Tree Physiology 26, 899–904

Interspecific variation in vessel size, growth and drought tolerance of broad-leaved trees in semi-arid regions of Kenya

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Received July 12, 2005; accepted October 5, 2005; published online April 3, 2006

Summary In semi-arid regions, trees often wither during the dry season. Withering is sometimes manifest as die-back, whereby whithering results in shoot death, which progresses downward from the uppermost part of the crown. In this study, we measured the relationships between height growth and diameter at breast height, die-back frequency and severity, vessel size and specific hydraulic conductivity of four evergreen (*Senna siamea* (Lamk) H.S. Irwin & Barneby, *Jacaranda mimosifolia* D. Don, *Azadirachta indica* A.H.L. Juss and *Acacia gerrardii* Benth.) and one deciduous (*Melia volkensii* Gürke) plantation tree species in Kenya, which has a conspicuous dry season. Die-back occurred readily in some species, but not in others. *Senna siamea* showed the highest specific hydraulic conductivity and the highest growth rate among the five species and was quite susceptible to die-back. Among species, height growth and specific hydraulic conductivity were positively correlated with vessel size and negatively correlated with die-back frequency, suggesting a trade-off between growth rate and drought tolerance. This implies that an adaptation to rapid growth under humid conditions leads to low drought tolerance. However, the deciduous tree *Melia volkensii* showed high specific hydraulic conductivity and growth, with no symptoms of die-back, implying that a mechanism associated with the deciduous habit results in drought avoidance by reducing the requirement for water during the dry season.

Keywords: deciduous tree, die-back, drought stress, water transport, xylem architecture.

Introduction

Soil water availability is an important environmental factor that greatly affects plant survival, growth and reproduction (Tyree and Sperry 1989, Mencuccini and Comstock 1997, Tyree et al. 1998, Henzler et al. 1999, Comstock 2000, Tsuda and Tyree 2000, Nardini et al. 2001, Vilagrosa et al. 2003). Drought stress leads to several physiological consequences, depending on diverse traits related to water movement in plants, such as stomatal behavior (Sperry et al. 1998, Hacke et al. 2000, Domec et al. 2005), photosynthetic capacity (Brodribb and Feild 2000), turgor loss point of leaf cells (Alder et al. 1996, Brodribb et al. 2003), and water transport capability of the xylem. These traits allow environmental adaptation to be achieved in many different ways.

Among several characteristics affecting plant water status, vessel size has been the focus of many studies (e.g., Zimmermann 1978, Dixon et al. 1984, Cochard and Tyree 1990, Sobrado 1996, Hacke and Sauter 1996, Lovisolo and Schubert 1998, Schubert et al. 1999, Thomas et al. 2004). There are two adaptive requirements affecting a vessel size, namely, water transportation efficiency and vulnerability to cavitation. On the one hand, water flow resistance in vascular tissue decreases with increasing vessel size, as predicted by the Hagen-Poiseuille law (Tyree and Zimmermann 2002). On the other hand, there is evidence that large vessels are more vulnerable to embolism or cavitation (Sperry et al. 1994, Davis et al. 1999). Xylem dysfunction, as a result of cavitation-induced embolism (Holbrook and Putz 1989), drastically lowers conductivity in stems (Cochard et al. 1992, Linton et al. 1998) and may ultimately lead to plant death (Magnani and Borghetti 1995).

Although there is considerable evidence that freezing-induced cavitation is enhanced by larger vessels (Ewers 1985, Pittermann and Sperry 2003), the relationship between vessel size and drought-induced cavitation remains unclear. In angiosperms, it is supposed that drought-induced cavitation occurs when the pressure difference between an adjacent water-filled conduit and an air-filled conduit is sufficiently large (Crombie et al. 1985, Tyree and Sperry 1989, Cochard et al. 1992, Salleo et al. 1996, Sperry et al. 1996, Tognetti et al. 1996). The air-water meniscus is pulled into the water-filled conduit through inter-conduit pores, resulting in rupture of the water column. According to Young-Laplace law, the pressure difference required to cause cavitation is inversely proportional to the diameter of the largest inter-conduit pore (Schultz and Matthews 1988, Tyree and Sperry 1989, Tognetti et al. 1996). If the diameter of the pit pore is positively correlated with vessel size, as suggested by Martinez-Vilata et al. (2002), a plant with large diameter vessels may be more vulnerable to drought-induced cavitation than a plant with small diameter vessels.

