Measurement of sap flow in roots of woody plants: a commentary

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Summary Measurements of sap flow in roots have recently been used to study patterns of resource acquisition by woody plants; however, the various thermometric methods employed have yielded disparate findings. These findings may be harmonized by accounting for the phenomenon of reverse sap flow in roots. We suggest that only methods capable of measuring slow and reverse rates of flow and that do not require assumptions of zero flow during the night are applicable to studies with roots. The heat ratio method and the constant power heat balance method fit these criteria, whereas the constant temperature heat balance, compensation heat pulse and thermal dissipation methods do not.

Keywords: heat pulse method, hydraulic lift, soil moisture, water uptake.


Heat-based sap flow gauges, which were developed for use on plant stems, have also been applied to woody roots to quantify water uptake by plants (Cabibel and Do 1991a, Howard et al. 1996, Lott et al. 1996, Green et al. 1997). In contrast to measurement of whole-plant transpiration (which gives no information about the source of water or net changes in soil water content, and which cannot identify the action of specific plants) direct measurement of sap flow in roots provides the opportunity to link resource acquisition with belowground form and function.

The number of heat-based sap flow techniques has increased in recent years (Swanson 1994, Edwards et al. 1996, Smith and Allen 1996) and these techniques have been widely employed in a variety of systems. In the last decade, four techniques have been applied to tree roots (Cabibel and Do 1991a, Cabibel 1994, Green and Clothier 1995, Howard et al. 1996, Lott et al. 1996, Moreno et al. 1996, Green et al. 1997, Burgess et al. 1998, Smith et al. 1999), and three different patterns of diurnal sap flow have been described for roots growing in dry soil. Discrepancies among studies based on different techniques raise the question of whether large differences in patterns of water uptake exist among trees or whether such differences are a result of methodological constraints.

Because flow rates and directions can differ markedly between roots and stems, heat-based sap flow techniques developed for stems may yield ambiguous or erroneous results when applied to roots. We review the theoretical constraints of recently used methods and illustrate some of the difficulties associated with each technique.

Sap flow techniques recently applied to roots The basic theory and operation of the sap flow techniques discussed in this paper (with the exception of the heat ratio method) have been described and reviewed by Smith and Allen (1996). Here we discuss how the method of operation of each technique constrains its ability to measure the rate and direction of sap flow in roots.

Variable power, constant temperature heat balance method (CTHB) The constant temperature heat balance method used by Lott et al. (1996) and Howard et al. (1996) consisted of a heating element wrapped around the outside of a straight section of root. The element was insulated with styrofoam and metal foil to minimize heat exchange with the external environment. Variable power was supplied to the heater coil to maintain its temperature constantly at 5 °C greater than the unheated root, as measured at a fixed position distal to the coil with respect to the tree crown. Usually, heat balance methods measure and deduct radial and axial conductive heat losses from the amount of heat supplied to the heater coil to determine how much heat is lost as a result of convective transport by moving sap. The mass of moving sap is calculated by the amount of heat it absorbs, its temperature increase (measured by thermocouples placed at either end of the heated root section), and its specific...
heat capacity (Smith and Allen 1996). Lott et al. (1996) and Howard et al. (1996) assumed that, under conditions of high sap flow during daylight hours, conductive heat losses were negligible relative to heat losses due to moving sap, and therefore did not require measuring. However, use of this assumption restricted measurements to daylight periods where rates of flow were expected to be fast.

The CTHB method is only capable of measuring sap flow if sap moves in the direction of the increasing temperature gradient between the unheated root and the heater coil. As pointed out by Smith and Allen (1996), sap flowing opposite to the direction of this gradient would cause the power supply to the heater coil to increase in an attempt to maintain the direction of the temperature gradient.

Thermal dissipation probe (TDP)

The thermal dissipation probe (Granier 1985) is based on comparisons between the temperature of a constantly heated probe and that of an unheated probe, both of which are implanted radially into the xylem of a plant. Cabibel and Do (1991a) implanted the unheated probe 8–10 cm distal to the heated probe (with respect to the crown). The distance separating the probes made thermal interference unlikely regardless of the rate and direction of sap flow.

