ORIGINAL ARTICLE

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Control of transpiration in three coffee cultivars: the role of hydraulic and crown architecture

Abstract Water use and hydraulic architecture were studied in the coffee (*Coffea arabica*) cultivars San Ramon, Yellow Caturra and Typica growing in the field under similar environmental conditions. The cultivars differed in growth habit, crown architecture, basal sapwood area and total leaf surface area. Transpiration per unit leaf area (E), stomatal conductance (g_s), crown conductance (g_c), total hydraulic conductance of the soil/leaf pathway (G_t) and the stomatal decoupling coefficient, omega (Ω) (Jarvis and McNaughton 1986) were assessed over a range of soil moisture and during partial defoliation treatments. The relationship between sap flow and sapwood area was linear and appeared to be similar for the three cultivars. Variation in g_c, E, and G_t of intact plants and leaf area-specific hydraulic conductivity (k_l) of excised lateral branches was negatively correlated with variation in the ratio of leaf area to sapwood area. Transpiration, g_c, and g_s were positively correlated with G_t. Transpiration and G_t varied with total leaf area and were greatest at intermediate values (10 m^2) of leaf area. Omega was greatest in Yellow Caturra, the cultivar with the greatest leaf area and a dense crown, and was smallest in Typica, the cultivar with an open crown. Differences in omega were attributable primarily to differences in leaf boundary layer conductance among the cultivars. Plants of each cultivar that were 40% defoliated maintained sap flows comparable to pretreatment plants, but expected compensatory increases in g_s were not consistently observed. Despite their contrasting crown morphologies and hydraulic architecture, the three cultivars shared common relationships between water use and hydraulic architectural traits.

Key words *Coffee arabica* · Hydraulic conductance · Sap flow · Stomata · Stomatal decoupling coefficient

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Introduction

The role of stomata in controlling transpiration has traditionally been inferred from leaf-level measurements of stomatal conductance made with porometers or gas exchange systems (Wullschleger et al. 1998). Extrapolation from leaf-level measurements to rates of whole-plant water use is problematic because the influence of stomatal movements on transpiration is diminished by the resistance to water vapor diffusion of boundary layers surrounding each leaf and the entire canopy. These boundary layers cause transpired water vapor to humidify the air near the leaves, uncoupling the vapor pressure at the leaf surface from that of the bulk air (Jarvis and McNaughton 1986). The degree of uncoupling is largely dependent on the ratio of stomatal to leaf boundary layer conductance rather than the absolute magnitude of boundary layer conductance. Jarvis and McNaughton (1986) quantitatively described the sensitivity of leaf or canopy transpiration to a marginal change in stomatal conductance in terms of a dimensionless decoupling coefficient omega (Ω), values of which range between zero and one. As Ω approaches 1, stomatal control of transpiration becomes progressively weaker because the vapor pressure at the leaf surface becomes increasingly decoupled from the vapor pressure of the bulk air. Generally, Ω increases as stomatal conductance increases, but in a manner determined by prevailing boundary layer conductance, leading to a range of values of Ω for a given species. Characteristics such as large leaf size, close plant spacing, and dense, compact crowns tend to reduce boundary layer conductance (Grace et al. 1980) and thus, increase values of Ω.

In addition to the influence of boundary layer conductance on transpiration, plant hydraulic architecture and its components influence transpiration through their effects on operating ranges of stomatal conductance. Hydraulic architecture is a term coined by Zimmermann (1978) to describe how the hydraulic conductivity of the xylem in various parts of a plant is related to the leaf area it must supply. Total daily sap flow is often highly correlated with hydraulic architecture components such as basal stem area and sapwood area, both within species (Köstner et al. 1992; Vertessy et al. 1995; Becker 1996; Andrade et al. 1998) and among similar co-occurring species (Vertessy et al. 1995). Such relationships allow prediction of stand water use in orchards or forests with relatively few dominant species. There is substantial evidence that stomatal conductance and transpiration are positively correlated with the hydraulic conductance of the soil/root/leaf pathway in diverse plant species and growth forms (Aston and Lawlor 1979; Küppers 1984; Meinzer et al. 1988; Meinzer and Grantz 1990; Sperry and Pockman 1993; Meinzer et al. 1995; Andrade et al. 1998). Such close coordination between vapor and liquid phase conductance can dampen variation of daily leaf water potential under a wide range of conditions (Whitehead et al. 1984; Meinzer et al. 1992), thus limiting the usefulness of leaf water potential as a predictor of stomatal conductance and transpiration. Stomatal conductance and transpiration on a leaf area basis have generally been found to increase in response to defoliation (Tschaplinski and Blake 1989; Meinzer and Grantz 1990; Ovaska et al. 1992; Pataki et al. 1998), further supporting suggested coordination between leaf area-specific liquid and vapor phase conductance.

In the present study, transpiration per unit leaf area, leaf water status, stomatal conductance, leaf boundary layer conductance, crown conductance and total hydraulic conductance of the soil/leaf pathway were measured concurrently in field-grown plants of three coffee (*Coffea arabica* L.) cultivars with contrasting growth habits and crown architecture. Measurements were made under well-irrigated and non-irrigated conditions, and also on plants subjected to partial defoliation treatments. Laboratory measurements to determine leaf-area specific hydraulic conductivity of excised lateral branches were also carried out. Our objectives were to explore patterns of water use by the three cultivars during periods of high and low soil moisture, to determine relationships between hydraulic architecture traits and control of whole-plant water transport, to characterize leaf-atmosphere coupling, and to examine cultivar responses of sap flow to manipulation of hydraulic architecture *via* partial defoliation. We hypothesized that (1) control of transpiration per unit leaf area in the three coffee cultivars would be characterized by close coordination between liquid and vapor phase conductance, that (2) apparent differences in regulation of transpiration per unit leaf area among cultivars would be governed by divergent hydraulic architecture rather than physiology, and that (3) differences in crown morphology would be reflected in differences in leaf-air coupling.

