Scientia Horticulturae 120 (2009) 8–13

Contents lists available at ScienceDirect

Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti

Sap flow in 'Hass' avocado trees on two clonal rootstocks in relation to xylem anatomy

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ARTICLE INFO

Article history:
Received 9 May 2008
Received in revised form 2 September 2008
Accepted 8 September 2008

Keywords:
Xylem vessel
Persea americana
Clonal rootstock
Root anatomy
Sap flow

ABSTRACT

The rates of sap flow and xylem vessel features were studied in two-year-old nongrafted and grafted avocado (*Persea americana* Mill.) trees. Daily sap flow rates were measured with heat and balance stem gauges in clonal Duke 7 (D7) and Toro Canyon (TC) trees and 'Hass' clonal scions grafted onto clonal D7 (H/D7) and TC (H/TC) rootstocks. Vessel features as size, number and total vessel area were determined histologically in the stem of the scion and rootstock and the roots of the grafted trees. Significant differences in the sap flow rate were found among the rootstocks, where D7 had a 29% higher sap flow rate than did TC (grafted and nongrafted trees). There were no differences among xylem vessel features in the stems of any of the varieties. However in the roots, D7 had wider and fewer vessels then TC do. Also, D7 had a 19% higher total vessel area than TC. These results suggest that the differences in water consumption of 'Hass' on different rootstocks may be associated with differences in the efficiency of the roots to absorb water across conductive tissue which may be linked to differences in the area of xylem vessels in the root.

1. Introduction

Avocado (*Persea americana* Mill.) is a very genetically diverse species comprised of three botanical races and their hybrids, viz. Mexican, Guatemalan and West Indian ecotypes (Newett et al., 2002). Avocado rootstocks have been selected from those races based fundamentally on the tolerance to Phytophthora root rot caused by the oomycete, *Phytophthora cinnamomi*, to salinity, and on adaptability to calcareous soils (Ben Ya'acov and Michelson, 1995). To the authors' knowledge, there are no published reports that relate the physiological and anatomical differences among avocado rootstocks to their ability to absorb and transport water.

Rootstocks should exert significant physiological effects on scions, including affecting the rate of water and nutrient absorption and translocation. If water availability is a problem in the leaves, the stomata will close and assimilation will be reduced. Therefore, the rootstock may significantly influence the productivity of the scion by affecting the tree water balance (Giulivo et al., 1985; Olien and Lakso, 1986; Klamkowski and Treder, 2002). Solari et al. (2006) suggested that the effect of rootstock on vegetative growth of peach trees was associated with balanced water relations, specifically to differences in hydraulic conductance in the vascular system of the rootstock. Studies that have examined hydraulic conductance in whole trees as well as individually in roots, stem and leaves showed that hydraulic resistance to water flow is higher in the roots than in the above ground shoots of the tree (Olien and Lakso, 1986; Tsuda and Tyree, 1997; Basile et al., 2003).

The anatomical characteristics of the water conduction system in plants can have a profound impact on the hydraulic conductivity of the tree (Tyree and Zimmerman, 2002). From an engineering point of view, the xylem is the water distribution network that transmits water from the root collection system to the main consumers, the leaves, in the upper parts of the plant (Karam, 2005). Recent anatomical studies of avocado (*P. americana* Mill.) trees have elucidated differences in vessel anatomy among races and cultivars. If the scion of a grafted tree is a different cultivar than the rootstock, which is generally the case in commercial groves, the difference in anatomical features between the scion and the rootstock seems to cause a discontinuity in the water conduction system that negatively impacts water transport (Reyes Santa Maria et al., 2002).

The objective of this research was to determine the effect of the xylem vessel network of two clonal avocado rootstocks on water consumption of 'Hass', the most widely planted avocado cultivar throughout the world.

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doi:10.1016/j.scienta.2008.09.012

2. Material and methods

2.1. Water use

This part of the research was conducted in a shaded glasshouse at the University of California, Riverside from June through August, 2005 and 2006. Climatic variables within the glasshouse during the experiment were recorded with Hobo H8 data loggers (Onset, Pocasset, Massachusetts, USA). Average day/night temperatures were 18 °C/36 °C and relative humidity ranged from 40 to 100%. The photosynthetic photon flux (PPF) was recorded above the canopy with two quantum sensors (Model Li 190, Li Cor, Inc., Lincoln, NE, USA) which were connected to an LI 1000 data logger (Li Cor, Inc.). The average PPF at midday was between 250 and 300 μmol m^{-2} s^{-1}. The vapor pressure deficit ranged from 0.48 mol m^{-3} in the morning to 1.57 mol m^{-3} in the afternoon.

Two-year-old avocado trees were used in this experiment. Treatments consisted of four rootstock/scion combinations were used, nongrafted clonal Duke 7 (D7) and Toro Canyon (TC) trees, and 'Hass' grafted onto clonal D7 (H/D7) or TC rootstock (H/TC). Duke 7 is a Mexican race rootstock and Toro Canyon is a Mexican × Guatemalan hybrid rootstock. One group of plants (used during 2005) was provided by ACW Farm (Fallbrook, CA) and propagated by the Hofshi method (Hofshi, 1996) and the second group (used in 2006) was provided by Brokaw Nursery, Inc. (Ventura, CA) and propagated by the Brokaw method (Brokaw, 1987). Trees were grown in 15-l plastic pots filled with 33% sand, 33% clay and 33% silt. During the experiment the plants were watered and fertilized daily at 9.00 a.m. with Hoagland's solution (Hoagland and Arnon, 1950). Tensiometers placed at a 20-cm depth in the soil were used for monitoring soil matric potential.

