Technical Brief

Device for Simulating High Rates of Sap Flow in Grapevines

J.M. Tarara[1]* and J.C. Ferguson[2]

Sap-flow gauges typically are tested by comparing their output to gravimetric measurements of water loss from a potted plant. However, a mature vine of *Vitis labrusca* cv. Concord, when potted, could not achieve the high rates of sap flow that were observed in similar vines in the field. This limited the range in which the sap-flow gauges could be tested and confidence in their accuracy at high flow rates. Consequently, a laboratory device was constructed to reproduce the high rates of sap flow that were observed in the vineyard on mature grapevines. The device allows gauge testing on a severed vine stem, thereby reproducing the thermal regime of a sap-flow measurement in the field. The design of the device is simple, and its component parts are low-cost and easily obtained from commercial sources. The device permits empirical determination of limiting factors in gauge performance as they vary with flow rate. It also permits the establishment of "zero-flow set" or gauge conductance on hydrated stem tissue. Evaluation of the heat-balance method under high rates of sap flow (>1500 g h^{-1}) showed that gauges made from designs that are standard in the literature consistently underestimated gravimetric measurements. Evidence suggests that gauges should be redesigned to accommodate thermal heterogeneity across the vine stem that occurs under high flow.

Key words: Vitis, heat-balance method, sap gauge, water use, transpiration, measurement, stem flow, woody species, methodology

Sap-flow gauges have been employed extensively to measure water use in both herbaceous [6,18,23,27] and woody plants [1,21,30,31], including grapevines [5,8,11,20,35]. Prior to deploying gauges in the field, standard protocol is to assess the accuracy of the instruments by comparing gauge output to gravimetric measurements of water loss from a potted specimen [7,20,34]. Large woody plants may restrict this testing for two reasons: it can be impractical to pot a sufficiently large specimen, and it may not be possible to duplicate the high flow rates of mature, field-grown plants. In the "heat-balance" sap-flow method, the principles of which are well described elsewhere [3,29,31], adequate testing at high flow rates is critical. Common gauge designs can fail under high flow rates if key assumptions of the method are violated [2,14,15,28].

Briefly, the heat balance method involves encircling a plant stem with a flexible heater, applying a known amount of energy to the stem, and then accounting for the dissipation of that energy within the system. Convection heat transfer occurs in the xylem sap stream; thus, the mass flow rate of water through the stem is measured by determining the convection portion of a stem heat balance. Heat transfer rates are determined from knowledge of the thermal properties of the stem and from measurements of stem temperature above, below, and radially adjacent to the heater. Main assumptions of the method include: (1) the heated stem segment is at steady-state; (2) there are negligible radiant and latent heat losses; and (3) there are negligible changes in temperature from the surface to the center of the stem at a given location along the stem axis (radial thermal homogeneity). At high flow rates, the heat-balance method can fail because the temperatures measured above and below the heater may not represent a uniform temperature across the stem [2,17]. Nevertheless, the heat-balance method remains attractive because it is noninvasive and requires neither knowledge of the cross-sectional area of the xylem vessels nor empirical transformations of the data, which are limitations of other sap-flow methods (such as heat pulse).

Because of low plant densities in vineyards relative to other crops, vineyard water use may seem low [9,20] on a per acre basis. However, on a per vine basis, rates of transpiration can be quite high, particularly in large, well-watered canopies (for example, 60 L d^{-1} for Thompson Seedless in California; L. Williams, personal communication). The purpose of this paper is to describe a device that was constructed to reproduce high rates of sap flow in woody stems, specifically grapevines, to assess the accuracy of standard heat-balance sap-flow gauges, and to facilitate the development of new gauge designs for use in mature grapevines.

Materials and Methods

Project background. Heat-balance sap-flow gauges were constructed in-house based on the U-shaped design [26] for use on 10-year-old vines of *Vitis labrusca* cv. Concord. Vine trunks typically were 32 to 40 mm in diameter, well below that (up to 90 mm diam) which the heat-balance method had been used successfully on other woody stems [28,30,31,32]. Leaf area per vine averaged 14 to 18 m^2. Vine density was 1500 vines ha^{-1}.

[1]Research Horticulturist, [2]Electronics Technician, USDA-ARS, Horticultural Crops Research Unit, 24106 N. Bunn Rd., Prosser, WA 99350.

