>Deciduous</td>
<td>Late dry season</td>
<td>0.83–0.93</td>
</tr>
<tr>
<td>Hopea ferrea (Dipterocarpaceae)</td>
<td>25</td>
<td>0.38</td>
<td>Evergreen</td>
<td>Throughout the year (dependent on individuals)</td>
<td>0.96–1.05</td>
</tr>
<tr>
<td>Syzygium cumini (Myrtaceae)</td>
<td>27</td>
<td>0.75</td>
<td>Evergreen</td>
<td>Late dry season</td>
<td>0.73–0.87</td>
</tr>
</tbody>
</table>

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ment of hydraulics, a vacuum pump method was used (Sack et al. 2002). After rehydration, measurements were conducted on the subsequent day of sampling. A shoot branch of ~20 cm in length was placed inside a clear chamber of hard plastic (8 l in volume) and the cut end of a twig was connected with a Tygon tube that led to a water (10 mM KCl solution) reservoir placed on an electronic balance in a room. The solution for the hydraulic measurements was filtered through a 0.2-mm pore diameter filter before introduction into the tubing system. Water fluxes from the balance through the twig were measured at four negative-pressure points from 30 to 80 kPa using a vacuum pump. The slope between the pressure points and water flow rates is the hydraulic conductance ($K$) (Sack et al. 2002). After measuring the whole-shoot hydraulic conductance ($K_{\text{shoot}}$), the leaves were removed and the hydraulic conductance of the defoliated twig ($K_{\text{defoliated}}$) was then measured. The lamina hydraulic conductance ($K_{\text{lamina}}$) was calculated as follows: ($1/K_{\text{lamina}}$) = ($1/K_{\text{shoot}}$) − ($1/K_{\text{defoliated}}$). After the measurement, the top part of the shoot was cut, a part of the 1-year-old stem was retained inside the chamber and the water flux was measured under sub-atmospheric pressure. The length of the stem was measured to standardize the $K$ values in terms of length, and the hydraulic conductivity of the twig ($K_{\text{twig}}$) was calculated. Because of rapid irradiance-induced variations in $K_{\text{lamina}}$ (Cochard et al. 2007, Voicu et al. 2008), all the hydraulics were measured under constant room lighting (10 µmol m$^{-2}$ s$^{-1}$ PPF). The influence of water viscosity because of the slight seasonal differences in the room temperature was corrected at 25 °C, following the procedure adopted by Yang and Tyree (1993).

After these measurements, the projected leaf area of each shoot was computed from the digital image obtained using a digital camera. A segment of the 1-year-old stem was fixed with formaldehyde–acetic acid–alcohol. Transverse sections of the stem with a thickness of 15–30 mm were taken with a sliding microtome (HM 400R; Micron, Walldorf, Germany) and double-stained with safranin and gentian violet. The transverse area of sapwood, the number of vessels per unit sapwood area (vessel density), the cross-sectional area and the long and short radii in each xylem vessel were determined on the digital images of the obtained transverse sections with a light microscope (ECLIPSE 80i; Nikon, Tokyo, Japan). More than 200 vessels in each twig sample were counted. The digital pictures were analysed using the image analysis software Image-J (Ver. 1.41, National Institutes of Health, Bethesda, MD).

On the basis of the anatomical characteristics, the theoretical hydraulic conductivity per unit sapwood area ($K_{\text{theo}}$) in twigs was calculated as:

$$K_{\text{theo}} = (1/A)(1-L)(\rho/\eta)\pi \sum_{i=1}^{n} \left(a_i b_i / 4 \left(a_i^2 b_i^2 / (a_i^2 + b_i^2)\right)\right)$$

where $A$ is the sapwood area (in square metres), $a$ and $b$ are the long and short radii in xylem vessels (in metres), respectively, $\rho$ is the density of water (997 kg m$^{-3}$ at 25 °C) and $\eta$ is the viscosity of water ($0.89 \times 10^{-3}$ MPa s at 25 °C). Equation (1) is obtained by applying Hagen–Poiseuille’s law to an elliptical pipe. The $a/b$ ratios were 1.4–1.5 in the examined trees. If $K_{\text{theo}}$ was calculated under an assumption that vessels are circular pipes, then the $K_{\text{theo}}$ values were overestimated.
Table 2. Xylem vessel diameter and the distribution parameters and the number of xylem vessels per unit sap area (vessel density). Different letters beside the mean values show significant differences among species by Scheffé’s F-test ($P < 0.05$).

