

Potential errors in measurement of nonuniform sap flow using heat dissipation probes

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Summary The empirical calibration of Granier-type heat dissipation sap flow probes that relate temperature difference (ΔT) to sap velocity (v) was reevaluated in stems of three tropical tree species. The original calibration was confirmed when the entire heated probe was in contact with conducting xylem, but mean v was underestimated when part of the probe was in contact with nonconducting xylem or bark. Analysis of the effects of nonuniform sap velocity profiles on heat dissipation estimates showed that errors increased as v and the proportion of the probe in nonconducting wood increased. If half of a 20-mm probe is in sapwood with a v of 0.15 mm s^{-1} and the other half is in nonconducting wood, then mean v for the whole probe can be underestimated by as much as 50%. A correction was developed that can be used if the proportion of the probe in nonconducting wood is known. Even with the entire heated probe in contact with conducting xylem, v would be underestimated when radial velocity gradients are present. In this case, the error would be smaller except when velocity gradients are very steep, as can occur in species with ring-porous wood anatomy. Errors occur because the relationship between ΔT and v is nonlinear. Mean ΔT along the probe is therefore not a measure of mean v , and users of heat dissipation probes should not assume that v is integrated along the length of the probe. The same type of error can occur when ΔT is averaged through time while v is changing, but the error is small unless there are sudden, step changes between zero and high sap velocity. It is recommended that relatively short probes (20 mm or less) be used and that probes longer than the depth of conducting sapwood be avoided. Multiple probes inserted to a range of depths should be used in situations where steep gradients in v are expected. If these conditions are met, heat dissipation probes remain useful and widely applicable for measuring sap flow in woody stems.

Keywords: *Anacardium excelsum*, *Bursera simaruba*, *Eucalyptus deglupta*, Granier, sap velocity, sapwood, transpiration.

Introduction

A variety of methods are now used for the measurement of sap flow in plant stems (Smith and Allen 1996). All use heat as a

tracer for sap movement, and each has advantages and limitations in terms of ease of use, cost, and the size of plant stem on which they can be used (Swanson 1994, Smith and Allen 1996). The heat dissipation method introduced by Granier (1985, 1987) measures sap velocity as the temperature difference between heated and unheated probes inserted radially into the stem. Heat dissipation increases and the temperature difference between the heated and unheated probe declines asymptotically with increasing sap velocity (Figure 1). The technique is relatively simple and inexpensive, and is now in wide use. Heat dissipation probes have already been used successfully in a number of studies of tree water use (Granier et al. 1990, Kelliher et al. 1992, Bréda et al. 1995, Loustau et al. 1996, Andrade et al. 1998), and heat dissipation estimates of water use have usually compared well with estimates from other sap flow techniques (Köstner et al. 1996, Köstner et al. 1998) or independent micrometeorological or gravimetric methods (Diawara et al. 1991, Granier et al. 1996b, David et al. 1997). An important potential limitation, however, is that

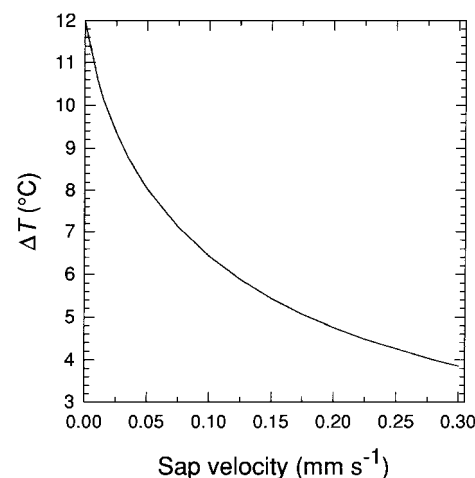


Figure 1. The temperature difference (ΔT) between the heated and unheated probe as a function of sap velocity. Based on the original calibration of Granier (1985, 1987) with $\Delta T_m = 12^\circ \text{C}$ (Equation 4).

the calibration of the heat dissipation method is based on an empirical relationship between temperature difference and sap flow (Granier 1985), rather than on the physical properties of heat transfer in sapwood (Smith and Allen 1996).