Materials and methods

Field site and plant material

The study was conducted from early March through mid-July, 1996 at the Hawaii State Coffee Trial site located near Eleele, Kauai, Hawaii ($21^0 54''$N, $154^0 33''$W, altitude about 90 m). A total of 19 coffee cultivars were present at the 0.53 ha site. The soil at the site was of the Makaweli stony silty clay loam series of the Low Humic Latosol great soil group (Foote et al. 1972). The soil was relatively free of rocks, and had a pH of 6.0. The cultivars were planted in paired rows in August 1987 at a spacing of 1.2 m between plants and 3.7 m between rows. Each row consisted of eight unpruned plants growing in full sun. The plants typically had one to three orthotropic (vertical) shoots bearing many plagiotropic (horizontal) branches. Three *Coffea arabica* cultivars with contrasting shoot morphologies were chosen for this study. Typica, the tallest of the three cultivars, had a conical, relatively open crown. San Ramon, the shortest of the three cultivars had a narrow conical shape, with a dense crown. Yellow Caturra was intermediate in height, had a flat top, with a dense crown. Mean height of these three cultivars at the study site was 3.7, 1.5, and 2.0 m for Typica, San Ramon, and Yellow Caturra, respectively. Additional characteristics of the three cultivars are summarized in Table 1. The measured plants were located within 40 m of each other. Each row was supplied with drip irrigation, and received a total of approximately 30 mm water in one to two applications per week, except when irrigation was withheld. Total precipitation during the study period was 234 mm, including a total of 8.6 mm of widely scattered precipitation during a 21-day period when irrigation was intentionally stopped.

Microclimate

An automated weather station was installed in an open area near the midpoint of the study site. Relative humidity and air temperature were measured with shielded sensors (HMP35 C, Campbell Scientific, Logan, Utah, USA) mounted at a height of 2 m. Ambient vapor pressure was calculated using humidity and temperature data. Photosynthetic photon flux density (PPFD) was measured by a quantum sensor (Li-190SB, Li-Cor, Lincoln, Neb., USA) mounted horizontally at a height of 3 m. Net radiation was measured with a Fritschen net radiometer (Model Q5, Micromet Systems, Seattle, Wash., USA) mounted horizontally at a height of 2 m. Wind speed was measured with a cup anemometer (Model 03101–5, R.M. Young, Traverse City, Mich., USA) mounted at a height of 3 m. Precipitation was measured with a tipping bucket rain gauge (Model TE525, Texas Electronics, Dallas, Tex., USA) mounted at a height of 3 m. Continuous readings from these sensors were recorded on a datalogger (CR10, Campbell Scientific), with 10-min averages stored in a solid state storage module (SM196, Campbell Scientific).

Leaf temperature was measured with fine-wire (0.08 mm) copper-constantan thermocouples affixed with thin porous surgical tape to abaxial leaf surfaces. Four leaves were monitored on each plant fitted with sap flow probes (see below). On these plants, thermocouples were attached to leaves of four mid-crown lateral branches oriented in the four compass directions. The four thermocouples on a given plant were connected in parallel in order to obtain an average leaf temperature for each plant. Leaf temperature was continuously recorded by a datalogger (CR10, Campbell Scientific), with storage of 10-min average values. The vapor pressure difference between the leaf interior and bulk air (V_a) was calculated using saturation vapor pressure at leaf temperature and the ambient vapor pressure calculated from the weather station readings.

Transpiration

All values of transpiration (E) reported in this study are per unit leaf area, and were derived from sap flow measurements, not

from porometry. Sap flow through the basal portion of the largest vertical branch of each plant was measured by the constant heating method (Granier 1987). Basal diameters of measured branches ranged from 35 to 95 mm. The system used allowed simultaneous measurement of branches on two plants of each of the three cultivars, a total of six plants. Sap flow was measured in one set of six plants from early March until mid-April 1996, and in another set of six plants from mid-April until mid-July 1996. Two 20-mm long 2-mm diameter probes (UP, Munich, Germany) were inserted radially near the base of each selected branch. Each pair of probes was separated vertically by a distance of 15–20 cm. The higher (downstream) probe was continuously heated by a constant current power supply (UP, Munich), with the lower (upstream) probe serving as a temperature reference. The protruding portions of each pair of probes were insulated with a layer of foam rubber surrounded by an outer shield of reflective car windshield liner in order to avoid radiant heating of the stem. Probe temperatures were recorded at 15-s intervals by a datalogger (CR10, Campbell Scientific), and 10-min averages were stored in a solid state storage module (SM196, Campbell Scientific). Sap flow density was calculated from the temperature difference between the probes based on a standard empirical relationship (Granier 1987). Mass flow of sap was obtained by multiplying flow density by the sapwood cross-sectional area, which was determined by injection of 0.1% indigo carmine dye into trunks with diameters similar to those of the measured plants. Trunks were cross-sectioned 3–5 cm above the injection points 2-h after dye injection and the colored sapwood measured to calculate the cross-sectional area of conducting xylem tissue. The sapwood thickness of measured branches was sufficient to avoid potential errors resulting from sapwood thickness being less than the length of sap flow probes. Leaf area distal to the probes was determined by counting all leaves distal to the probes and multiplying the total number of leaves by mean area per leaf. Leaf counts were made at the beginning of the study, and subsequently at 4-week intervals. Mean area per leaf was calculated from subsamples of 100 leaves of each cultivar measured with a leaf area meter (Model 3000 A, Li-Cor). Transpiration per unit leaf area (E) was calculated by dividing mass flow of sap by the leaf area distal to the sap flow probes. The three dataloggers used in this study were synchronized weekly.

Leaf water potential

Leaf water potential (Ψ_L) was measured with a pressure chamber (Model 1000, PMS, Corvallis, Ore., USA). On selected days Ψ_L was determined four times: predawn (around 0600 hours), 1000 hours, 1300 hours, and 1600 hours. At each time, measurements were made on a total of six leaves of two adjacent plants of each cultivar. In order to minimize errors due to water loss, leaves were enclosed in plastic bags and placed in darkness immediately upon removal from plants.