In arid and semi-arid regions of Kenya, drought-induced embolism and the consequent decrease in xylem conductivity often result in symptoms of die-back, in which a tree withers downward from the top. The tree species grown in plantations in Kenya vary in growth and tolerance to drought stress. Some species tend to have low hydraulic conductivity and experience little die-back, whereas other tree species are quite vulnerable to die-back during dry seasons. Such variability provides an opportunity to study how hydraulic anatomy influences the requirements for water transportation efficiency and drought tolerance under conditions of high water stress.

We investigated inter-specific variation in the growth and drought tolerance as assessed by the frequency and extent of and water relations of five plantation tree species in Kenya: evergreen *Senna siamea* (Lamk) H.S. Irwin & Barneby, deciduous *Melia volkensii* Gürke, evergreen *Jacaranda mimosifolia* D. Don, evergreen *Azadirachta indica* A.H.L. Juss and evergreen *Acacia gerrardii* Benth.

Materials and methods

Study sites

The field study was conducted at a research site in Tiva, Kitui Prefecture, Kenya (01°19′ S, 36°55′ E, 1127 m above sea level). The site experiences a rainy (October to May) and a dry (June to September) season. Mean annual precipitation is about 619 mm (from 1995 to 1999). The precipitation during our study was 421 mm in 1995, 396 mm in 1996, 985 mm in 1997, 817 mm in 1998 and 474 mm in 1999. Mean monthly precipitation is 1 to 4 mm during the drought season and 17 to 226 mm in the rainy season (1995 to 1999). The experiments were carried out in August during the drought season, i.e., 3 months after the short rainy season had ended.

Plant material and sampling

A pilot experimental plantation with 15 tree species (both indigenous and introduced) was established at the research site in November 1995 to identify suitable species for afforestation in the semi-arid environment of the Kitui district. This plantation has been neither irrigated nor fertilized since its establishment.

We chose five species: two legumes (*Senna siamea* and *Acacia gerrardii*), two members of the meliaceae (*Melia volkensii* and *Azadirachta indica*) and one member of the Bignoniaceae (*Jacaranda mimosifolia*). The experiments were carried out on 4-year-old planted trees at the study site. Two species, *M. volkensii* and *A. gerrardii*, are indigenous to Kenya; *S. siamea*, *J. mimosifolia* and *A. indica* are introduced species from tropical Asia, Brazil and India, respectively. *Melia volkensii* is deciduous; *S. siamea*, *A. indica* and *J. mimosifolia* are evergreen trees. *Acacia gerrardii* is usually evergreen, although it is occasionally deciduous.

Plant growth conditions and die-back

We measured tree height and diameter at breast height (DBH; 1.3 m) of 10 individuals per species. Trees in the study plot were in various conditions with some apparently healthy, some experiencing die-back and others dead. To assess die-back length, a branch was selected from the top of the crown and the leader shoot was cut into 1-cm segments. If the xylem endodermis tissue visible at the cut surface was green, the shoot was considered to be alive; if the endodermis was brown, the shoot was considered dead. We measured the total length of dead tissue on each leader shoot and report this as dieback length (i.e., dieback severity). All leader shoots were measured if the main stem branched into several leaders at the base. Second-order shoots were not included, because the leader shoots seemed adequate to represent the extent of die-back. Four years after planting, annual height growth of all trees exceeded the die-back length. We also calculated the frequency of individual trees showing die-back symptoms (i.e., die-back length > 0.0 cm) for each species.