Granier et al. (1990) asserted that the original calibration, based on measurements in three species, was independent of tree species or wood anatomy. Smith and Allen (1996) advised that the technique should be calibrated for each new species on which it is used, at least until a physical basis for the calibration can be developed. During our initial tests for a study of tree water use, heat dissipation probes used with the original calibration sometimes appeared to underestimate water flow through excised stems from several species. For a given flow, heat dissipation was lower, and the temperature difference higher than was expected based on the original calibration. Similar observations were made independently in another laboratory (S.D. Wullschlegel, Oak Ridge National Laboratory, Oak Ridge, TN, personal communication). Further tests in our laboratory suggested that errors were related to nonuniform sap velocity along the length of the heated probe. Implicit in the design and recent use of heat dissipation probes is that the heated probe integrates temperature, and therefore sap velocity, along its length (Granier et al. 1994, Lu 1997). The effect of variable flow along the length of single probes has not been addressed, even though probes longer than the reported depth of sapwood have been used in some studies (Granier 1987, Granier et al. 1990, Saugier et al. 1997). Here, we reevaluate the heat dissipation probe calibration in stems of three tree species and present an analysis of the effects of nonuniform sap velocity profiles on heat dissipation estimates, along with a correction that can be applied in some circumstances to account for these effects.

Materials and methods

Terminology and units follow those of Edwards et al. (1997). Sap velocity refers to the speed of sap (sap flux density) measured at a point or along a probe. Sap flow refers to the volume or mass of sap flowing through a stem per unit time.

Probe design and the Granier calibration

Probe design was similar to that of Granier (1985). Two cylindrical probes 1.5 mm in diameter were inserted radially into the stem to a depth of 20 mm, one 100 mm downstream of the other. Aluminum tubes (2 mm outside diameter) were pushed into predrilled holes before inserting the probes, both of which were coated in thermally conductive paste. The distal 20 mm of each probe was wrapped in a coil of insulated constantan wire, and the downstream probe was heated by applying a known voltage across the heating element, giving a constant power output of 0.2 W. The temperature difference between the probes was measured with T-type thermocouple junctions inserted halfway along each probe. The thermocouples were joined at the constantan side and the copper leads connected to a data logger (21X, Campbell Scientific, Inc., Logan, UT) set to record the temperature difference every 5 s and store the mean every 60 s.

Granier (1985) found for three species (*Pseudotsuga menziesii* (Mirb.) Franco, *Pinus nigra* Arnold and *Quercus pendunculata* Ehrh.) that:

$$v = 0.119k^{1.231}, \quad (1)$$

where v is sap velocity (mm s^{-1}) and k is related to the temperature difference between the two probes (ΔT):

$$k = \frac{(\Delta T_m - \Delta T)}{\Delta T}, \quad (2)$$

where ΔT_m is the temperature difference when $v = 0$ (Figure 1). Granier (1985, 1987) determined the coefficients in Equation 1 by fitting a nonlinear regression to the measured relationship between v and k . The rate of sap flow (L s^{-1}) is calculated as:

$$F = vA, \quad (3)$$

where A (m^2) is the cross-sectional area of sapwood.

Variation in sap velocity with depth

If sap velocity varies along the length of the probe, then heat dissipation and probe surface temperature will also vary. The purpose of the thermally conductive aluminum sleeve is to minimize temperature gradients along the probe (Granier 1985). The parameter ΔT as measured by the probe thermocouples is therefore assumed to be equivalent to the mean value of the temperature "profile" along the probe. Equations 1 and 2 were rearranged to predict the temperature at any point along the probe from the velocity of sap past that point (Figure 1):