Conductances

Stomatal conductance (g_s) was measured with a steady state porometer (Model Li-1600, Li-Cor) on six leaves of each plant fitted with sap flow gauges. The six leaves measured per plant were chosen to be representative of the range of light exposure during each set of measurements. On days chosen for porometry, four sets of measurements were taken between 1000 and 1600 hours unless precipitation interfered with measurements.

Crown conductance (g_c), the total vapor phase conductance (encompassing both g_s and boundary layer conductance - g_b), was calculated as

$$g_c = EP/V_a \qquad (1)$$

where E is transpiration, P is atmospheric pressure, and V_a is the vapor pressure difference between the leaf interior and bulk air. Values of g_c are expressed on a unit leaf area basis.

Boundary layer conductance (g_b) was estimated from leaf dimensions and prevailing wind speed using a relationship proposed by Nobel (1991):

$$g_b = 255/(d/v)^{0.5} \qquad (2)$$

where d is the mean length of the leaf in the downwind direction (average of length plus width) and v is the wind speed near the foliage. This empirical method thus estimates the conductance of the boundary layer adjacent to the leaf surfaces. Repeated spot measurements of wind speed were made with a heated thermistor anemometer (Model 8330, TSI, St. Paul, Minn., USA) at five points adjacent to foliage on a transect at mid-crown height through a representative plant of each of the three cultivars. Local attenuation of wind near the leaves of the study plants was estimated by taking the average ratio of the spot measurements in the plants and simultaneously recorded wind speed at the automated weather station nearby. This attenuation ratio was multiplied by values of wind speed continuously measured at the weather station to obtain values of v used in Eq. 2. The length and width of 60 randomly selected leaves of each cultivar were measured and averaged to provide mean values of d for each cultivar.

Leaf area-specific total hydraulic conductance of the soil/leaf pathway (G_t) for the branches fitted with sap flow probes was determined as

$$G_t = E/\Delta\Psi \qquad (3)$$

where $\Delta\Psi$ is the difference between soil water potential and leaf water potential (Ψ_L) at a given time. Derivation and use of G_t have been recently reviewed (Wullschleger et al. 1998). In the current study, G_t was calculated from midday values of Ψ_L and E, when rates of E were relatively constant. Predawn Ψ_L was used to estimate soil water potential (Tardieu and Simonneau 1998). Sap flow gauges indicated zero sap flow when predawn Ψ_L samples were taken and leaves typically were covered with dew at these times, supporting the assumption that discrepancies between soil Ψ and Ψ_L caused by transpiration at predawn sampling times would be negligible.

Besides G_t, a dimensionless index of potential plant architectural constraints on water supply in relation to transpirational demand was obtained for each branch monitored with sap flow sensors by dividing the total leaf area distal to the sensors by the sapwood area at the point of sensor installation (LA/SA). LA/SA is roughly equivalent to the inverse of the so-called Huber value, originally defined as the cross sectional xylem area divided by the fresh weight of the leaves distal to the point of xylem area measurement (Zimmermann 1978).

Stomatal control of transpiration

The sensitivity of transpiration to a marginal change in g_s was evaluated using the dimensionless decoupling coefficient Ω, described by Jarvis and McNaughton (1986) with a modification by Martin (1989) that allows for radiative coupling between leaves and the atmosphere:

$$\Omega = (\varepsilon + 2 + g_r/g_b)/(\varepsilon + 2 + (g_r + g_b)/g_s + g_r/g_b) \qquad (4)$$

where ε is the ratio of the increase of latent heat content to increase of sensible heat content of saturated air, and g_r is a longwave radiative transfer conductance of the canopy.

Branch hydraulic conductivity measurements

Hydraulic conductivity of lateral branches was assessed for the three cultivars by techniques developed by Sperry et al. (1988). Woody lateral branches from mid-crown portions of field-grown plants were cut under water to prevent air entering into the xylem. Selected branches had basal diameters ranging from 4 to 8 mm. In the laboratory, stem segments from harvested branches were recut under water and immediately connected to plastic tubing supplied with degassed, acidified distilled water under gravitational pres-

sure (around 0.01 MPa) from an elevated beaker. Flow rates through segments were measured volumetrically to determine hydraulic conductivity. Six segments were measured simultaneously in the apparatus used. Leaf area distal to each segment was measured on a leaf area meter (Model 3000 A, Li-Cor) to allow leaf area-specific hydraulic conductivity (k_l) to be calculated.

Manipulations

In order to characterize cultivar responses to drying soil, irrigation was withheld from all plants for 21 days, from 19 May (day of year 140) through 9 June 1996 (day 161). In order to characterize cultivar responses to leaf area reduction, 20% of the leaf area was removed from branches fitted with sap flow probes on one plant of each cultivar on day 191. Three days later (day 194), an additional 20% of the original leaf area was removed from the same branches. Plants were receiving regular irrigation at this time. The appropriate number of leaves to be removed was determined from the average area per leaf for each cultivar. Transpiration (E), g_s, g_c and Ψ_L were measured in manipulated and control plants prior to and following defoliation.

Results

Mean basal sapwood area and leaf area of the branches fitted with sap flow gauges were 2–3 times greater for Typica and Yellow Caturra than for San Ramon (Table 1). The mean value of the ratio LA/SA was lowest for Typica and highest for Yellow Caturra. Although the absolute difference between extreme values of LA/SA was small, Yellow Caturra had about 67% more leaf area per sapwood area than Typica. Mean daily sap flow for Typica and Yellow Caturra was more than twice that of San Ramon, but when expressed on a leaf-area basis, Typica and San Ramon had higher mean values of E than Yellow Caturra.