Specific hydraulic conductivity measurements

Sample branches (current-year shoots) for conductivity measurements were collected from various parts of each tree, from the crown to near the stem base. For each species, three branches were collected from living trees ranging in height from 3.5 to 5.5 m, with mean diameters at the endodermis of 6.29 mm (3.13–8.32) for *S. siamea*, 5.71 mm (4.44–6.70) for *M. volkensii*, 6.89 mm (5.62–8.30) for *J. mimosifolia*, 5.78 mm (4.13–8.21) for *A. indica* and 5.20 mm (3.68–7.08) for *A. gerrardii*. Segments with a healthy epidermis obtained from the harvested branches were transported to the laboratory in a plastic bag containing enough water to cover the cut ends of the segments. In the laboratory, each segment was soaked in distilled water inside a plastic bag for 2–12 h to prevent further drying. All samples were measured within 2–12 h after sampling. Experiments were conducted at least three times for each branch, for a total of 45 to 54 measurements per species. Each segment was recut under water, and specific hydraulic conductivity of the segment measured following the method of Ikeda and Suzaki (1984). The length of segments were 7.17 cm (6.35–9.84) for *S. siamea*, 10.36 cm (7.07–11.6) for *M. volkensii,* 9.74 cm (6.96–12.9) for *J. mimosifolia* and 7.03 cm (6.04–11.6) for *A. indica. Acacia gerrardii* has extremely short internodes and a shorter segment (2.20 cm, 1.40–2.28) was used in order to exclude nodes from the sample, as water flowed from the nodes making it impossible to measure the amount of water conducted through the stem segment. A Marriotte tube was used to deliver filtered (0.2 µm) distilled water to the basal end of the excised stem segment at a constant outlet pressure. The hydraulic head was set in the range of 4.56 to 17.8 kPa depending on the sample to keep a measurable water flow rate. Once the hydraulic head was set for each segment, it was held constant during the measurement. Water flowing from a segment was collected in a preweighed 1.5-ml micro tube lined with moist tissue paper for 100 s. The amount of water collected was determined by weighing. We used a 50-ml beaker to collect water when the water flow rates exceeded 1.5 ml for 100 s.

Specific hydraulic conductivity (K_c, m^2) can be expressed as (Ikeda and Suzaki 1984, Tyree and Ewers 1991):

$$K_c = (Q\eta l)/(AtP) \quad (1)$$

where Q is volume of flowing water obtained under pressure (m^3) η is viscosity (Pa s) of flowing water at temperature T (22.0–23.8 °C), l is length of the cut segment (m), A is cross-sectional area of the xylem (m^2), t is duration of water supply (s) and P is relative pressure (Pa). We calculated P as: $P = mgh$, where m, g and h are the density of the water (m_{H_2O} = 1000 kg m^{-3}), gravity (m s^{-2}) and relative length (m), respectively. We calculated η as: $\eta = aT + bT^2 + cT^3 + d$, where a, b, c and d are coefficients ($a = -5.60418 \times 10^{-5}$; $b = 0.09879 \times 10^{-5}$; $c = -0.00072 \times 10^{-5}$; and $d = 178.449 \times 10^{-5}$) at temperature T.

Xylem anatomy and measurements of vessel size

From the same branches used for the determination of K_c, at least three transverse sections per branch were obtained to analyze xylem anatomy and calculate vessel size. Thin sections (about 30–40 µm thick) were cut with a microtome, stained in a solution of alcohol, glycerol and safranin red, washed and then mounted in Caledonian balsam on microscope slides. We photographed each cross section with a digital camera and analyzed all images with image analysis software. Vessel diameter was measured in cross sections with a fluorescence microscope and an ocular micrometer. All vessels within one section, which was defined by rays and included inner and outer areas of xylem, were sampled in such a manner that we measured at least 100 vessels per stem. Vessel size was calculated with LIA32 software, which is used for leaf area calculations (Yamamoto 1995), scaled inside the cross-sectional photograph.

Statistical analysis

Comparisons of parameters between tissues or among species were made by one-way ANOVA followed by an honestly significant difference test. Student t tests were used to assess significant interspecific variations in tree height and DBH and variations in the frequency and serverity of die-back among species. For this purpose, the standard error (SE) of tree height, DBH, die-back length and K_c was approximated by the SE of the slope of the least squares regression. All analyses were carried out with the Statistica software package (Stat Soft, Tulsa, OK).

Results

Variation in tree growth and die-back

Four years after planting, there were significant interspecific differences in tree height and DBH (Figure 1), whereas at the time of planting all seedlings were similar in height. Four years after planting, mean tree heights of *S. siamea*, *M. volkensii* and *J. mimosifolia* were larger than those of the other two species ($P < 0.05$, $n = 10$). However, *Melia volkensii* had the largest DBH, followed by *S. siamea*. The difference between these two species was significant ($P < 0.05$), whereas the other three species had a significantly smaller DBH than *S. siamea* and *M. volkensii* ($P < 0.05$).