$$\Delta T = \frac{\Delta T_m}{(v/0.119)^{1/1.231} + 1}. \quad (4)$$

If a portion of the probe is inserted into nonconducting xylem while the remainder is in sapwood with relatively uniform sap velocity, then it can be assumed that the measured ΔT is a weighted mean of ΔT in the sapwood (ΔT_{sw}) and ΔT in the inactive xylem (ΔT_m):

$$\Delta T = a\Delta T_{\text{sw}} + b\Delta T_m, \quad (5)$$

where a and b are the proportions of probe in sapwood and inactive xylem ($b = 1 - a$), respectively. This approach assumes that the thermal properties of inactive xylem are the same as sapwood when $v = 0$. If the depth of sapwood is known, then Equation 5 can be rearranged to find the actual temperature and sap velocity in the sapwood:

$$\Delta T_{\text{sw}} = \frac{\Delta T - b\Delta T_m}{a}. \quad (6)$$

Equations 3–6 were used to compare probe estimated and actual sap velocity under a variety of experimental conditions, including insertion through conductive sapwood into inactive xylem. Sensitivity analyses were used to explore the conse-

quences of varying the amount of conducting sapwood in contact with the probe and to simulate the effect of the sap velocity gradients typically observed in the stems of ring-porous and diffuse-porous tree species. These calculations assume probe length = 20 mm and $\Delta T_m = 12^\circ\text{C}$.

Experimental calibration

Heat dissipation probes were tested in Hawaii and Panama using stems from three tropical tree species: *Eucalyptus deglupta* Blume, Myrtaceae; *Anacardium excelsum* (Bert. & Balb.) Skeels, Anacardiaceae; and *Bursera simaruba* (L.) Sarg., Burseraceae. Sections of stem were cut from branches with a pruning saw, brought to the laboratory, recut and smoothed with a razor blade (the mean dimensions of the stem sections used are given in Table 1). Bark was removed from near the upstream end and the stem connected to a reservoir of deionized water using plastic tubing, hose clamps and motorcycle inner tube rubber. Two pairs of heat dissipation probes were installed on opposite sides of, and offset along the length of, the stem. Probes were inserted to a depth of 20 mm, with the proximal end of the heating element flush with the cambium. Power was supplied to the probes and ΔT_m recorded after reaching a constant temperature. Water was then passed through the stem by increasing the height of the water reservoir, or by applying a slight positive pressure to the reservoir for higher flow rates (no difference was observed when flow was induced by suction applied to the downstream end of the stem). Water flowing from the downstream end of the stem section was collected on a balance connected to the same data logger as the probes. The resolution of the balance was 0.1 g. Mass flow through the stem was increased in steps to a high rate, then decreased, with ΔT allowed to reach a constant value at each level. Flow was then stopped and ΔT_m compared with the starting value. After each test, a dye (indigo carmine) was added to the reservoir and allowed to pass through the stem. The stem was then cut transversely at the level of each heated probe and the pattern of staining examined to determine the sapwood cross-sectional area and depth of sapwood at the point of probe insertion.

The pattern of dye staining was often uneven and patchy, suggesting gradients in sap velocity within the stem rather than a sharp boundary between sapwood and inactive xylem. As a more definitive test of the effects of inactive xylem on ΔT (Equations 5 and 6), a 10-mm thick block of wood was held against a stem section and the heated probe inserted through

the block and into active sapwood. The wood block was made from a 100-mm length of sapwood from the same branch as the stem section, and was cut with a semicircular transverse cross section so that it could be held tightly against the bark of the stem with cable ties. The probe and inactive block of sapwood were installed 50 mm from the down stream end of the stem section. At the end of the calibration test a 9-mm diameter, hollow cork borer was pushed against the transverse face of the sapwood immediately downstream of the probe. The borer allowed separate collection and determination of flow near the probe as a fraction of total mass flow. This fraction was a constant proportion of total mass flow over a range of flow rates, and was used to correct the flow velocity estimates used in the calibration test.