The relationship between sap flow and sapwood area appeared to be similar for the three cultivars (Fig. 1). However, it should be pointed out that these two variables are not completely independent, since sapwood area is used to calculate total sap flow. The small-statured San Ramon had the lowest sap flows and sapwood
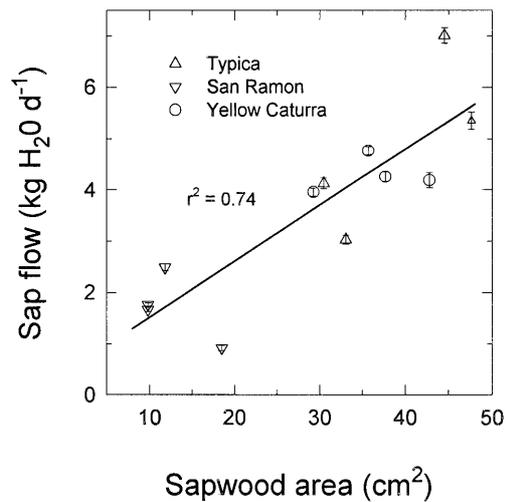

Fig. 1 Mean daily sap flow in relation to sapwood area of the three cultivars. Total daily sap flow totals are for 0600–2000 hours. Measurements were made on four individuals of each cultivar. Symbols are means±1 SE of 29–34 days of measurements on a single individual of each cultivar. *Solid line* is a fitted linear regression: $y=0.43+0.11\ x$, $P<0.05$

areas. Sapwood area for Yellow Caturra ranged from near 30 to about 44 cm^2 and its daily sap flow totals were near 4 kg. Typica sapwood area ranged from around 30 to near 50 cm^2 and its daily sap flow totals ranged from near 3 to 7 kg.

Variation in g_c, E, and G_t among cultivars was negatively correlated with variation of LA/SA (Fig. 2A-C). These three indices of in situ water use and vapor and liquid phase conductance appeared to initially decline sharply, then more gradually with increasing LA/SA. Variation in k_l measured on excised lateral branches in a laboratory was also negatively correlated with variation in LA/SA (Fig. 3).

A positive linear dependence of E and g_c on G_t was found in all three cultivars (Fig. 4A, B). The dependence of E and g_c on G_t appeared to be similar among the three

Table 1 Morphological and water-use characteristics of the four vertical branches per cultivar in which sap flow was measured. Values are means±1 SE. LA/SA is the ratio of branch leaf area to the sapwood cross-sectional area where the sap flow probes were inserted. Daily totals of sap flow and transpiration (E) are from measurements made on 30 days under well-watered conditions

Cultivar	Basal sapwood area (cm^2) n=4	Leaf area (m^2) n=4	LA/SA (m^2 cm^{-2}) n=4	Sap flow (kg H$_2$O day^{-1}) n=120	E (mol m^{-2} day^{-1}) n=120
Typica	39±4	11.7±2.0	0.30±0.03	4.9±0.2	25.3±0.8
San Ramon	13±2	5.0±0.5	0.42±0.05	1.7±0.1	20.7±0.7
Yellow Caturra	37±3	18.0±2.7	0.49±0.06	4.3±0.1	14.9±0.5

Table 2 Values of r^2 for the relationship between transpiration (E) and crown conductance (g_c) vs. predawn and midday Ψ_L. Data represent 20 days of measurements made on four individuals per cultivar

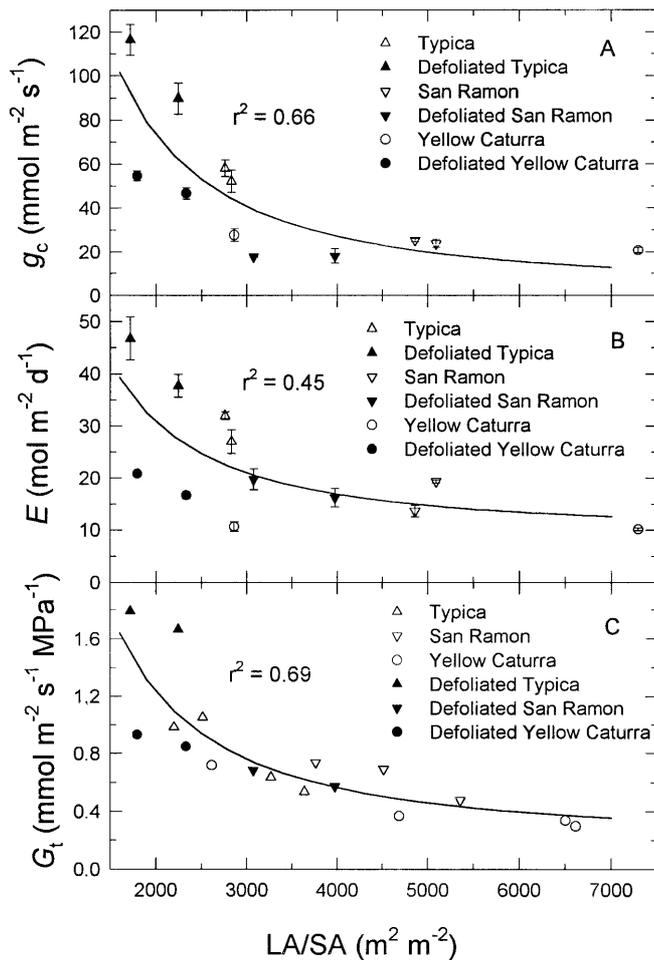| Cultivar	E vs. predawn Ψ_L	E vs. midday Ψ_L	g_c vs. predawn Ψ_L	g_c vs. midday Ψ_L
Typica	0.00	0.00	0.01	0.00
San Ramon	0.03	0.00	0.20	0.01
Yellow Caturra	0.12	0.24	0.05	0.31

Fig. 2 **A** Crown conductance (g_c), **B** total daily transpiration (E) and **C** leaf area-specific total hydraulic conductance of the soil/leaf pathway (G_t) in relation to the ratio of leaf area to sapwood area (LA/SA). Symbols for A and B are means±1 SE, $n=3$–9. *Solid lines* are fitted nonlinear regressions: (A) $y=1.93+6383953/x^{1.5}$, $P<0.05$, (B) $y=9.36+1915639/x^{1.5}$, $P<0.05$, and (C) $y=0.20+92456/x^{1.5}$, $P<0.05$

cultivars, but Typica consistently operated at higher values of G_t and therefore, g_c and E than the other two cultivars. In contrast with the dependence of transpiration and vapor phase conductance on plant hydraulic properties (Fig. 2A, B; Fig. 4A, B), little or no dependence of g_c or E on predawn or midday Ψ_L, ranging from –0.1 to –2.5 Mpa, was observed (Table 2). Positive linear relationships between independently measured g_s and G_t were found for the three cultivars (Fig. 5). Unlike the common relationship for the three cultivars seen between g_c, E and G_t, the relationships between g_s and G_t appeared to be distinct for each cultivar. Both E and G_t appeared to initially increase, then decrease with increasing plant size (Fig. 6A, B), suggesting coordination between water use and water transport efficiency throughout plant development.