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Mean (µm)</th>
<th>Median (µm)</th>
<th>Skewness</th>
<th>Kurtosis</th>
<th>Vessel density (no. mm$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vitex peduncularis</td>
<td>21.7b</td>
<td>20.5b</td>
<td>0.85a</td>
<td>0.82a</td>
<td>304b</td>
</tr>
<tr>
<td>Xyilia xylocarpa</td>
<td>26.1b</td>
<td>25.0c</td>
<td>0.37b</td>
<td>−0.71b</td>
<td>391b</td>
</tr>
<tr>
<td>Hopea ferrea</td>
<td>13.3a</td>
<td>15.6a</td>
<td>0.03c</td>
<td>−0.77b</td>
<td>854a</td>
</tr>
<tr>
<td>Syzygium cumini</td>
<td>25.6b</td>
<td>26.6c</td>
<td>−0.22c</td>
<td>−0.52b</td>
<td>430b</td>
</tr>
</tbody>
</table>

by 5–8%. $L$ is the cavitation ratio (0–1) in the xylem vessels obtained from cryo-SEM observation, as follows.

**Cryo-SEM observation**

To examine the state of progression of xylem cavitation, direct observation of transverse sections of 1-year-old twigs was conducted by a cryo-SEM in the early wet (just after full leaf expansion in deciduous trees), middle wet, early dry (before leaf shedding in deciduous trees) and late dry (after leaf shedding in deciduous trees) seasons (Canny 1997, McCully et al. 2009). At dusk, a shoot with leaves was put directly into liquid nitrogen in situ. After obtaining an equilibrium temperature (disappearance of the bubble sound), the frozen shoot was separated from the tree with scissors. Two 1-year-old twigs (~9 mm in diameter) were collected from individual trees. The twig samples were kept in dry ice, transferred to a laboratory and stored at −80 °C until the cryo-SEM observation.

The transverse faces of the stems were cleanly cut with a sliding microtome (HM 500E; Micron, Germany) under −20 °C and then were observed with a cryo-SEM (S4500; Hitachi, Tokyo, Japan). The vessels that had been filled with water and the cavitated vessels could be easily distinguished by white and black colours on the cryo-SEM images, respectively (Utsumi et al. 1998), and the ratio of the number of cavitated vessels to the number of total vessels (cavitation ratio, $L$) was calculated.

**Statistical analysis**

Statistical comparisons were conducted with the software StatView (version 4.5J; ABACUS Concepts, Berkley, CA). Differences and interactions among the species and seasons were tested using a two-way ANOVA in each variable. To clarify the seasonal trends within a species or the differences among species, multiple comparisons on average in each variable were conducted using Scheffé’s method as a post hoc test of ANOVA. Statistical significance was recognized at $P < 0.05$. The cavitation ratios were compared between the wet and dry seasons and among species using two-way ANOVA.

**Results**

**Seasonal changes in microclimate, leaf phenology and gas exchange**

The first rain (2–3 mm day$^{-1}$) was recorded on 12 and 13 February in 2007 in the DEF and the MDF, respectively (Figure 1). Following the onset of the dry season in November 2006, no rainfall of more than 10 mm day$^{-1}$ occurred until the middle of March 2007. In deciduous trees, the green leaves were retained until the middle dry season (January). Bud break of new leaves occurred during the late dry season (February) (Table 1). Thus, the green-less period was not lengthy for each tree (Sukwong et al. 1975).

Leaves of the evergreens measured in February showed a pronounced drop in stomatal conductance and net photosynthetic rates (Figure 1). The seasonal peaks in $G_{\text{max}}$ and $A_{\text{max}}$ were found during the wet season, and the timing of the peak depended on the species. The low $G_{\text{max}}$ and $A_{\text{max}}$ during the dry season indicated severe drought.

**Xylem anatomy**

All the species had diffuse porous hardwood. The frequency distribution of the mean diameter of individual xylem vessels in 1-year-old twigs and the distribution parameters are represented in Figure 2 and Table 2, respectively. The vessel diameter distributions showed a unimodal pattern in all species. Evergreen Hopea had the narrowest vessel width on average and the highest vessel density. In the distribution patterns of vessel diameters, deciduous Vitex and Xyilia had higher skewness than evergreen Hopea and Syzygium. The positive values of skewness in deciduous trees indicate that some large vessels are included in their sapwood. Although the rare and large vessels in deciduous trees contribute to a large water flow based on Hagen–Poiseuille’s law (Tyree and Ewers 1991), there was no clear difference in the sapwood-area-specific $K_{\text{twig}}$ between the groups of deciduous trees and evergreen trees (Table 3).