Results and discussion

Effects of inactive xylem

Heat dissipation probes underestimated the k value predicted by the original Granier calibration when part of the probe was in contact with inactive xylem (Figure 2). Up to half of the probe was in contact with inactive xylem in the *Eucalyptus* stems and k was underestimated by 48% when the mean velocity for the whole probe was 0.15 mm s^{-1} (Figure 2a). In the *Anacardium* stem, 10% of the probe was in inactive xylem and k was underestimated by 17% when v was 0.14 mm s^{-1} (Figure 2b). Sap velocity will be underestimated if the same situation occurs during routine use of the probes. Experimental manipulation of the proportion of the probe in inactive xylem confirmed this effect. Mean velocity for the whole probe was underestimated when the probe was inserted through a wood block of known thickness and into active xylem (Figure 3). Correction of probe ΔT estimates with Equation 6 resulted in a calibration relationship that conformed well to the original Granier calibration, regardless of species (Figures 2 and 3). Even the corrected relationships began to deviate from the Granier calibration when v was very high, but such high velocities probably do not occur *in vivo*. If the entire probe was in contact with active sapwood, the original calibration appeared valid without correction of probe ΔT (Figure 2c). The error in probe velocity estimates increased rapidly with increases in both actual velocity in the sapwood and the proportion of the probe in inactive xylem (Figures 4 and 5). At a moderate sap velocity in the sapwood of 0.05 mm s^{-1} (0.18 m

Table 1. Dimensions of excised stem segments used for the calibration tests of heat dissipation probes presented in Figures 2 and 3. Parameter ΔT_m is the temperature difference between heated and unheated probes when $v = 0$ and a is the proportion of the heated probe in contact with active xylem (Equations 5 and 6).

Species	Diameter (mm)	ΔT_m ($^\circ\text{C}$)	Depth of sapwood (mm)	a	Figure
<i>Eucalyptus deglupta</i>	67	8.1	12	0.6	2a
<i>Eucalyptus deglupta</i>	61	10.2	9	0.5	2a
<i>Anacardium excelsum</i>	43	10.4	18	0.9	2b
<i>Bursera simaruba</i>	56	8.0	24	1.0	2c
<i>Eucalyptus deglupta</i>	44	10.4	8	0.4	3

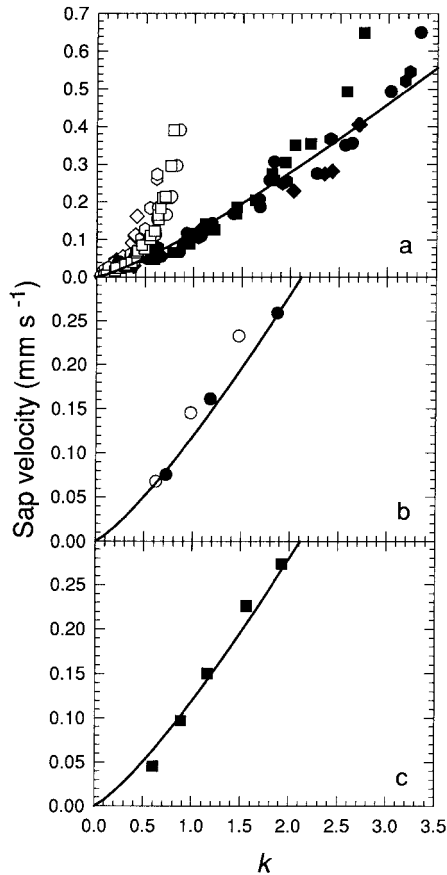


Figure 2. Sap velocity through excised stem sections in relation to k , before (open symbols) and after (closed symbols) correcting ΔT for the proportion of probe in contact with nonconducting wood. The line in each panel represents Granier's (1985) calibration. Sap velocity for the uncorrected data is the mean \bar{v} for the whole probe. Sap velocity for the corrected data is v in the sapwood. (a) Two stems each with two pairs of probes; (b) and (c) one stem with one pair of probes; in (c) the sapwood was deeper than the length of probe and no correction was necessary. Species and stem dimensions are given in Table 1.

h^{-1}), v in the sapwood was underestimated by 8% when a was 0.9 and 35% when a was 0.5. At a high sap velocity of 0.15 mm s^{-1} , v was underestimated by 15% and 52% when a was 0.9 and 0.5, respectively (Figure 5).