Leaf characteristics and representative measurements used to determine values of Ω are presented in Table 3. Wind speed measured in the foliage of Yellow Caturra
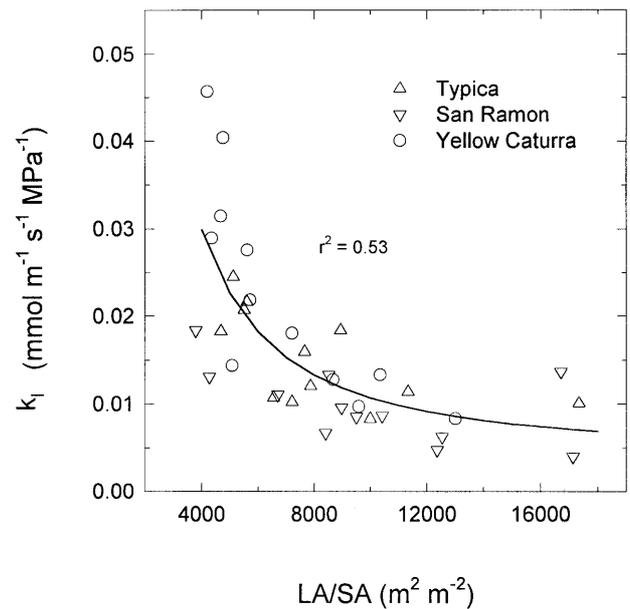

Fig. 3 Leaf area-specific hydraulic conductivity of excised branches (k_l) in relation to the ratio of leaf area to sapwood area, LA/SA. *Solid line* is fitted nonlinear regression: $y=0.0000008+0.12/x^{1.5}$, $P<0.05$
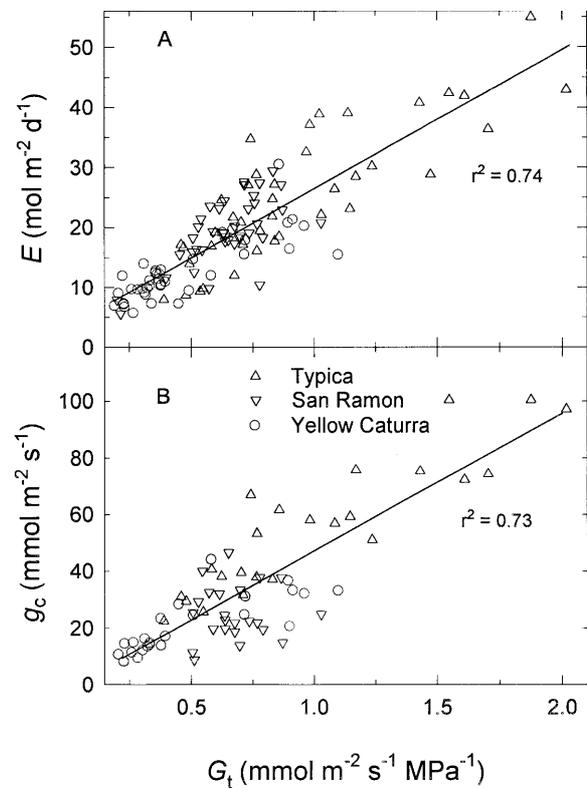

Fig. 4 **A** Total daily transpiration (E), and **B** crown conductance (g_c) as functions of leaf area-specific total hydraulic conductance of the soil/leaf pathway (G_t) for the three cultivars. Measurements were made on four individuals of each cultivar. *Solid lines* are fitted regressions: (A) $y=3.51+23.05\ x$, $P<0.05$; (B) $y=-1.20+48.51x$, $P<0.05$

Table 3 Area per leaf, mean leaf length in the downwind direction (*d*), wind speed near the foliage (*v*), wind speed at the study-site weather station, stomatal conductance (g_s), leaf boundary layer conductance (g_b), and the stomatal decoupling coefficient, Ω of the three cultivars. Values are means±1 SE. Wind speed and g_s were measured on well-watered plants at 1300 hours on 6 different days. Equation 2 was used to calculate g_b and Ω was calculated from Eq. 4. Means for Ω were significantly different (Fisher's LSD, $P<0.05$)

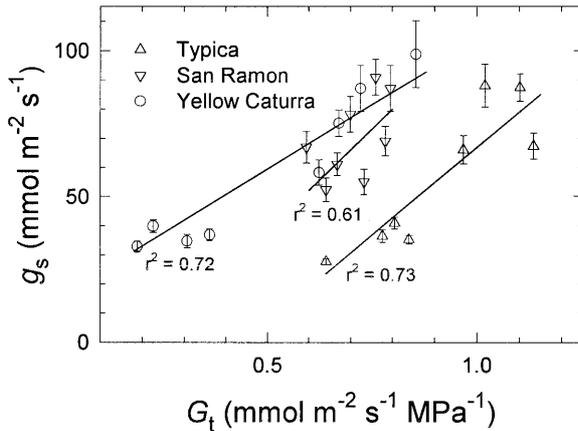| Cultivar	Area per leaf (cm^2) $n=100$	d (cm) $n=60$	v (m s^{-1}) $n=6$	Wind speed at weather station (m s^{-1}) $n=6$	g_s (mmol m^{-2} s^{-1}) $n=6$	g_b (mmol m^{-2} s^{-1}) $n=6$	Ω $n=6$
Typica	39.2±0.9	8.7±0.2	0.44±0.06	2.92±0.37	76±10	567±37	0.38±0.03
San Ramon	30.9±0.6	7.2±0.1	0.23±0.03	2.92±0.37	87±12	449±29	0.47±0.03
Yellow Caturra	42.4±0.8	8.7± 0.2	0.17±0.02	2.92±0.37	97±7	351±23	0.56±0.02

