



Interconnection of seasonal temperature, vascular traits, leaf anatomy and hydraulic performance in cut *Dodonaea* 'Dana' branches

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ABSTRACT

Dodonaea 'Dana' is an Israeli hybrid with purple tinted leaves, cultivated for cut foliage branches. Cut *Dodonaea* branches showed strong seasonal variations in longevity, wilting after one week in winter, while displaying a vase life of three weeks in summer. We examined the relationship between functional anatomy, including vessel, stomata and trichome densities, vessel member length and leaf thickness, and water status of cut branches during vase life over two consecutive seasons, in relation to the average monthly day temperature. All the vascular and leaf anatomy traits examined were significantly correlated with seasonal average monthly day temperature. On day one of vase life the branch water status was positively correlated with vessel, stomata, and trichome densities, and negatively correlated with vessel member length and leaf thickness. However, on day 16, the branch water status was negatively correlated only with vessel member length and diameter, implying different relative importance of anatomical parameters for surviving water stress in the vase. Our results suggest that *Dodonaea* 'Dana' branches exhibit a strong interconnection between environmental parameters and postharvest performance, showing temperature-related seasonal anatomical changes, which lead to differential hydraulic performance during vase life.

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1. Introduction

Adaptation to water stress is dependent on plant water economy (thicker cuticle, trichomes, leaf shedding), and on efficient water transport (xylem vessel characteristics). In each case, structural changes play a crucial role in plant survival. This is true for plants perpetually growing in dry environments, as well as for plants which experience occasional water stress, and also for longevity of cut branches in the vase.

Vessel diameter is perhaps the most important xylem structure parameter regarding water flow. According to Poiseuille's law, vessel radius is proportional in the 4th power to water conductance. Therefore, wider vessels mean much higher conductivity. On the other hand, occlusion in wider elements could significantly reduce water transport. Some researchers have pointed out that wider conduits are also more sensitive to air embolisms (Zimmermann and Milburn, 1982; Salleo and Lo Gullo, 1986; Tyree and Dixon, 1986; Lo Gullo and Salleo, 1993; Lo Gullo et al., 1995; Van Ieperen et al., 2001; Hacke et al., 2009). Air embolisms are especially problem-

atic in wounded or cut branches, as the exposed surface allows air entrance. As a result of water tension, air enters via the wound and causes embolisms. Another aspect of vessel width is its effect on plant support, where narrow vessels provide stronger support to the stem (Tyree and Ewers, 1991; Tyree, 2003).

Xylem conduit length and number also have an impact on water conductance. Longer xylem conduits transport water more effectively (Zimmermann and Milburn, 1982; Comstock and Sperry, 2000; Nijse et al., 2001), but they are also more vulnerable to cavitation (Zimmermann and Milburn, 1982; Hacke et al., 2009). A higher conduit number means more redundancy in the stem structure, and therefore, might be advantageous in embolized or wounded stems.

Different structural parameters of the leaf are important in regard to water use efficiency. The stomata control transpirational water loss, and therefore, stomata density is an important factor determining water relations. However, it is not completely clear whether under hot and/or dry climate conditions stomata density decreases or increases (Beerling and Chaloner, 1993; Xu and Zhou, 2008; Fraser et al., 2009). While high transpiration helps to cool the plant, it also facilitates rapid water loss. A higher stomata number might allow a better control of transpirational water loss, while on the other hand, a decrease in stomata number would reduce evap-

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orative surfaces. It should also be noted that in addition to stomata number, stomata closure, which occurs during periods of water stress, also controls water loss. Other structural leaf features are less ambiguous regarding water economy. Thus, trichome density is widely acclaimed as an adaptive trait to dry or hot conditions (Quarrie and Jones, 1977; Pérez-Estrada et al., 2000; Aronne and De Micco, 2001). Similarly, thick leaves with more developed, wax-encrusted cuticles are a well known feature of xeromorphic plants (Dickson, 2000).

The relationship between plant anatomy and function, or the relationship between environmental factors and plant structure have been extensively studied and reviewed (Fahn et al., 1986; Tyree and Ewers, 1991; Comstock and Sperry, 2000; Tyree, 2003). In addition, in the field of postharvest physiology, several attempts have been made to relate pre-harvest growth conditions (Paul et al., 1992; Slootweg et al., 2001; Twumasi et al., 2005) or anatomy (Nijse, 2001) to postharvest performance of cut flowers and branches. However, data combining environmental factors with anatomy and hydraulic performance of plants are still lacking.