Underestimates of true sapwood velocity occur because the relationship between ΔT and v is nonlinear (Figure 1). For this study, it was assumed that when sap velocity was nonuniform, ΔT was a measure of the mean temperature difference along the probe. Agreement between velocity- k relationships corrected on the basis of this assumption (Equation 6) and Granier's (1985) original calibration suggests that this assumption is valid (Figures 2 and 3). The error occurs because mean ΔT is not a measure of mean v . Uncorrected ΔT measurements therefore should not be used to estimate v even when a small length of the probe (e.g., 2 mm of a 20-mm probe) is in contact with nonconducting xylem or bark.

The potential for error in calculation of velocity and mass flow depends on the assumptions made about sapwood area

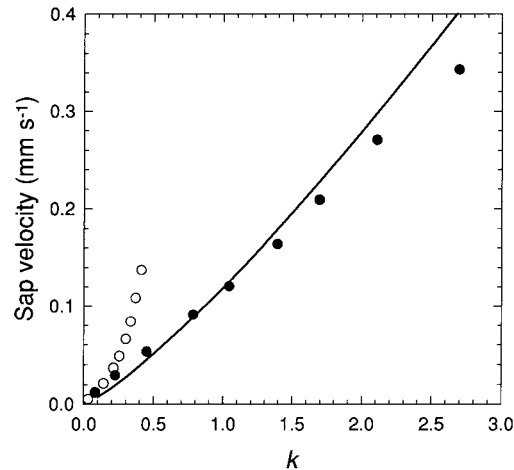


Figure 3. Sap velocity in relation to k measured with a heated probe inserted through a block of wood and into conducting sapwood, before (○) and after (●) correcting ΔT for the proportion of probe in contact with nonconducting wood. Sap velocity for the uncorrected data is the mean \bar{v} for the whole probe. Sap velocity for the corrected data is v in the sapwood. The line represents Granier's (1985) calibration. Species and stem dimensions are given in Table 1.

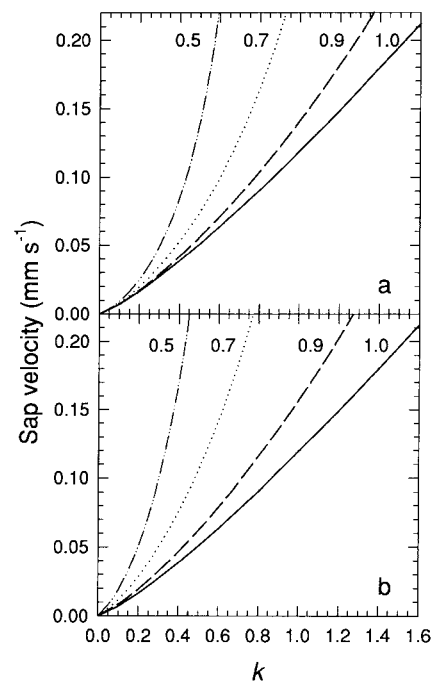


Figure 4. Sap velocity as a function of k , based on the Granier (1985) calibration and Equation 5, when the proportion of the probe in contact with active xylem is 1.0, 0.9, 0.7 or 0.5. (a) Sap velocity represents the mean value for the whole probe, including parts in nonconducting wood; (b) sap velocity represents the actual sap velocity in the sapwood.

and probe averaging of v . Previous users have assumed that the probe measures the mean of sap velocity along its length. The uncorrected k values presented in Figures 2–4a were therefore compared with velocity calculated by dividing actual mass