Fig. 5 Mean stomatal conductance (g_s) in relation to leaf area-specific total hydraulic conductance of the soil/leaf pathway (G_t) of the three cultivars. Symbols are means±1 SE, $n=48$. *Solid lines* are fitted linear regressions: (Typica) $y=-53.64+120.66x$, $P<0.05$, (San Ramon) $y=-31.38+139.26x$, $P<0.05$, and (Yellow Caturra) $y=15.71+87.70x$, $P<0.05$

Fig. 6 A Total daily transpiration (*E*), and **B** leaf area-specific total hydraulic conductance of the soil/leaf pathway (G_t) in relation to measured branch leaf area for four individuals of each of the three coffee cultivars. Symbols are means±1 SE, $n=3–5$. *Solid lines* are fitted nonlinear regressions: (A) $y=9.59+2.77x+-0.21x^2+0.004x^3$, $P<0.05$, and (B) $y=0.16+0.14x+-0.01x^2+0.0002x^3$, $P<0.05$

was the most attenuated relative to that measured in the open air at 3 m height at the nearby weather station, resulting in the lowest value of g_b, and the highest value of Ω. Conversely, wind speed measured in Typica foliage was the least attenuated, resulting in the highest g_b and lowest Ω of the three cultivars. The relationship between Ω and g_s for each cultivar is shown in Fig. 7. At intermediate values of g_s of 75 mmol m^{-2} s^{-1} values of Ω were 0.38 for Typica, 0.43 for San Ramon, and 0.49 for Yellow Caturra, indicating that all three cultivars were usually in a moderately decoupled state with respect to stomatal control of transpiration. As expected, values of Ω declined when g_s was decreased by drought or afternoon reduction in stomatal aperture, and increased as g_s increased.

Results of the two-step partial defoliation experiment are presented in Fig. 8 and Table 4. Net radiation measured by a sensor at the study site ranged from a low of around 15.5 MJ m^{-2} day^{-1} on day 193 to a high of around 19.5 MJ m^{-2} day^{-1} on day 195 (Fig. 8 A). Because net radiation is a major driving variable for sap flow, daily totals of sap flow were therefore normalized by net radiation to avoid variation associated with differences in radi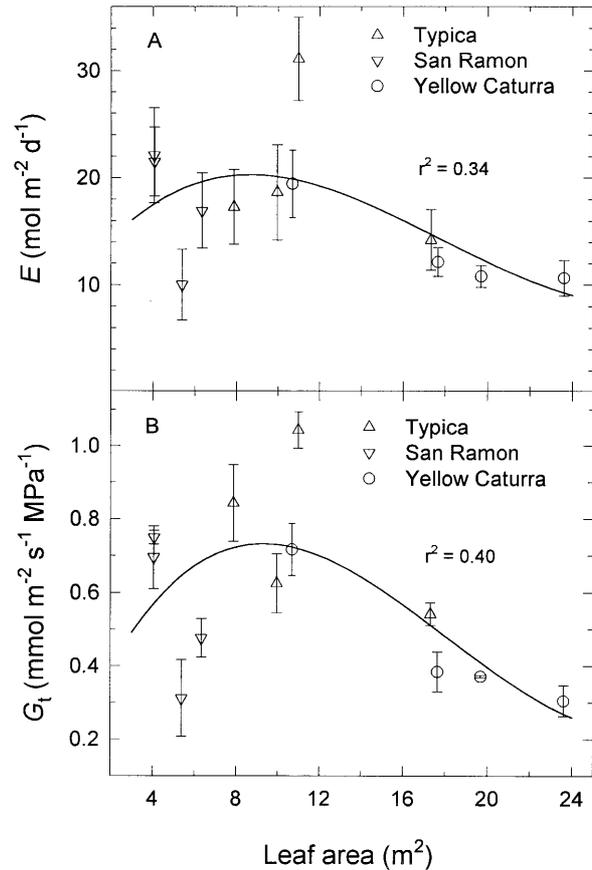ative input (Fig. 8B). Normalized sap flow remained nearly constant in all three cultivars following each successive removal of 20% of the original branch leaf area, indicating that compensatory increases in leaf-level transpiration had occurred. Increased g_s was seen in partially defoliated Typica and San Ramon plants, and G_t increased in partially defoliated plants of Typica and Yellow Caturra (Table 4). However, these increases were not statistically significant.

Table 4 Stomatal conductance (g_s) and leaf area-specific total hydraulic conductance of the soil/leaf pathway (G_t) of two plants of each cultivar before and in relation to successive partial defoliation treatments of one plant of each cultivar. Defoliation treatments are described under manipulations in the materials and methods section. Each measurement interval includes data from three days under well-watered conditions. Units for g_s and G_t are mmol m^{-2} s^{-1} and mmol m^{-2} s^{-1} MPa^{-1}, respectively. Values are means±1 SE, n=72 and 6 for g_s and G_t, respectively. For each plant, parameter means for the three intervals were subjected to one-way ANOVA (P <0.05). None were found to be statistically different
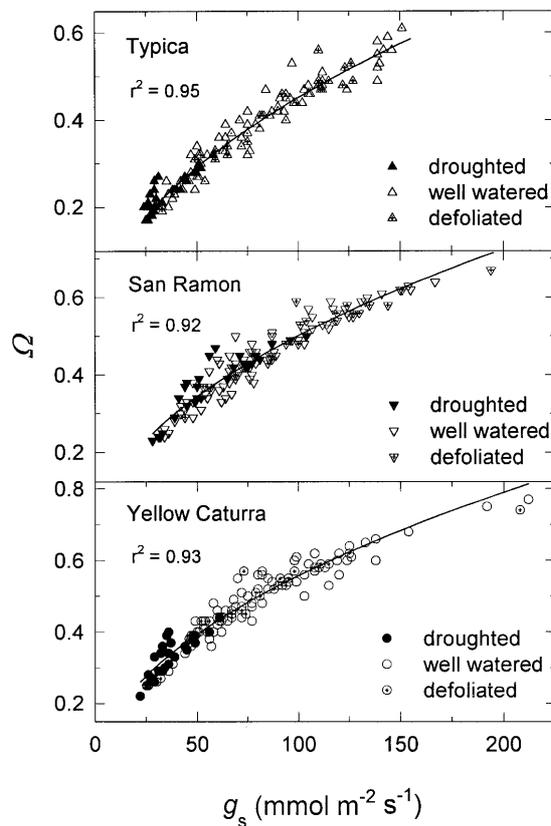
Parameter – interval	Typica untreated plant	Typica treated plant	San Ramon untreated plant	San Ramon treated plant	Yellow Caturra untreated plant	Yellow Caturra treated plant
g_s - pretreatment	64±4	85±5	82±6	86±6	76±6	85±7
g_s - defoliation #1	76±4	84±4	91±5	98±5	83±6	84±6
g_s - defoliation #2	68±3	94±3	86±5	107±6	78±5	82±4
G_t - pretreatment	0.84±0.10	1.04±0.05	0.75±0.02	0.70±0.00	0.37±0.00	0.72±0.07
G_t - defoliation #1	0.72±0.15	1.35±0.31	0.82±0.11	0.62±0.06	0.34±0.04	0.91±0.11
G_t - defoliation #2	1.18±0.03	1.81±0.14	0.64±0.08	0.68±0.11	0.32±0.01	0.92±0.02