*Corresponding author [jtarara@tricity.wsu.edu; Fax: 509-786-9277]

Manuscript submitted December 2000; revised April 2001. This research was publically funded through the U.S. Dept. of Agriculture and is considered to be in the public domain.

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Gauges first were tested in the greenhouse on a 10-year-old, potted Concord vine that had been excavated from the vineyard while dormant. Trunk diameter averaged 45 mm and vine leaf area was estimated at 2 to 3 m^2 during the test period. The pot (76-l) was sealed to prevent soil evaporation and the entire assembly placed on a precision load cell (LCAE-45KG, Omega, Stamford, CT) with an accuracy of ±5 g for a 40-Kg load. Sap-flow measurements underestimated transpiration calculated gravimetrically by 16% on a cumulative 24 hr basis. Maximum flow rates exceeded 550 g h^{-1}, with most daily maxima about 450 g h^{-1}. Subsequently, 20 heat-balance sap-flow gauges were operated simultaneously in a commercial, furrow-irrigated vineyard for 94 days during the summer of 1999. Maximum midsummer flow rates estimated by the sap-flow gauges exceeded 3000 g h^{-1}, although daily maxima averaged 1350 g h^{-1} across all vines. From these data, cumulative estimates of vine water use were calculated. Midseason values under full canopies were about 10 L d^{-1} per vine. Estimates of total vine water use for a 120 day period were 183 mm per acre. Compared with values determined by lysimetry for well-watered, drip-irrigated vines in the same area (417 mm; [9]), ours were unrealistically low. This result called into question the accuracy of the sap-flow gauges on rapidly transpiring vines.

Device construction. The first model we considered for a gauge-testing device was a simple pipe through which water could flow via a hydraulic head [10,16] or be pumped. Grapevine stems have been shown to be excellent conductors of water, responding to hydrostatic pressure from an adjacent water column attached to the base of a severed trunk [25]. However, we rejected the analogy because flow through a pipe is in a single turbulent column, whereas flow through a vine trunk is through many, relatively narrow, vessels. Radial thermal homogeneity in the stem is critical to the success of the heat-balance method [2] and flow pattern influences temperature distribution [2,4,17]. Bundling small tubes within a pipe [16] was rejected because the heat capacity and thermal conductivity of the materials would not be representative of grapevine trunk tissue. For studying flow through a grapevine stem *in situ,* the best model is a severed trunk section from a vine of appropriate diameter.

The sap-flow simulator device consisted of components to control water delivery to a severed trunk section and components to monitor continuously the ensuing flow rate (Figure 1). Water was supplied from a laboratory tap with a hose barb at pressures up to about 0.35 MPa (≈50 psi). Reinforced PVC tubing (6.4 mm i.d.; Tygon, Akron, OH) delivered the water to a 15-turn needle valve (Swagelok-Nupro, Willoughby, OH). Thus, unlike the simple hydraulic head approach [10,16,25], precise manual control of the flow rate was possible for practically unlimited duration. The user set an approximate stem flow rate via a stock glass flow meter (Brooks Instruments, Hatfield, PA). A pressure gauge was plumbed inline for reference. Iron pipe fittings were selected to match closely the diameter of the trunk specimen. A severed trunk from which all loose bark had been stripped was attached to the pipe fittings by a neoprene rubber coupler fastened with hose clamps. A hole (4 mm diam) was drilled and tapped into the top of the pipe fitting to allow air to bleed during the initial startup of the simulator device, thereby minimizing embolisms. The port also was used for injection of dye into the water stream. Water exiting the trunk section was funneled into a covered reservoir on a precision load (previously specified). The trunk was oriented horizontally to facilitate collection of the exit water. Flow rates were calculated directly from the change in mass of water on the load cell. Both the load cell and the sap-flow gauge were monitored and controlled by a datalogger (CR 10X, Campbell Scientific, Logan, UT). A variable-power circuit [33] was included so that over a wide range of flow rates, a fixed temperature difference was maintained above and below the heated segment. Measurements were recorded at 5 s intervals and averaged every 12 min. Experimental runs varied from several hours to several days.