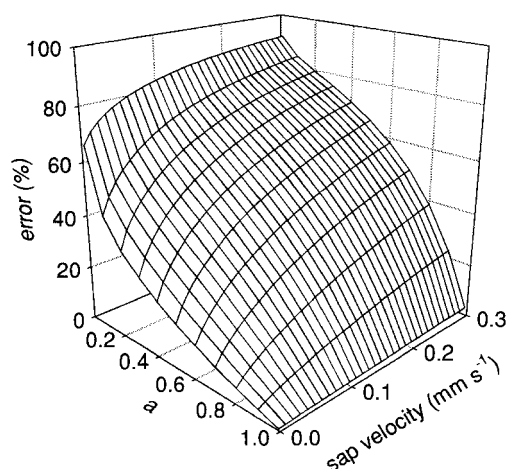


Figure 5. Error in measured sapwood sap velocity as a function of sapwood sap velocity and the proportion of the probe in contact with active xylem (a). Error is the percent by which the probes underestimate sapwood sap velocity, after the raw probe velocity is divided by a (based on the assumption that the probe measures the mean v along its length—see text for details).

flow by the cross-sectional area of wood sampled by the probe. Sapwood area was overestimated, and the resulting velocity was the mean velocity for the whole probe, including portions of the probe in contact with nonconducting wood (Figures 2 and 3, open symbols). After applying the correction to probe ΔT estimates (Equation 6), k was representative of velocity in the sapwood. Corrected k was therefore compared with true velocity in the sapwood, calculated as mass flow divided by the cross-sectional area of sapwood (Figures 2 and 3, closed symbols). Both k and v were increased after correction, and correction increased both the horizontal and vertical scales of the curves presented in Figures 2 and 3. Larger errors in estimated v occur if no compensation is made for either sapwood area or the nonlinear averaging of k and v (Figure 4b). In this case, uncorrected k was compared with v in the sapwood.

Similar errors may occur when small (< 100-mm diameter) stems or branches of fast-growing species are incorrectly assumed to be comprised entirely of sapwood. If the heated probe is longer than the actual sapwood depth, errors in F resulting from underestimated v will tend to be cancelled by opposing overestimates of sapwood area (Figure 6). Estimated mass flow may approach or exceed actual mass flow as stem diameter increases. For an 80-mm stem, estimated mass flow was higher than actual mass flow if 90% of the heated probe was in sapwood, but less than actual mass flow if 70% of the probe was in sapwood (Figure 6). Opposing errors may therefore result in an apparently reasonable estimate of mass flow even when there are large errors in measured sap velocity.

How often do users of heat dissipation probes encounter a depth of sapwood that is less than probe length? The probes first described by Granier (1985) and used in this study were 20 mm in length. Similar probes are commercially available in lengths of 20 mm (UP GmbH, Munich, Germany), 30 mm (Dynamax, Houston, TX) or 80 mm (Dynamax). Use of probes

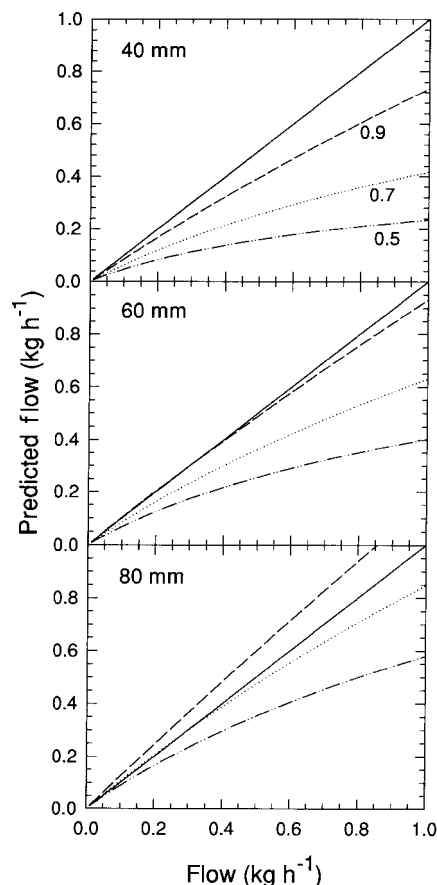


Figure 6. Mass flow predicted for whole stems from heat dissipation measurements, as a function of actual flow. Predicted flow is the flow calculated from probe measurements if the user incorrectly assumed the entire stem was sapwood, when in fact only a proportion (0.9, 0.7, 0.5) of the probe was in contact with active xylem. The solid lines represent the 1:1 relationship between predicted and actual flow. Calculations are for probes 20 mm in length, used with stems 40, 60 or 80 mm in diameter.