**Seasonal changes in leaf and twig hydraulic traits**

Results of two-way ANOVA show that there were significant differences among species and seasons and in the interactions between season and species in all hydraulic traits in leaves and twigs, except for the interaction between seasons and species in leaf-area-specific $K_{\text{twig}}$. LMA was significantly higher in evergreen trees than in deciduous trees (Table 3). However, hydraulic traits in leaves and twigs were more dependent on species than leaf phenology. Xyilia had the highest sapwood-area-specific $K_{\text{twig}}$ among the species, along with the lowest HV. This indicates that the high hydraulic efficiency of twigs in Xyilia supports a large leaf area within a shoot. The values of $\Psi_{c}$ also overlapped between evergreen and deciduous trees. The lowest $\Psi_{c}$ among the species was found in...
evergreen *Hopea*, along with the lowest leaf-area-specific \( K_{\text{twig}} \) and \( K_{\text{lamina}} \). In contrast, the highest \( \Psi_o \) among the species was found in evergreen *Syzygium*, along with the highest leaf-area-specific \( K_{\text{twig}} \) and \( K_{\text{lamina}} \) among the species.

Regarding seasonal changes (Figure 3), depression in \( \Psi_o \) during the dry season (i.e., effective osmotic adjustment) was found in deciduous *Vitex* and evergreen *Hopea*, and they exhibited relatively low sapwood-area-specific \( K_{\text{twig}} \) throughout the year. Furthermore, leaf osmotic adjustment during the dry season was more dependent on species than on leaf phenology. No reduction in \( K_{\text{lamina}} \) and \( K_{\text{twig}} \) during the dry season was found in any of the trees, except that sapwood-area-specific \( K_{\text{twig}} \) in *Xylia* decreased progressively from the wet to dry season. However, a substantial portion of the xylem function was retained throughout the seasons in all species.

A direct observation was conducted to examine whether cavitation occurred in xylem vessels within 1-year-old twigs using cryo-SEM (Figure 4, data not shown in the mid-wet season). The annually averaged cavitation ratios were 14.2% in evergreen *Hopea* and 18% in deciduous *Syzygium*. The percentage of cavitated xylem vessels in the wet and dry seasons was 7 and 18% in deciduous *Vitex*, 54 and 33% in deciduous *Xylia*, 27 and 16% in evergreen *Hopea* and 44 and 51% in evergreen *Syzygium*, respectively. There was no common trend in the seasonal change in the cavitation ratio among species (\( P > 0.05 \) when compared between the wet and dry seasons). The values of \( K_{\text{theo}} \) calculated from the cavitation ratio and vessel radii were relatively consistent with those of sapwood-area-specific \( K_{\text{twig}} \) directly measured using a vacuum method (Table 3).

### Discussion

One major goal of this study was to examine the differences in water relations and hydraulic traits between drought-deciduous and evergreen trees. In general, stomatal conductance and net photosynthetic rate were higher in deciduous trees than in evergreen trees in tropical dry forests (Goldstein et al. 1989, Eamus 1999, Sobrado 1993, Ishida et al. 2006). If soil water potential was similar between the MDF and DEF, the high transpiration rates because of high stomatal conductance in deciduous trees would be compensated by wider vessels, low leaf water potential in daytime or high HV (deceased transpiration surface). In the present study, no differences in leaf and twig hydraulic traits and xylem anatomy in twigs were observed, and these traits were more dependent on species than leaf phenology (Table 2, Figure 2). Furthermore, no difference in leaf osmotic potential was found between deciduous and evergreen trees and leaf osmotic adjustment was more dependent on species than leaf phenology. Because a parallel correlation between leaf osmotic potential at full turgor and daytime leaf water potential was frequently found (Ishida et al. 1992), daytime leaf water potential would also be dependent on species. Deciduous *Xylia* with large vessel areas and sapwood-area-specific \( K_{\text{twig}} \) had the lowest HV (Table 3). High stomatal conductance and transpiration rates in deciduous trees would be supported by total water balance among xylem anatomy, HV and leaf water potential within a shoot (Shimizu et al. 2005).