The 15-turn fine meter valve was automated by connection to a 12-V, 4.5 rpm, reversible gear motor (part no. 155820, Jameco Electronics, Belmont, CA) and a 6.4-mm bore (1/4-inch) miniature slip clutch (U-MSCB-4, Small Parts, Inc., Miami

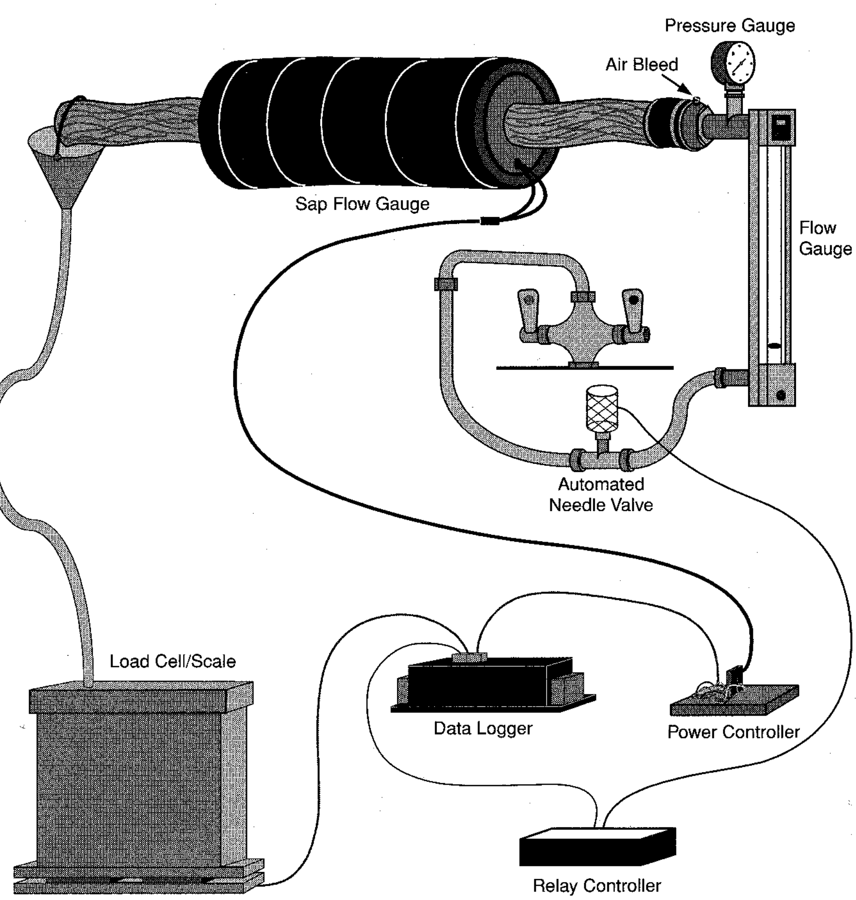

Figure 1 Schematic diagram of sap-flow simulator device (not drawn to scale).

Lakes, FL). The slip clutch eliminated the risk of damaging the needle valve by over-turning it. The aperture of the valve was monitored by the datalogger, which controlled a relay driver (SDM-CD16, Campbell Scientific, Logan, UT) and the on-time of the motor (the number of turns of the needle valve). The direction of rotation was controlled by the polarity of the 12-V power supply via the relay driver. Algorithms were written to automatically produce multiple step changes in flow rate over several hours or to produce flow rates following a sinusoidal curve. The sine curve reproduced the diurnal patterns of flow rate (transpiration) that could be observed in the field (Figure 2). Details of the hardware-software system are available from the authors upon request. Step changes in flow rates were used to assess the linearity of the sap-gauge system and to determine its time constant at various flow rates. Sinusoidal patterns of flow were used to test control algorithms for the variable-power approach [13,17,33].

Results and Discussion

Using freshly severed, dormant Concord trunks (34 to 38 mm diam), initial trials with input pressures of about 0.3 MPa (≈40 psi) achieved flow rates up to 3000 g h^{-1}. Maximum flow rates were limited by the conductivity of the stem at the pressure available from the tap. Values up to 600 g h^{-1} have been reported for grapevines [5] of similar diameter to our trunks, whereas much higher values have been measured in tropical vines [10] and tree branches [32] of similar diameter. The maximum attainable flow rate in the simulator diminished over time (Figure 3a). We suspect that secondary metabolites progressively clogged xylem vessels because a gelatinous exudate was observed continuously at the terminus of the trunk section (M. Goffinet, personal communication). The exudates may have been the manifestation of a wound response. They either formed at, or migrated to, the cut ends of the trunk segment; trimming a few cm from each end of the severed trunk restored maximum flow rates to nearly their original values (Figure 3b). Injection of dye (methylene blue) into the xylem streams of freshly-cut and two-week-old severed trunks showed a relatively uniform decrease radially in the proportion of xylem elements that were conducting water (Figure 4). Through visual inspection of the dye patterns on the freshly-cut and well-used trunks, we concluded that the horizontal orientation of the stem in the simulator device did not lead to gravity-induced preferential flow along the "bottom" of