between 10 and 50 mm has been reported, with Granier et al. (1990) using probes 20 or 50 mm long in sapwood 40–80 mm in depth. The radial depth of sapwood varies widely with age and between individual trees, species, and growth environments (Whitehead and Jarvis 1981). A minority of studies report values less than 20 mm, but values in the 20 to 50 mm range are more common (Phillips et al. 1996, Wullschlegel et al. 1998). Coniferous species usually have sapwood at least 20 mm in depth (Whitehead and Jarvis 1981), whereas some species with ring-porous wood anatomy have a more shallow layer that is 20 mm or less in depth (Swanson 1994, Phillips et al. 1996). The best approach for heat dissipation methods may be to use relatively short probes and to avoid contact with inactive xylem. Care should be taken to insert the entire heated probe beneath the level of nonconducting cambium and bark. If sapwood depth is substantially greater than probe length, multiple probes can be used to obtain a profile of sap velocity with depth (Granier et al. 1994, Granier et al. 1996a, Phillips et al. 1996). Equation 6 can be used to estimate the true sap

velocity in the sapwood if the use of probes longer than the radial depth of sapwood cannot be avoided. Note that Equation 6 assumes that the thermal properties of active and inactive xylem are the same. This assumption may be incorrect if the probe extends from sapwood into heartwood with a low water content (Whitehead and Jarvis 1981). For this reason, and because of additional uncertainties about the amount of temperature averaging that occurs along the probes, the use of very long probes is not recommended. For example, if an 80-mm probe is fitted with three thermocouple junctions, do the individual ΔT values measured at points along the probe represent local estimates of v , or a combination of local v and ΔT averaged by conduction along the probe?

Effects of gradients in sap velocity

Potential errors resulting from contact with inactive xylem are large, but a more common situation may be gradients in sap velocity along individual heat dissipation probes. Sap velocity is usually low in the immature xylem beneath the cambium, increases some distance inside the cambium and then declines again in older sapwood (Swanson 1994). With many exceptions, radial patterns of v in coniferous and diffuse-porous species are usually more even or Gaussian, whereas those of ring-porous species are more likely to be sharply uneven (Phillips et al. 1996). Sap flow in the ring-porous genera *Ulmus* and *Quercus* occurs primarily through the early wood of the most recent growth ring (Granier et al. 1994, Swanson 1994). Equation 4 was used to test the effects of two hypothetical radial profiles on heat dissipation probe estimates of mean v along the profile (Figure 7). Averaging ΔT systematically underestimates mean v for the reasons described above. Deviation from the Granier calibration with the diffuse-porous pattern was small, even though v varied more than twofold along the probe. Using the Granier calibration, a mean v of 0.15 mm s^{-1} would be underestimated by 8%. Deviation with the ring-porous pattern was more serious, and a mean v of 0.15 mm s^{-1} would be underestimated by 45%. In the ring-porous example, the situation is similar to that arising when a probe is in partial contact with inactive xylem—flow velocities are high over part of the probe and close to zero over the remainder (Figure 7). Similar errors may occur when there is variation in sap velocity between early and late wood within the same annual ring (Whitehead and Jarvis 1981, Anfodillo et al. 1993), but it can be argued that heat transfer between early and late wood will reduce the size of error when the annual rings are narrow.