Fig. 7 The stomatal decoupling coefficient Ω in relation to stomatal conductance (g_s) for Typica, San Ramon, and Yellow Caturra. Each symbol represents the mean of six g_s measurements. *Solid lines* are fitted nonlinear regressions: Ω_{typica}=−0.09+0.055 $x^{0.5}$, P<0.05, $\Omega_{san\ ramon}$=−0.04+0.054 $x^{0.5}$, P<0.05, and $\Omega_{yellow\ caturra}$ =−0.0004+0.056 $x^{0.5}$, P<0.05

Fig. 8 A Daily totals of net radiation measured by a sensor at the study site, and **B** daily sap flow totals normalized by net radiation for days 188–196, 1996. Days 188–190 were prior to removal of 20% of the foliage of one measured plant of each cultivar on the morning of day 191; a second partial defoliation of 20% was performed on the same plants on the morning of day 194

Discussion

As predicted, control of transpiration in the three coffee cultivars was characterized by close coordination between vapor and liquid phase conductance, and apparent differences in regulation of transpiration among cultivars was governed by divergent hydraulic architecture rather than sto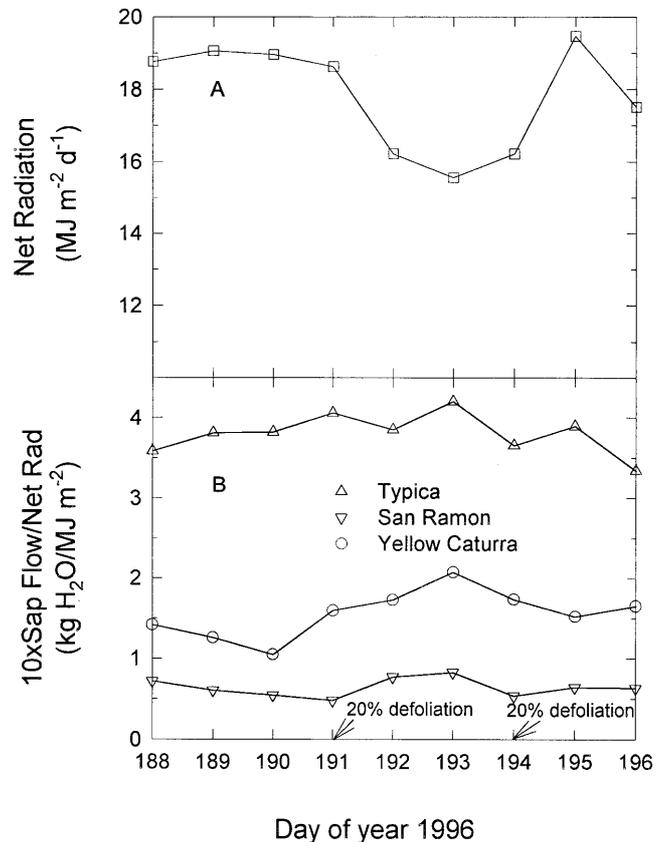matal physiology. Common relationships between indices of plant water transport and hydraulic architectural traits found for the three cultivars imply that the hydraulic properties of sapwood were likely similar among the three cultivars. When hydraulic architecture was manipulated *via* partial defoliation, sap flow was comparable to pretreatment levels. However, expected concurrent increases of g_s and G_t were not consistently observed for each cultivar. Possible reasons for these discrepancies

will be discussed below. Consistent with our hypothesis, Typica, the cultivar with the most open crown, had a greater degree of leaf-air coupling (lower values of Ω) than the two other cultivars studied. Since the three cultivars usually had similar operating ranges of g_s (Fig. 7), differences in values of Ω were mainly due to differences in g_b (Table 3), and thus, crown architecture.

In contrast to the weak correlation of E and g_c with Ψ_L (Table 2), both E and g_c were closely related to G_t. Similar linear relationships between E and G_t, g_c and G_t, and g_s and G_t among the three cultivars suggested that vapor phase conductance and therefore transpiration were limited by G_t over the entire range of G_t observed. Similar linear relationships between E and G_t and g_s and G_t were reported among four woody species growing in a Brazilian savanna (Meinzer et al. 1999), but curvilinear relationships between these traits have been found in other woody species (Sperry and Pockman 1993; Meinzer et al. 1995), indicating a threshold value of G_t above which E and g_s became independent of G_t. The values of G_t in the present study were all below 2 mmol m^{-2} s^{-1} MPa^{-1}, which were low relative to those reported in the other studies cited above, and would have fallen on the relatively linear part of the asymptotic curves obtained in those studies.