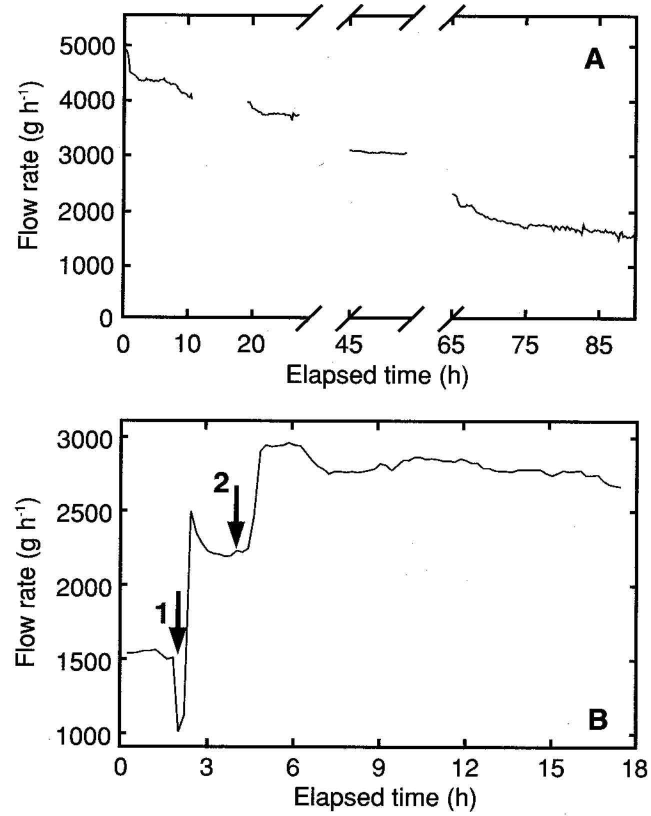

Figure 3 Time-dependent decrease in flow of water through a severed grapevine trunk installed on sap-flow simulator device (**A**), due to clogging of xylem vessels by exudates. Input pressures ranged from 0.28 to 0.36 MPa (42 to 52 psi). Gaps in data are overnight periods when exiting water was not collected. (**B**) Restoration of higher flow rates through the same severed trunk, by trimming the equivalent of one stem diameter from the ends of the trunk segment. Arrow 1 corresponds to cut made on the downstream end of the trunk; arrow 2 corresponds to cut made on upstream end of the trunk segment.

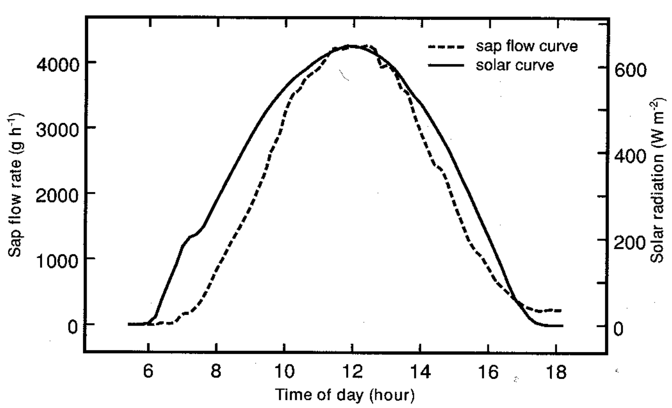

Figure 2 Incident solar radiation (solid line) measured during a day with 12 hr daylength and simulated diurnal curve of sap flow (dashed line) reproduced by use of an automated, fine needle valve that controls water delivery to the sap-flow simulator device. Solar radiation was measured with a pyranometer (model 8-48, Eppley, Newport, RI). The simulator device is controlled by an algorithm that reproduces a sinusoidal pattern of sap flow following the daily curve of solar radiation.