Figure 7 suggests that estimates of sap velocity from heat dissipation probes are relatively insensitive to moderate radial variations in v (the diffuse-porous pattern). A similar analysis was presented by Lu (1997), who described a method for reducing error resulting from flow variation around the circumference of individual trees while minimizing the number of data logger channels required. Thermocouples from two sets of heat dissipation probes inserted in the same tree were connected in parallel to provide mean ΔT . When there was a twofold difference in v between pairs of probes inserted into mango and cashew trees, the error in v estimated from mean ΔT was no more than 6% (Lu 1997). However, users should

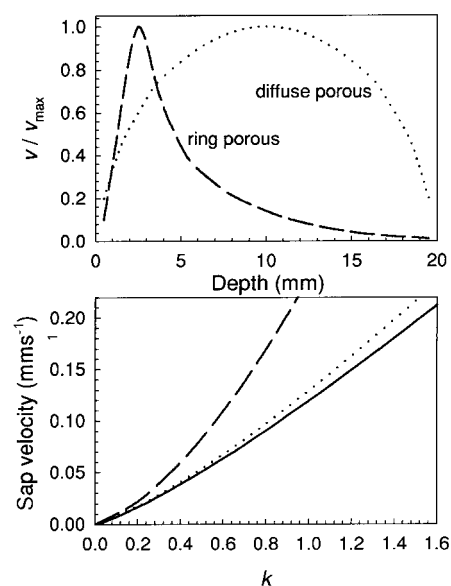


Figure 7. Typical gradients in v with depth for ring-porous and diffuse-porous species (Ěermák et al. 1992, Zang et al. 1996), and their effect on the relationship between mean v and heat dissipation estimates of k . The solid line represents the relationship between v and k when v is uniform across the radial profile.

always be aware that the heat dissipation method systematically underestimates mean v when gradients in v exist, and that the error can be large in certain situations. If steep gradients in v are expected, then the length of probes should be minimized and multiple probes used to record v at a range of depths below the cambium. If sapwood is deep and v declines with depth, then a short probe in contact with only the outer sapwood may overestimate the mean velocity of the whole radial profile. Granier et al. (1996a) and Köstner et al. (1996) used a correction factor to account for this effect in *Pinus sylvestris* L. after first measuring radial profiles in a representative tree.

Temporal averaging of ΔT when sap velocity is changing causes the same type of error in estimated sap velocity as do spatial gradients in ΔT and sap velocity. Heat dissipation probes are normally connected to a data logger set to record mean ΔT over intervals of up to 60 min. Mean ΔT underestimates mean v when v varies during the averaging interval. However, in the same way that estimates of mean v are insensitive to moderate radial variation in v , errors resulting from temporal averaging of ΔT may only be significant when there are sudden step changes between zero and high sap velocities. Estimated mean daytime sap velocity was reduced by less than 1% when the averaging interval of ΔT measurements in *Coffea arabica* L. plants growing in full sun was increased from 10 min to 60 min, even when v increased in the morning from less than 0.001 mm s^{-1} to more than 0.11 mm s^{-1} in less than 120 min (Clearwater and Meinzer, unpublished data). As a precaution, an averaging interval of 30 min or less should be used when frequent, rapid fluctuations between zero and maximum sap velocities are expected.

Conclusions

Heat dissipation probes do not truly integrate sap velocity along their lengths. They integrate heat dissipation, but this cannot be directly related to sap velocity because of the non-linear relationship between ΔT and v . Sap velocity can be seriously underestimated if portions of the heated probe are in contact with inactive xylem or bark. A correction can be applied if the length of the inactive portion is known (Equation 6). Sap velocity will also be underestimated if gradients in sap velocity occur along the length of the heated probe. However, errors with flow gradients are less serious provided v does not approach zero at any point along the probe. For these reasons, users of heat dissipation probes should clearly account for the length of the probe used, the depth of sapwood into which it was inserted, and assumptions and corrections used when calculating v and F . Errors can be minimized by using shorter probes, and multiple probes inserted to a range of depths to record flow gradients.

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