We noted variation in the frequency and severity of die-back among species. The frequency of die-back in *S. siamea* was 100%, compared with 0% for *M. volkensii* and *A. gerrardii*. The other species experienced die-back, but with significantly lower frequencies than observed in *S. siamea* ($P < 0.05$, n = 10). The severity of die-back, which was not closely correlated with the frequency of die-back, was greatest in *J. mimosifolia*, followed by *A. indica* and *S. siamea*. Thus, *S. siamea* showed a high incidence of die-back but little serious damage, whereas *A. indica* and *J. mimosifolia* suffered severe damage despite a lower frequency of die-back.

Specific hydraulic conductivity

Branch K_c differed substantially among the species (Figure 2). Branch K_c was highest in *S. siamea*, followed by *M. volkensii* and *J. mimosifolia*, and the difference among these three species was significant ($P < 0.05$, $n = 5$). Branch K_c was highly and positively correlated with mean tree height ($r = 0.99$, $P <$ 0.01).

Vessel size and specific hydraulic conductivity

The vessel area frequency distributions were skewed to smaller sizes in all species and we observed few large vessels (Figure 3). We found significant differences in mean vessel size among the five species; *S. siamea* had the largest vessels (12×10^3 µm^2), followed by *M. volkensii* (9.5), *J. mimosifolia* (8.0), *A. indica* (6.5) and *A. gerrardii* (6.0). Maximum vessel size followed the same order. Branch K_c was positively correlated with mean vessel area ($r = 0.90$, $P = 0.037$, $n = 58$; Figure 4). Tree height was positively correlated with mean vessel area ($r = 0.90$, $P = 0.037$). The intra-specific correlation between the mean vessel area and K_c was positive ($r = 0.79$, $P <$ 0.05, $n = 18$) only in *S. siamea*. Vessel size was also positively correlated with the frequency of die-back ($r = 0.88$, $P < 0.05$).

Discussion

Vessel size was positively correlated with K_c and tree height growth, suggesting that trees with larger vessels are able to transport more water, facilitating more rapid growth (Cochard and Tyree 1990, Sperry et al. 1994, Hacke and Sauter 1996, Utsumi et al. 1999). This interpretation does not contradict the fact that no correlation was detected between vessel size and stem diameter growth estimated as an increase in DBH, be-

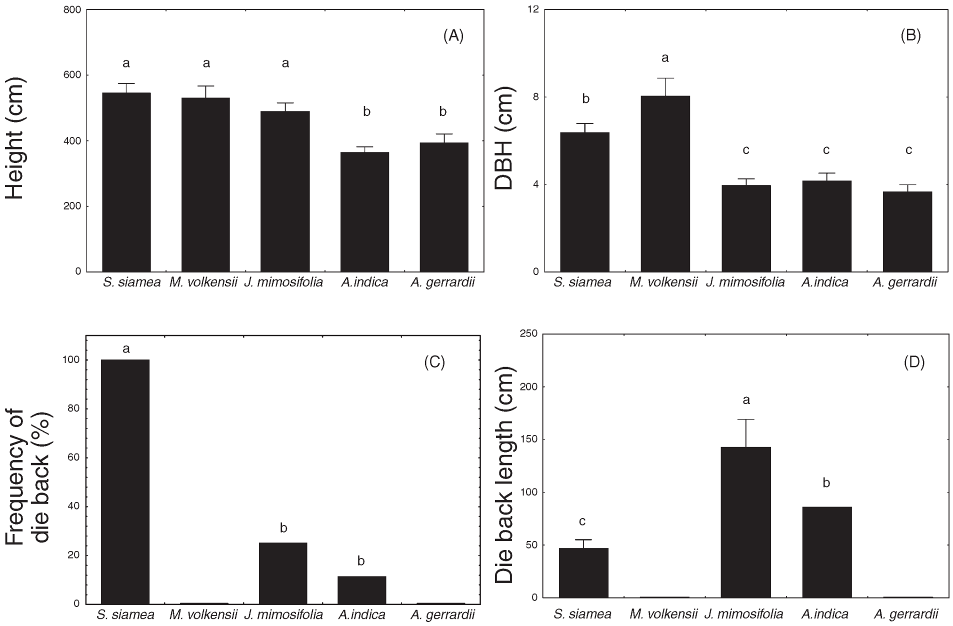

Figure 1. Height (A) and diameter at breast height (DBH; B) of 4-year-old trees of the study species *S. siamea*, *M. volkensii*, *J. mimosifolia*, *A. indica* and *A. gerrardii*. Also shown are the frequency of die-back (C) and die-back length (D) of the species. Within a panel, different letters indicate significant differences ($P < 0.05$). Black bars and error bars indicate means and standard deviations, respectively.