Daytime xylem water potential is maintained at values unlikely to cause catastrophic cavitation (Tyree et al. 1998, Nardini and Salleo 2000). Our results showed that deciduous *Xylia* and evergreen *Syzygium* with higher sapwood-area-specific \( K_{\text{twig}} \) and \( \Psi_o \) had higher cavitation ratios than deciduous *Vitex* and evergreen *Hopea* with lower sapwood-area-specific \( K_{\text{twig}} \) and \( \Psi_o \) (Table 3). If the low leaf osmotic potential at full turgor was connected with low leaf water potential in the daytime, then deciduous *Vitex* and evergreen *Hopea* would have low vulnerability to xylem cavitation (Tyree and Ewers 1991). Increasing cavitation resistance in vessels under drought is inversely related to total pit area per vessel rather than vessel diameter (Hacke and Sperry 2001, Wheeler et al. 2005, Hacke et al. 2006, Choat et al. 2008), and rare large pit pores may strongly affect vulnerability to drought-induced embolism (Sperry and Tyree 1988, Choat et al. 2003, Wheeler et al. 2005). Recent studies have found negative cor-

### Table 3. Mean values in leaf dry mass per area (LMA), maximum water vapour stomatal conductance (\( G_{\text{max}} \)) and leaf water and twig hydraulic properties in 1-year-old twigs. Different letters beside the mean values show significant differences among species by Scheffé’s \( F \)-test (\( P < 0.05 \)).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Unit</th>
<th>Deciduous trees</th>
<th>Evergreen trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>LMA</td>
<td>g m(^{-2})</td>
<td>1.15b 1.44a</td>
<td>1.36c 1.65b</td>
</tr>
<tr>
<td>( G_{\text{max}} ) during the wet season</td>
<td>mol m(^{-2}) s(^{-1})</td>
<td>0.439a 0.332ab</td>
<td>0.136c 0.299b</td>
</tr>
<tr>
<td>Area of individual xylem vessels</td>
<td>( \mu \text{m}^2 )</td>
<td>431a 617b</td>
<td>204c 546ab</td>
</tr>
<tr>
<td>Long radius/short radius ratio in individual xylem vessels</td>
<td></td>
<td>1.45ab 1.44a</td>
<td>1.40a 1.50b</td>
</tr>
<tr>
<td>( K_{\text{theo}} )</td>
<td>kg m(^{-1}) s(^{-1}) MPa(^{-1})</td>
<td>3.4a 6.3b</td>
<td>1.7c 3.5a</td>
</tr>
<tr>
<td>HV</td>
<td>( 10^{-4} ) m(^{2}) m(^{-2})</td>
<td>1.23a 0.56b</td>
<td>1.00a 1.23a</td>
</tr>
<tr>
<td>( K_{\text{lamina}} )</td>
<td>( 10^{-4} ) kg m(^{-2}) s(^{-1}) MPa(^{-1})</td>
<td>0.72a 0.45b</td>
<td>0.39b 1.85c</td>
</tr>
<tr>
<td>leaf-area-specific ( K_{\text{twig}} )</td>
<td>( 10^{-5} ) kg m(^{-2}) s(^{-1}) MPa(^{-1})</td>
<td>2.1a 2.8a</td>
<td>1.3b 3.6c</td>
</tr>
<tr>
<td>sapwood-area-specific ( K_{\text{twig}} )</td>
<td></td>
<td>1.9a 7.7b</td>
<td>1.3a 3.4c</td>
</tr>
<tr>
<td>( \Psi_o )</td>
<td>MPa</td>
<td>-1.43a -1.15b</td>
<td>-1.75c -0.81d</td>
</tr>
</tbody>
</table>
relations between wood density and minimum leaf water potential (Meinzer 2003, Ackerly 2004, Bucci et al. 2004, Santiago et al. 2004) or leaf osmotic potential at full turgor (Ishida et al. 2008, Meinzer et al. 2008), indicating that high xylem construction cost in stems is needed to increase resistance to drought-induced cavitation (Hacke et al. 2006).

There is evidence showing that deciduous trees are more vulnerable to drought-induced xylem embolism and have low wood density in an Australian dry forest (Choat et al. 2003, 2005). In contrast, Sobrado (1997) showed that there was no difference in the vulnerability curves between coexisting evergreen and deciduous trees in a neotropical dry forest. In the present study, not only wood density but also $\Psi_o$ overlapped between deciduous and evergreen trees, indicating that the difference in vulnerability to xylem cavitation could be due to species more than leaf phenology.