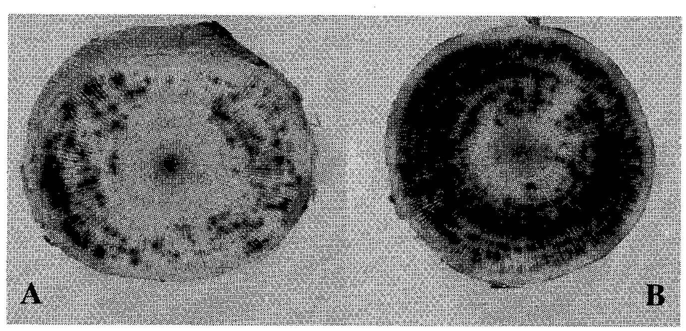

Figure 4 Cut stem sections of *Vitis labrusca* cv. Concord, stained with a xylem mobile dye. (**A**) Stem used for two weeks in the sap-flow simulator device. (**B**) Freshly severed stem (< 1 h). Dark areas are colored by dye and indicate sap flow, whereas lighter areas indicate no flow. Center of stem on both specimens is not dyed.

the trunk. Trunks excised while dormant remained useable longer than trunks from actively growing vines. Each severed trunk was used in the simulator for about one week, then discarded. Twenty-one 10- and 11-year-old Concord trunks were used during the experiments.

One functional consideration was that a trunk on the simulator device was under pressure, but a transpiring vine *in situ* is under tension. Thus, there was concern that the device could have forced water through vessels that might have been unused under field conditions. We examined the pattern of conductive xylem vessels in an actively growing, transpiring vine of the same age (11 years) and similar trunk diameter (34 to 38 mm) as our laboratory specimens. The vine was severed above the ground, at night; the severed stem immediately was placed in a container of dyed water, left in the vineyard for 48 hr, then sectioned. The dye revealed a toroidal flow pattern (Figure 5b). An undyed stem section, showing a small disc of nonconducting tissue at the center, is presented for comparison (Figure 5a). On average, the zone of xylem in which sap was conducted comprised about 77% of the stem's cross-sectional area. Subsequently, a freshly severed trunk of similar diameter was installed in the simulator device, under pressure, and dye injected into the port. The result was a similar toroidal flow pattern to that obtained in the field (Figure 5c) with about the same proportion of stem cross-sectional area (≈79%) comprised of conducting elements. Another fresh trunk segment was obtained and the simulator device placed under vacuum (≈0.1 MPa) with a vacuum aspirator to simulate the effect of water movement under tension due to transpiration. Dye again showed a toroidal flow pattern and a zone of conductive vessels similar to the previous tests (82% of cross-sectional area; Figure 5d). The apparent differences in dye intensity among Figures 5b, 5c, and 5d were due to different dye concentrations in the field and laboratory tests, not to a difference in the density of conducting elements. The lower concentration of dye evident in Figure 5c resulted from a single pulse of dye being injected into the simulator's water stream, whereas in Figures 5b and 5d both stems were under tension and continuously absorbed the dyed solution.

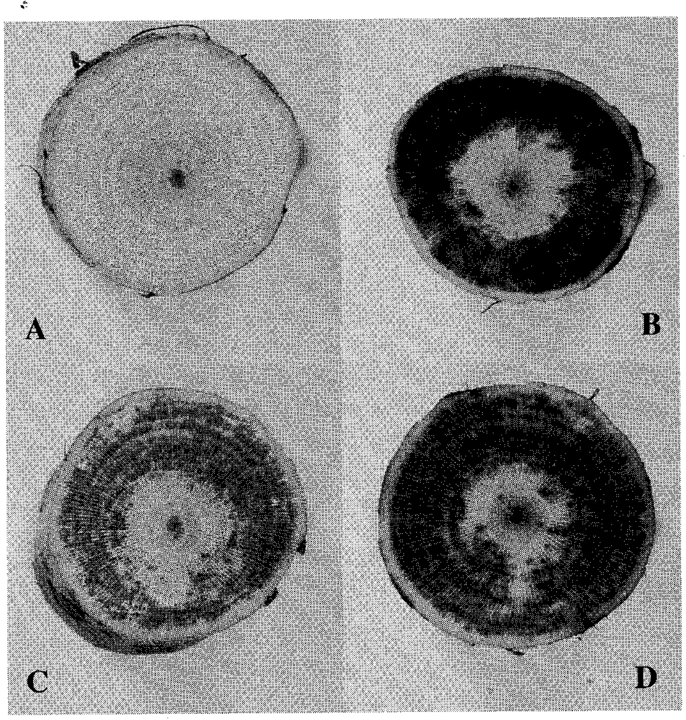

Figure 5 Cut stem sections of *Vitis labrusca* cv. Concord, stained with a xylem mobile dye. (**A**) Undyed stem for comparison; note dark central disc. (**B**) Stem under transpiration stream (tension) in vineyard. (**C**) Severed stem under pressure in sap-flow simulator. (**D**) Severed stem under tension in sap-flow simulator. Increased dye intensity in (**B**) and (**D**) is due to the vine continuously absorbing a dyed solution, whereas in (**C**) a single pulse of dye was injected into the upstream water.