cause water-transport efficiency is more likely to affect vertical growth than radial growth. These trends agree with previous studies (Lovisolo and Schubert 1998, Schubert et al. 1999, Thomas et al. 2004) and with the Hagen-Poiseuille rule that the amount of water transported is proportional to the fourth power of vessel radius.

Vessel size was positively correlated with frequency of die-back, implying that trees with smaller vessels are less vulnerable to cavitation and embolism and thus more tolerant of drought. Although the effect of plant vessel size on drought tolerance is controversial, the tendency for vessel density and size to decrease from humid to dry climates and from tropical to cool-temperate zones (Dixon et al. 1984) seems to support the hypothesis that increasing vessel size lowers drought tolerance.

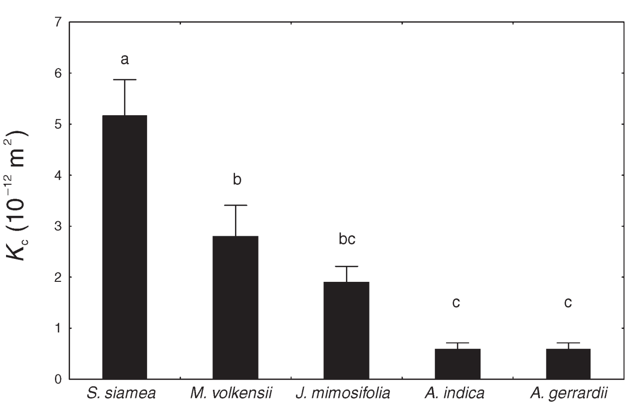

Figure 2. Specific hydraulic conductivity (K_c) of branches of 4-year-old trees of the study species *S. siamea*, *M. volkensii*, *J. mimosifolia*, *A. indica* and *A. gerrardii*. Different letters indicate significant differences ($P < 0.05$). Black bars and error bars indicate means and standard deviations, respectively.

The inversely related effects of vessel size on conductivity or growth and die-back frequency suggest a trade-off between effective water transportation and drought resistance: i.e., a species with a high growth rate is more vulnerable to drought stress. Thus, a species can be located somewhere along a continuum of varying water relations characteristics, with the extremes of a drought-tolerant (or low growth rate) species and high growth (or low drought tolerant) species. *Senna siamea* showed high conductivity and growth, although it was susceptible to die-back, implying that this species is at the extreme of the high growth rate among the study species. Species at the other extreme included *Azadirachta indica* and *Acacia gerrardii,* which had low conductivity and growth, and showed the lowest incidence of die-back. *Jacaranda mimosifolia* showed intermediate characteristics.

Melia volkensii was characterized by high conductivity, but showed no symptoms of die back, suggesting that this species cannot be positioned on the continuum of growth and drought tolerance. This may be explained by the deciduous habit of this species. High transpiration enhances embolism (Holbrook et al. 1989, Cochard et al. 1992, Sperry et al. 1994, Magnani and Borghetti 1995, Linton et al. 1998, Davis et al. 1999, Tyree and Zimmermann 2002), especially under drought stress. Deciduous species shed leaves during the dry season, which can prevent high pressure within a vessel and resultant embolism. Deciduous trees can therefore be regarded as having a mechanism to attain high drought avoidance as well as high conductivity or growth rates.