Trees with similar trunk diameters and leaf areas were used in this study because preliminary tests showed that trunk diameter and leaf area affect sap flow, which was measured in this study. At the end of the experiment, root dry weight was measured to determine the relationship between root biomass and sap flow. Prior to dry weight determination the root systems were washed and dried in a forced draft oven at 60 °C for 48 h.

The area of every leaf of each tree and the calculation of the total leaf area per tree were determined non-destructively by multiplying the squared value of the length of the leaf midrib by a pre-determined conversion factor. Separate conversion factors were determined for each cultivar because these factors were related to the shape of the leaf which was different for each cultivar. It was determined that it was not necessary to use both the length and width to get a better estimation of leaf area because the width was related to the length for each cultivar and so an area proportional to the length × width was similar to the area proportional to the square of the length. To determine the conversion factors, 10 mature leaves from each of 3 trees per cultivar (for a total of 30 leaves per cultivar) were collected from potted trees in a glasshouse. The detached leaves were immediately transported in a plastic bag to a copy machine where a photocopy was made of each leaf. The image of each leaf was cut from the photocopied page and the leaf image was weighed. The midrib length was determined from this copy. A piece of graph paper of a known area (30 cm^2) was also photocopied and weighed to determine the surface area: weight ratio. The surface area/weight ratio of the graph paper photocopy was then used to determine the unknown surface area of the leaf photocopy. This scaling allowed each conversion factor to be calculated (dividing the leaf area by the squared value of the length of the midrib). The conversion factors of all 30 sampled leaves per cultivar were averaged to obtain the mean conversion factor for converting midrib length to leaf area for each cultivar. The leaf area conversion factors (measured area/midrib length^2) were 0.36, 0.30 and 0.31 for 'Hass', D7 and TC, respectively.

Three experiments were conducted with trees in containers, each with four single-tree replications of each tree or scion/rootstock combination (D7, TC, H/D7, H/TC). Two experiments were conducted during 2005, from July 26 to 28 and from August 4 to 6. The third experiment was conducted from August 19 to 21, 2006. Trees were arranged in the glasshouse in a completely randomized design.

Sap flow rate was monitored with a Dynagage sap flow system (Dynamax, Inc., Houston, TX, USA) based upon the heat balance technique (Steinberg et al., 1989) with SGA13 sensors linked to a CR10 data logger (Campbell Scientific, Inc., Logan, UT, USA). A four-channel stem gauge was attached to the base of the stem, approximately 5 cm above the graft union and was covered with insulation to prevent extraneous heat flow over which was placed aluminum foil to reduce the effect of external radiation. The data logger was programmed to record the output every 15 min and the data were downloaded and analyzed every day using Flow32 WIN analysis software (Dynamax, Inc.). All trees were monitored for 3 days and the sap flow rate per day was calculated between 8:00 and 20:00 h, when a majority of the total sap flow occurred.

To test the operation and accuracy of the equipment, daily water loss was determined from gravimetric measurements of soil water content for 8 days. For soil water content determinations during the 8-day period, pots with the soil and trees were placed on an electronic balance and weighed continuously during the day. The pots were wrapped in aluminum foil, which covered the soil surface throughout the experiment so that the only water loss was from transpiration.

The experiment was arranged in a complete randomized block design with three replications and periods of tree days as a blocking factor. All data were statistically analyzed with SPSS software 11.5 for Windows TM (SPSS Inc., Chicago, IL, USA) and significance differences among treatment means were determined with Duncan's multiple range test at $P \leq 0.05$. The relationship between sap flow and weight loss, measured gravimetrically, was determined by linear regression analysis.

2.2. Xylem vessel anatomy

This part of the research was conduced in the Propagation and Histological Laboratories at the Catholic University of Valparaiso, Chile.

Histological sections of the xylem were prepared from three of the trees used in the water use experiment plus three additional trees (at approximately the same state of development as those used in the water use experiment) of each of H/D7 and H/TC) to determine the diameter and number of vessels in the stem of the scion and the stem and roots of the rootstock on the grafted trees. Root and stem samples were fixed in a formalin, acetic acid and alcohol solution (10 formalin:5 acetic acid:50 ethanol, by volume) (Ruzin, 1999). The tissue was embedded in a water-soluble wax. Sections that were 16–18 μm thick were cut from the embedded stem and 5 μm thick sections were cut from the embedded root using a rotary microtome (Spencer 820 Microtome, American Optical Co., Buffalo, NY, USA). Sections were stained with safranin and fast green. For 'Hass' (scion) stem analysis, six cross sections were obtained from 5 cm above the graft union. For analysis of the stem of the rootstocks of grafted trees, six cross sections were obtained from 5 cm below the graft union. For root sections, five root samples were collected 2.5 cm above root tips from second-order roots (diameters between 1 and 2 mm) from each tree (30 samples per rootstock) (Fig. 1).