Sap flow past the heated probe increases dissipation of heat by convection, thereby reducing the difference in temperature (δT) between the heated and reference probe in proportion to the rate of sap flow. Because heat is dissipated regardless of the direction of sap flow, the method yields scalar rather than vector measurements of sap flow.

To calculate sap flow, a maximum value of δT, corresponding to the temperature difference when sap flow is zero, must be obtained. This value (denoted δT₀) by Cabibel and Do (1991b) and δTₐₔ by Granier (1985) is measured at night when it is assumed that sap flow has ceased.

Compensation heat pulse method (CHPM)

The CHPM employs two temperature probes, implanted radially into xylem tissue and spaced asymmetrically from a similarly inserted line heater element. The midpoint of the two probes is located a specific distance downstream (i.e., closer to the tree crown) from the heater. A pulse of heat is released into the sap stream by the heater and carried by flowing sap toward the midpoint between the temperature probes. When both probes reach the same temperature, the heat pulse is judged to have moved to the point midway between the probes, and heat pulse velocity can be calculated as a function of distance and time. Heat pulse velocity can only be measured by the CHPM if it is sufficient to carry the heat pulse toward the fixed point before it dissipates by conduction. The threshold below which heat pulse velocities cannot be measured is dependent on the sensitivity of the temperature probes and the thermal diffusivity of the xylem. The minimum velocity measurable by the CHPM is 3.6–7.2 cm h⁻¹ (0.01–0.02 mm s⁻¹), according to Becker (1998), or 4 cm h⁻¹, according to Burgess et al. (1998).

Heat ratio method (HRM)

The HRM employs two temperature probes implanted in the xylem equidistant from a line heat source, one proximal and one distal to the crown. Heat pulse velocity (Vₘ) is related logarithmically to the ratio of temperature increase at each sensor position following the release of a pulse of heat (Marshall 1958):

\[ Vₘ = \frac{k}{x} \ln \left( \frac{v₁}{v₂} \right), \]

where k is thermal diffusivity of wet wood, x is the distance between heat source (heater) and temperature sensors, and v₁ and v₂ are the increases in temperature (relative to ambient) at equidistant points, x cm from the heater, proximal and distal to the crown, respectively.

Hence, during typical daytime conditions with a moderately moist soil, the probe proximal to the crown is heated to a greater temperature (by convection plus conduction) than the distal probe, giving a temperature ratio > 1. At times when sap flow is reversed (e.g., Burgess et al. 1998), the distal probe is then heated to a greater degree than the proximal probe, yielding ratios < 1, the logarithm of which yields a negative value. As rates of flow approach zero, convection ceases to heat either probe preferentially and ratios approach unity. The logarithm at unity is zero and hence zero sap flow yields a zero value. Gravimetric validation of the HRM in plant stems suggests that it is capable of measuring slow rates of flow with considerable accuracy (Figure 1). The HRM has limitations.

Figure 1. Accuracy of the heat ratio method (HRM) at low rates of sap flow. Weight loss from a potted 8-year-old Eucalyptus marginata J. Donn ex Sm. tree was measured with a digital recording balance (± 20 g) and compared with rates of sap flow measured by the HRM. The HRM was installed as described by Burgess et al. (2000), except that the temperature probes were spaced 0.5 cm either side of the line heater element. The right-hand axes indicate sap velocities corresponding to the rates of volumetric flow (left axes) measured during the experiment. The dashed line represents a 1:1 relationship.
when measuring fast rates of flow. Marshall (1958) suggested that Equation 1 only applies if $v_1/v_2 < 20$. This equates to sap velocities of about 45 cm h$^{-1}$ (where $x = 0.6$ cm). Higher rates (e.g., in some vine species) can be accommodated by increasing probe spacings.