Dodonaea 'Dana' is an Israeli hybrid of *Dodonaea viscosa* L. (Sapindaceae). It is a medium evergreen shrub (about 3 m in height) with decorative foliage that is used as filler branches in flower bouquets. However, *Dodonaea* 'Dana' cut branches suffer from impaired water balance in winter, while in summer the branches survive in vases for up to three weeks (Shtein et al., 2009). This wilting phenomenon has been shown to result from impaired water conductance, which might be caused by seasonal anatomical changes affecting the water status of the cut branches. In the present research we monitored water balance of the whole cut branches during vase life. These measurements were performed every two months during two consecutive seasons, in order to assess the influence of seasonal changes on longevity parameters and water balance. In parallel, we measured the corresponding seasonal changes of several anatomical traits of xylem vessels and leaves of the cut branches. This approach gives a deeper perspective on the interrelation between seasonal changes, anatomical parameters, and the water status of the cut branches during vase life.

2. Materials and methods

2.1. Plant material and treatments

Branches of *Dodonaea* 'Dana' were harvested from plants grown under constant irrigation in an experimental plot located at the ARO. The branches were 1–2 months old at the time of harvest. The branches were placed in a bucket with water immediately after harvest and brought to the laboratory. The base ends of the branches were trimmed off and the lower lateral branches were removed. Unless otherwise stated, the branches were held during vase life in a preservative solution, containing 50 $\mu\text{L L}^{-1}$ TOG-6 (GADOT-Agro Ltd., Israel), composed of active chlorine (5 mg mL^{-1}) complexed with sodium dichloroisocyanurate (Philosoph-Hadas et al., 1996). All experiments were performed in a standard controlled observation room maintained at 20 °C and 60–70% RH, with a 12 h photoperiod provided by cool-white fluorescent tubes and regular lamps illumination at a light intensity of 14 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

When using excised leaves, each leaf was held in a 50 mL plastic tube with a hole in the lid, containing a preservative solution (TOG-6), and held under the same conditions detailed above for cut branches.

The branches were harvested every two months during the years 2006–2008. The temperature data during these years were obtained from the Israel Meteorological Service (<http://www.ims.gov.il/IMSENG/All.Tahazit/homepage.htm>).

2.2. Determination of tissue anatomy parameters

Stem sections were excised at 30 cm distance from the top of the branch. Samples of 10 replicates (branches) taken from different plants were used for each measurement date.

For measurements of vessel diameter and density, transverse hand sections were made using a razor blade. The sections were stained for lignin with acid phloroglucinol. The measurements were made on a selected area of approximately 25% of each transverse section.

For measurements of vessel member length, 10 stem sections taken from 10 separated branches (per each sampling date) were macerated in acetic acid–hydrogen peroxide according to Franklin (1945), stained with safranin, and mounted on a slide in a glycerin–gelatin medium. Samples of 10 vessels were monitored in each slide for each branch.

For measurements of leaf thickness, microtome sections were excised from the upper mature leaves. The leaf sections were fixed in formaline:acetic acid (FAA):ethanol 70% (5:5:90), dehydrated in a graded ethanol solution series, and then embedded in paraffin wax. Leaf cross sections of 10 μm thickness were cut with a rotary microtome and stained with either toluidine blue O (TBO) or safranin-fast green.

For trichome and stomata counts, leaf epidermal imprints were made. The leaves were coated with nail polish, and after drying, the imprints were removed by adhesive tape and mounted on microscope slides. Trichomes were counted on an area of 9.4 mm^2 , and stomata on an area of 1.5 mm^2 . These areas represent the whole image size at the corresponding magnifications.

The samples were examined and photographed using a Zeiss microscope connected to a camera. The counts and measurement were made using ImageJ software (Rasband, W.S., ImageJ, U.S. National Institutes of Health, USA, <http://rsb.info.nih.gov/ij/>, 1997–2008).

2.3. Determination of water balance parameters

Solution uptake rate, transpiration rate, branch FW, and the ratio between the rate of solution uptake and transpiration during vase life were determined by weighing the vases plus the branches at specific time intervals (1–7 days) and calculated on the basis of these data (Turner, 1981). Transpiration and solution uptake rates were expressed on the basis of the initial FW divided by the number of vase life days included in the measuring interval. The vases were sealed with aluminum foil to prevent evaporation from the vase solution. Five to six replicates, each containing two to three cut branches, were used for each sampling date.

2.4. Statistical analysis

Analysis of variance (ANOVA) (JMP Statistical Software; SAS Institute Inc., Cary, NC) was used to determine differences between treatments. Tukey post hoc means comparisons were made to compare the significantly different treatments.

Linear correlations were made using Excel (Excel 2007, Microsoft).

3. Results

3.1. Seasonal variation in the water uptake of cut branches

The FW of cut *Dodonaea* branches during vase life was monitored every two months from October 2006 until August 2008, in parallel to the recorded maximum daily temperature at harvest (Fig. 1a). The branches were harvested on a specific day of the indicated month. The maximum temperature recorded on this day

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