The ratio LA/SA is a morphological index of potential transpirational demand in relation to water transport capacity, and the association of both G_t, at a whole-plant level, and leaf area specific hydraulic conductivity, at an individual branch level, with LA/SA (Figs. 2, 3) suggests that variation in LA/SA was an important component of variation in water transport efficiency on a leaf area basis. Andrade et al. (1998) reported a relationship between G_t and LA/SA for several diverse tropical forest tree species similar to that shown in Fig. 2C. Furthermore, it was observed that normalizing g_c and g_s by LA/SA caused contrasting stomatal responses to humidity among these species to converge (Meinzer et al. 1997a), and normalizing transpiration by branch LA/SA also caused contrasting behavior within individual trees and among species to converge. These observations suggest that caution should be exercised in interpreting variation in transpiration and gas exchange in relation to variation in leaf area-based hydraulic properties. Contrasting patterns of transpiration among individuals having similar amounts of sapwood with similar hydraulic properties may reflect variation in LA/SA rather than intrinsic differences in the hydraulic properties of the water transport pathway. Thus, in drawing inferences about hydraulic limitations on gas exchange it should be specified whether developmental and environmental changes in morphological indices such as LA/SA are being considered.

The maintenance of sap flow despite partial defoliation demonstrates a dynamic response to a change in LA/SA. This finding has practical implications for managing irrigation in pruned orchards, because it cannot be assumed that whole-plant water requirements would be reduced in proportion to the leaf area removed. Significant increases in g_s were expected, but not consistently measured in partially defoliated plants. It is possible that the sampling procedure employed in measuring g_s was inadequate to detect an increase that may have occurred. Alternatively, it is likely that defoliation allowed more wind to circulate through the canopy, increasing wind speed and g_b (Eq. 2), which would allow g_c and sap flow to increase without a concomitant increase in g_s. Increased g_b would also reduce humidification of air near the leaf surface. Given the reported sensitivity of coffee stomata to decreasing humidity (Gutierrez et al. 1994), this should prevent g_s from increasing, consistent with our findings for Yellow Caturra. These relationships illustrate the dynamic balance between components of vapor phase conductance and leaf area-based hydraulic properties. Such adjustments serve to balance actual flux (transpiration) with hydraulic properties and suggest that transpiration itself is somehow being sensed. Monteith (1995) has proposed that the stomatal response to humidity relies on the stomata sensing the bulk leaf transpiration rate itself, but Meinzer et al. (1997b) provide evidence that stomata may instead sense the epidermal or cuticular transpiration rate. In contrast to the poor correlation between variation of Ψ_L and transpiration found in the current study (Table 2), other studies have shown direct responses of g_s and transpiration to Ψ_L and not E per se (Saliendra et al. 1995; Fuchs and Livingston 1996; Comstock and Mencuccini 1998). Although our data are inconsistent with models of continuous feedback between Ψ_L and g_s (Cowan 1965), they are not inconsistent with models invoking water-potential set-points, where rapid stomatal closure is associated with discrete thresholds (Comstock and Mencuccini 1998). That Typica developed substantially more negative predawn Ψ_L than the two other cultivars (–1.8 vs –1.0 MPa) when irrigation was withheld and was less vulnerable to loss of hydraulic conductivity (Tausend et al. 2000) suggests that these cultivars may differ in their water-potential set-points.

The relationship between E, G_t and leaf area (Fig. 6) is similar to relationships between maximum g_s and leaf area index reported for the *Coffea arabica* cultivar Yellow Catuai (Gutierrez 1993) and transpiration and leaf area reported for sugarcane (Meinzer et al. 1992). In sugarcane it was suggested that such coordination of stomatal regulation with leaf hydraulic properties as plant size and leaf area increase would prevent decreases in Ψ_L in well-watered plants that could cause decreases in hydraulic conductivity resulting from cavitation. The patterns also suggest that LA/SA and/or shoot/root ratios undergo a developmental progression. Leaf water potential plotted as a function of total leaf area for the three coffee cultivars in this study (data not shown) indicated a trend of slightly less negative water potential as total leaf area increased, consistent with the parallel changes presented in Fig. 6 and the examples of sugarcane and coffee mentioned above.

Values of Ω determined in the present study were lower than those reported for the coffee cultivar Yellow Catuai (Gutierrez 1993), which had a crown architecture very similar to that of Yellow Caturra. In the former

study, lower values of g_b were obtained utilizing the resistance subtraction method, which calculates g_b as: $g_b = 1/(1/g_c - 1/g_s)$. A previous study of four tropical tree species in which estimates of g_b obtained from the resistance subtraction method were compared with those obtained from leaf dimensions and wind speed near the foliage found that values of g_b obtained by resistance subtraction were about one-third of those obtained by the other method. This resulted in values of Ω 15–32% higher than those calculated using wind speed and leaf dimensions (Meinzer et al. 1997a). Consistent with this, at a g_s of 100 mmol m^{-2} s^{-1}, Ω of Yellow Catuai was about 25% higher than the value obtained for Yellow Caturra in the present study. Despite this discrepancy, the current study established that different crown morphologies were associated with distinct ranges of Ω, such that the denser crowns of Yellow Caturra and San Ramon were more decoupled with respect to stomatal control of E than Typica.

We conclude that differences in the three cultivars' behavior with respect to control of E were governed by differences in hydraulic and crown architecture rather than stomatal physiology. Contrasting hydraulic architecture resulted in different operating ranges of G_t for each cultivar, but E and total vapor phase conductance were similar among all three cultivars at a given value of G_t. The dynamic nature of the balance between E and leaf area-based hydraulic properties was reinforced by short-term responses to "instantaneous" manipulation of hydraulic architecture by partial defoliation. Differences in crown architecture, through their effects on g_b and Ω, resulted in a distinct relationship between g_s and G_t for each cultivar, so that g_s at a given value of G_t increased with Ω. Stomatal adjustments to prevailing boundary layer conditions in intact and partially defoliated crowns led to similar relationships between E and G_t for all cultivars. Responses of transpiration to manipulations of hydraulic and crown architecture were thus consistent with balancing of vapor flux rather than g_s with G_t and imply stomatal sensing of the transpiration rate itself.

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