With the sap-flow simulator device, we recommend using the longest trunk segment that is feasible to minimize potential difficulties from preferential flow patterns in the radial aspect. Scholander [24] reported an average vessel length of 0.6 m in temperate *Vitis labrusca* (noncultivated) and maximum lengths of 3 m. Our trunks were obtained from a vineyard with a cordon height of 1.5 m, yielding 0.9 to 1.2 m of useable trunk length for laboratory experiments. The distribution of active xylem elements from the dye experiments suggests that the flow pattern through the severed trunk in the simulator device does indeed mimic that of a trunk connected to a full canopy in the field.

An ancillary application of the simulator device is the maintenance of a well-hydrated trunk segment under zero flow for the determination of the "zero-flow set" or gauge conductance (K_g) value that is required in the heat-balance method. The value of K_g primarily is due to gauge materials and design, but can change slightly with stem geometry [2,14]. Typically, K_g is set nightly in the field, under the assumption that before dawn, sap flow is zero. However, with our potted vine, we measured nocturnal transpiration of 15 to 25 g h^{-1} with both the sap-flow and gravimetric methods (data not shown). Errors in K_g are most troublesome at low rates of sap flow, when heat loss by radial conduction is a large fraction of the entire heat balance [2, 22]. Rather than setting a potentially incorrect predawn K_g in the field, we opted to establish the value for each gauge in the laboratory on the simulator device, accepting the smaller error that would result from variations in stem geometry in the vineyard [14].

After large step changes in sap flow (±500 g h^{-1}) that we created with the simulator, the time constant of the system, defined as the time for the gauge to reach 63% of the final target value, was about 25 min at low to moderate flow rates (<700 g h^{-1}) and within 12 min at high flow rates (>1000g h^{-1}). The time constant of the system is a function of flow rate; knowledge of the time constant facilitates programming the variable power control algorithms to ensure responsiveness in the field.

Finally, the accuracy of the sap-flow gauges was evaluated. The original set of gauges, based on standard designs in the literature, performed well up to about 500 g h^{-1}, the upper threshold of our greenhouse measurements. Several seminal studies on the dynamics of the heat-balance method defined "high" flow rates as 150 to 200 g h^{-1}, albeit for stem diameters somewhat smaller than those of our vines [2,15,22]. Above 500 g h^{-1}, apparent thermal heterogeneity across the stem (Figure 6) caused the gauges to underestimate sap flow by as much as 66%; hence

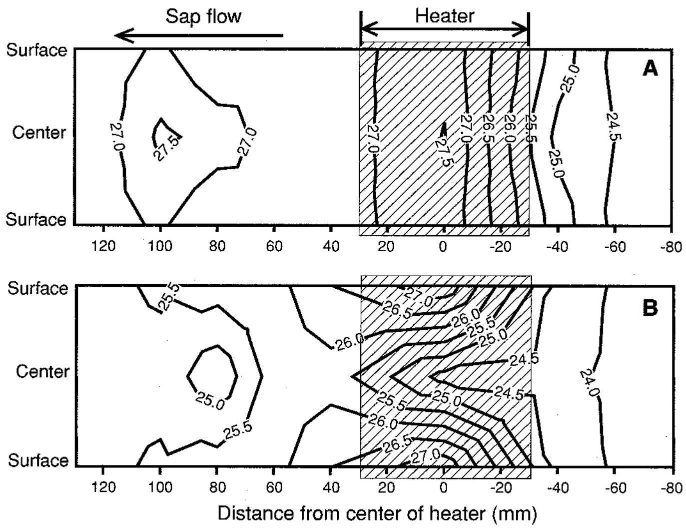

Figure 6 Temperature profiles from the surface to the center of the stem tissue, from 80 mm upstream to 130 mm downstream of the heated stem segment plotted on a longitudinal stem section. Flow direction is right to left. Trunk diameter averaged 38 mm; heater width was 60 mm. Thermocouples were installed at 11 locations along the stem axis, beneath the bark ("surface") and near the center of the stem ("center") but outside the nonconducting pith/heartwood disc. Input power was 1.0 W. (**A**) Radially homogeneous temperatures evident at 450 g h^{-1} ("low" flow rate). (**B**) Thermal heterogeneity evident in the radial aspect at 1050 g h^{-1}. For downstream thermocouples relatively near the heater, which is typical for traditional heat-balance sap-flow gauges, surface temperatures may not represent true tissue temperature at that axial position.