**Constant power heat balance (CPHB) method**

The CPHB method does not use a constant temperature gradient across the measurement apparatus and therefore has the potential benefit over the CTHB of being able to measure sap flow, even if it reverses direction. However, if reverse flows are to be measured, minor modifications must be made to data collection. As sap flow, and therefore the temperature difference between the thermocouples placed at either end of the heated root section approaches zero, calculations of sap flow become implausibly high or undefined (Smith et al. 1999). These values must be discarded and instead, sap flow is assumed to be zero according to predetermined criteria. Smith et al. (1999) assumed flow was zero if the absolute temperature difference between sap entering and leaving the heated root section was < 2.0 °C, whereas Sakuratani et al. (1999) used a value of 0.2 °C.

The second important aspect of data collection is that the sign of the temperature differential across the two ends of the heat section, rather than the absolute value, must be recorded.

**Patterns of sap flow in roots in dry soil determined by different sap flow methods**

**CTHB**

Lott et al. (1996) and Howard et al. (1996) measured sap flow in the roots and trunk of *Grevillea robusta* Cunn. by the CTHB method. A full diurnal pattern of sap flow is not available for this study, because measurements were restricted to daytime. The daytime pattern of sap flow in roots followed the pattern of sap flow in the trunk—a steady increase in flow toward noon, followed by a steady decrease in flow toward the evening.

**TDP**

Cabibel and Do (1991a) used the TDP to measure sap flow in the trunk and lateral roots of apple (*Malus pumila* Mill.), and compared rates of sap flow in lateral roots growing either with or outside of a patch of wet (irrigated) soil. They found that roots growing within the patch of wet soil had a pattern of sap flow in synchrony with that of the trunk, whereas the pattern of sap flow in roots growing in dry soil was approximately 12 h out of phase with that in the trunk. Hence, peak sap flow was recorded close to midnight (see Figure 2). This phase shift or lag in sap flow was attributed to a combination of low water availability, transport distance and recharge of tissue water stores.

**CHPM**

Green et al. (1997) repeated the study of Cabibel and Do (1991a) with the CHPM in place of the TDP technique and reported that, in contrast to the findings of Cabibel and Do (1991a), sap flow in apple roots (*Malus domestica* Borkh. cv. Braeburn) was in phase with sap flow in the trunk. Green et al. (1997) attributed the differences between the two studies to either a difference in technique or a difference in hydric status of the trees.

**HRM**

Burgess et al. (1998) used the HRM to measure sap flow in roots of *Grevillea robusta* Cunn. and *Eucalyptus camaldulensis* Dehnh. var. *obtusa* Blakely. In both species, sap flow was generally in phase with that in the trunk. Moreover, sap flow reversed in response to hydraulic lift in roots in dry soil. Reverse flow was greatest during the night when the gradient in water potential favored efflux of water from roots and was least balanced by the gradient between the canopy and the atmosphere. On some occasions, the water potentials developed in the crown during the day were not sufficiently low to reduce root water potential below that of the extremely dry topsoil. Hence water did not enter lateral roots and move to-

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**Figure 2.** Upper panel: patterns of sap flow measured by Cabibel and Do (1991a) in lateral roots of apple growing in wet soil (dotted line) and dry soil (solid line). Sap flow in the root growing in dry soil was approximately 12 h out of phase with that in wet soil, and the pattern of evapotranspiration (ETP, dashed line). Redrawn from Cabibel and Do (1991a) (Figure 5; p 761) with permission from Elsevier Science. Lower panel: a reinterpretation of Cabibel and Do’s (1991a) scalar measurements, where flow rates have been assigned a negative value, suggesting that reverse flow in the root growing in dry soil may have been responsible for the apparent phase-shift noted by Cabibel and Do (1991a).
ward the crown. Under such conditions, only roots with access to soil of higher water content (e.g., the taproot) supply the transpiring canopy and, in addition, provide water to lateral roots. This situation may arise either because of particularly dry soil or particularly low rates of transpiration. An example of the latter is shown in Figure 3.