In conclusion, our results suggest that in the four evergreen species studied there is an inherent trade-off between height growth and drought tolerance, probably arising from the opposite effects of vessel size on water transportation efficiency and vulnerability to cavitation. However, die-back intensity or frequency was affected not only by vessel size but also by other water-related characteristics. The deciduous tree *M. vol-*

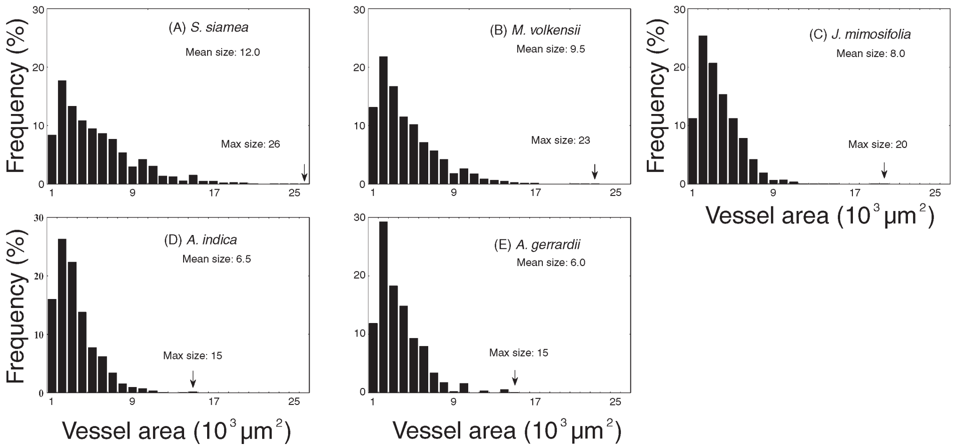

Figure 3. Frequency distributions of vessel sizes of 4-year-old trees of the study species (A) *S. siamea*, (B) *M. volkensii*, (C) *J. mimosifolia*, (D) *A. indica* and (E) *A. gerrardii*. The mean and maximum vessel sizes of each species are shown in each graph.

kensii, which had both a high water transport efficiency and high drought avoidance, appeared to be exempt from the growth–drought tolerance trade-off owing to its deciduous nature. This raises the question of the apparent cost of being deciduous, i.e., a deciduous species must "waste" leaves that are still "working" (Kikuzawa 1995). We suggest that the cost of being deciduous is outweighed by the advantages conferred in term of high drought avoidance during the dry season in this region. However, this suggestion needs to be tested through careful comparative evaluation of the economy of losing leaves in response to high stress during the dry season (e.g., die-back) and the physiological or energetic costs of losing leaves by leaf shedding.

Acknowledgments

The authors thank Mr. James Kimondo and the staff of the Kenya Forestry Research Institute in Kitui, Kenya, for their support. We also thank Dr. Takefumi Ikeda for infrastructural support and technical assistance and Drs. Shoko Sakai and Haruhiko Taneda for helpful discussions. We appreciate JICA's acceptance of this research, and we thank the JICA Office and chief advisor, Mr. Ioki Atsushi of the JCA and the JCA staff.

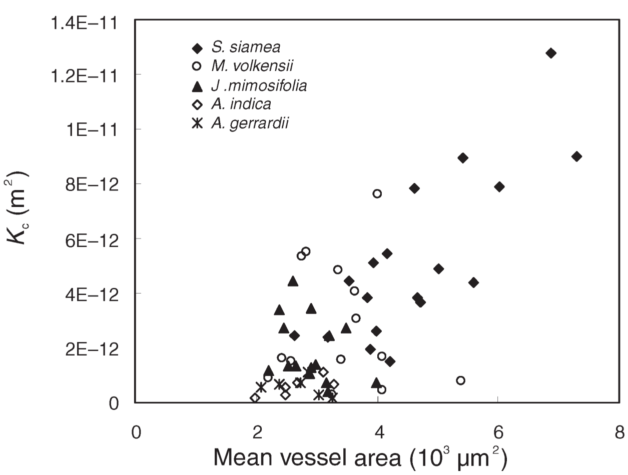

Figure 4. Correlation between vessel size and specific hydraulic conductivity (K_c) of branches of 4-year-old trees of the study species *S. siamea*, *M. volkensii*, *J. mimosifolia*, *A. indica* and *A. gerrardii*. Mean cross sectional area of a single vessel was positively correlated with K_c ($r = 0.90$, $P = 0.037$, $n = 58$). The intra-specific correlation was positive ($r = 0.79$, $P < 0.05$, $n = 18$) only for *S. siamea*.

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