Another goal of this study was to examine the role of xylem cavitation in leaf shedding during the dry season in deciduous trees. There is clear evidence that prolonged drought induces xylem cavitation and results in leaf shedding and plant death in seedlings of tropical forest trees (Engelbrecht and Kursar 2003, Tyree et al. 2003). Drought-induced embo-
lism in stems was linked to the timing of leaf drop (Sobrado 1993, 1997) and leaf shedding was preceded by a large decline in $K_{\text{leaf}}$ (Brodribb and Holbrook 2003) in some deciduous trees in the neotropics. However, no remarkable depression in leaf and twig hydraulic efficiency during the dry season was found in the present study (Figure 2). The observation by cryo-SEM also showed that no distinct expansion in cavitation during the dry season was found (Figure 4). These results indicate that leaf abscission in drought-deciduous trees is not always associated with large xylem cavitation (Brodribb et al. 2002, Choat et al. 2006) or xylem conduits can be easily refilled after leaf shedding in deciduous trees, even if xylem cavitation is linked to leaf shedding. Brodribb et al. (2002) also reported that a substantial portion of the xylem function was retained even during the dry season, enabling the plants to do leaf flushing for the driest period without a remarkable drop in xylem water potential.

The long leaf lifespan in evergreens has an advantage in that it enables carbon assimilation to start quickly following the onset of the wet season without the construction of new leaves with high LMA (i.e., high investment of carbon cost on leaves). On the other hand, the early leaf flushing and maintenance of hydraulic capacity in stems during the dry season give drought-deciduous trees an advantage in that the new leaves will be ready to quickly start carbon assimilation following the onset of rain. Such early flushing in deciduous

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Figure 4. Digital images of the transverse surface of twigs in the early wet, the early dry and the late dry seasons in deciduous trees (*Vitex* and *Xyilia*) and evergreen trees (*Hopea* and *Syzygium*) by using cryo-SEM. The xylem conduits with black colour indicate cavitated vessels, and xylem conduits with white colour indicate vessels filled with water.
trees has been observed not only in Thailand, but also in India (Singh and Kushwaha 2005), Java (Rivera et al. 2002), Australia (Williams et al. 1997), Brazil (Rivera et al. 2002) and Costa Rica (Rivera et al. 2002, Gutiérrez-Soto et al. 2008). The green-less period in each tree is not lengthy, and the synchrony of the timings of leaf fall and bud break among tree species is low (Elliott et al. 2006). The unique phenological behaviour has posed researchers with the question of what factors act as the trigger of leaf phenological behaviour. Recent attention has focused more on the photoperiod than on rainfall or soil water as an environmental cue in leaf bud break (Borchert and Rivera 2001, Rivera et al. 2002, Elliott et al. 2006, Williams et al. 2008). Williams et al. (2008) examined the timing of leaf flushing in 24 tree species in Thailand. The result showed that 38% of these species exhibit a pattern of photoperiod control, 25% show a pattern of rainfall control and the remaining 37% did not have phenological patterns consistent with either photoperiod or rainfall as the proximate trigger of leaf flushing, indicating that there is a large variation in the mechanisms for regulating leaf phenology among species. The maintenance of hydraulic capacity in stems during the dry season would be considered an important factor for allowing early leaf flushing in drought-deciduous trees.

Because drought-deciduous and evergreen forests exhibit allopatric distribution in Southeast Asia, it is apparent that their habitats are dependent on soil properties. In drought-deciduous forests in Thailand, MDFs develop in eutrophic limestone areas and drought-deciduous forests or drought dipterocarp forests (DDFs) develop in areas of shallow, sandy soil (Rundel and Boonpragob 1995). The top-canopy heights are taller in MDF than in DDF, and dipterocarp trees are predominant in DDF. Rooting depth in individual trees or forests strongly affects water relations and water use. Previous studies have hypothesized that coexisting evergreens have a deeper root system than deciduous trees (Sobrado 1993, Eamus 1999). On the other hand, several studies involving stable hydrogen isotopes in xylem sap have revealed that evergreens tended to access water primarily from shallower soil than deciduous trees in the Mediterranean (Valentini et al. 1992) and Brazilian savannas (Jackson et al. 1999). Unfortunately, in Thailand, the differences in rooting depth of woody plants with different leaf phenologies are not well known. Probably, eutrophic soil in MDFs or shallow soil with poor nutrients in DDFs favours trees with a deciduous leaf pattern and thick soil with poor nutrients in DEFs favours trees with an evergreen leaf pattern (Rundel and Boonpragob 1995, Ishida et al. 2006, Murata et al. 2009). However, because forest fires frequently occur in MDF and DDF during the dry season, other factors, such as fires and historical human activity, most likely affect the origin and maintenance of natural forests in Thailand.

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