**CPHB**

Smith et al. (1999) used the CPHB method to demonstrate reversal of sap flow in roots of the same stand of *G. robusta* studied by Burgess et al. (1998). As reported by Burgess et al. (1998), Smith et al. (1999) found that when the water potential of soil surrounding the tap root was lower than that developed in the crown as a result of transpiration, sap in the tap root flowed continuously in reverse throughout both day and night. Sakuratani et al. (1999) measured sap flow in the roots of *Sesbania rostrata* growing in a split-root experimental apparatus. Sap flow in a root growing in a watered, wet soil compartment was compared to that in a root growing in an unwatered, dry soil compartment. This experimental design is similar to the scenario investigated by Cabibel and Do (1991) under field conditions. Sakuratani et al. (1999) demonstrated reversal of sap flow in the root growing in dry soil, as water was transferred from the root growing in wet soil.

**Can methodological differences mask patterns of sap flow?**

The diurnal sap flow pattern for *G. robusta* found by Burgess et al. (1998) and Smith et al. (1999) during very dry conditions was similar to that established for apple by Cabibel and Do (1991a), if the direction of flow is ignored (see Figure 2). We suggest that because the TDP technique is largely constrained to scalar measurements of sap flow, the interpretation of Cabibel and Do (1991a) should be modified. If the sap flow data presented are assigned a negative value, the diurnal trend suggests that the dynamics of sap flow are in phase with that in the trunk. Furthermore, the trends become almost identical to those reported by Burgess et al. (1998) and Smith et al. (1999) for roots in soil with a water potential lower than the minimum canopy potential (see Figure 3).

Therefore, we suggest that roots within the area of wet (irrigated) soil absorbed water in synchrony with evaporative demand and sap flow in the trunk, whereas roots in dry soil exuded water in inverse proportion to demand for water elsewhere in the plant. Such lateral transfer and exudation of water have been demonstrated by measuring changes in soil water content in split root experiments (reviewed by Caldwell et al. 1998) and in combination with the CPHB method (Sakuratani et al. 1999). Burgess et al. (2000) recently linked efflux of water from roots to patterns of reverse sap flow by using a combination of thermometric, dye tracing and isotopic techniques.

Large effluxes of water into dry soil during the night should be accompanied by high rates of uptake by roots growing in wet soil, unless there is considerable stored water. Such trends are not apparent in Cabibel and Do’s (1991a) data. However, the absence of such a trend might be a result of a second potential problem associated with the TDP. Because sap continues to flow during the night in roots that are redistributing water, the maximum temperature difference between heated and unheated probes used to define zero flow would not be a true maximum ($\delta T_{\max}$) equating to actual zero flow.

Our explanation of the apparent “phase shift” in diurnal sap flow measured in lateral roots of apple helps avoid the inference of a rapid increase in sap flow immediately following sunset as a result of refilling of root and stem tissue water stores (Cabibel and Do 1991a). Regardless of any lag in flow between trunk and root (Goldstein et al. 1998), the gradient in water potential between the canopy and the atmosphere is generally greatest in the daytime and usually reaches a maximum around midday. Thereafter, sap flow should decrease steadily as refilling progresses (Goldstein et al. 1998). The pattern would be a bell-shaped curve. The data presented by Green et al. (1997), Lott et al. (1996) and Howard et al. (1996) cannot directly address this issue because slow and reverse rates of flow were not measurable with the methods employed.

**Conclusions**

Evidence for reverse sap flow in tree roots from sap flow, stable isotope and soil water content studies (see Caldwell et al. 1998), argue strongly for the use of techniques that provide a full picture of sap flow throughout the diurnal and seasonal cycles. The heat ratio method and constant power heat balance method (with correct data handling) fulfill this requirement because they can measure changes in direction and magnitude of sap flow. Other heat-based techniques remain useful within their constraints, but should be used with caution on roots in the light of phenomena such as reverse flow. Furthermore, caution must be exercised with methods that require calibration during an assumed period of zero sap flow. Sap flow does not necessarily cease in plant organs at nighttime and cessation need not be confined to nighttime. These methods should
be calibrated when zero flow can be verified, for example, by severing xylem tissue. Sakuratani et al. (1999) reported a novel way to calculate radial heat loss from heat balance gauges (sheath conductance) without the need for zero flow. This approach will be helpful where severing roots is not practicable.

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References