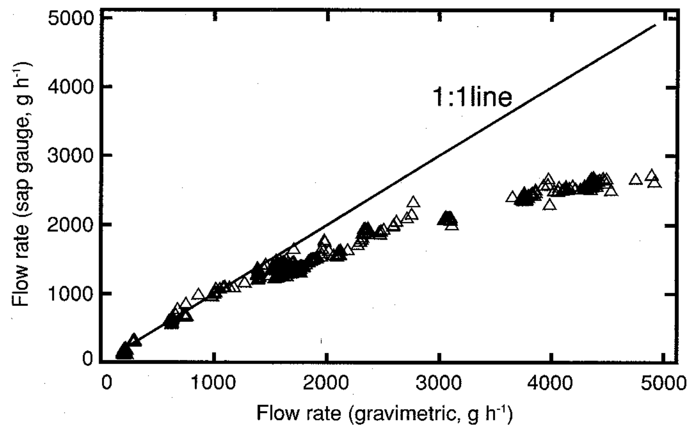

Figure 7 Rates of sap flow attained with severed trunks (n = 21) of *Vitis labrusca* cv. Concord on sap-flow simulator device. Heat-balance sap-flow gauges agreed with gravimetric measurements to within 10% at low to moderate rates of sap flow (<1000 g h^{-1}), but consistently underestimated flow at high rates (>2000 g h^{-1}).

our suspicious estimates of vine water use in the field. Thermal heterogeneity in the radial aspect increases the likelihood that thermocouples at the stem surface do not measure a representative tissue temperature, thus yielding underestimates of sap flow. Some researchers have addressed this difficulty by inserting thermocouples into the stem to a depth where the measurement is expected to represent an average radial temperature [10,17,19,34]. We chose to maintain a noninvasive design and instead placed the thermocouple junctions at positions along the stem surface where thermal homogeneity would exist at high flow rates. The original, poorly performing gauges were subsequently redesigned and tested. Flow rates calculated from the gauge signals agreed well (within 10%) with those computed from mass balance at low to moderate flow rates (up to 1500 g h^{-1}; Figure 7). However, at high flow rates (>2000 g h^{-1}), gauge and balance diverged, with the sap-flow gauge underestimating transpiration by as much as 50% at 5000 g h^{-1}. We are continuing to redesign and test gauges specifically at very high flow rates (>3000 g h^{-1}).

A key strength of the heat-balance method is in estimating cumulative daily water use rather than in estimating a precise flow rate at a given time, because some of the errors that occur in the method, such as violation of steady state at either end of the day, self-compensate over a 24 hr interval [2,12]. In our case, large errors at high flow rates are troublesome because they induce larger errors in cumulative water-use estimates than do errors that occur at low flow rates. For high-flow plants, an underestimate of 25% at an instantaneous flow rate of 100 g h^{-1} has a much smaller effect on estimates of total daily water use than does a 25% error at an instantaneous rate of 1500 g h^{-1}.

Conclusions

The device described herein, the sap-flow simulator, is a useful tool for researchers working with sap-flow gauges on unfamiliar woody species or on large plants where modifications to existing gauge designs may be required because of stem morphology or high flow rates. The method is destructive, but it allows repeated testing in situations where potted specimens may be unavailable or impractical to maintain. The simulator device is simple in design, inexpensive, and allows the testing of gauge performance under a variety of controlled flow rates. For plants exhibiting nocturnal flow, the device also provides an alternative method of establishing the required K_g before field installation. Because the actual plant under study is used in the device, the thermal properties of the gauge-stem system are identical to those encountered in the field. Individual factors affecting the performance of the gauge, such as environmental heating of the stem, can be evaluated in a more controlled setting than the field, leading to more robust measurements when gauges ultimately are deployed in the vineyard.

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