

## • Review •

## Granier's Thermal Dissipation Probe (TDP) Method for Measuring Sap Flow in Trees: Theory and Practice

Ping LU<sup>1\*</sup>, Laurent URBAN<sup>2</sup>, ZHAO Ping<sup>3</sup>

(1. CSIRO Plant Industry, Darwin Laboratory, PMB 44, Winnellie, NT 0822, Australia;

2. INRA/CIRAD-Flhor, Station de Bassin-Martin, BP 180, 97455 Saint-Pierre, La Réunion, France;

3. South China Institute of Botany, The Chinese Academy of Sciences, Guangzhou, 510650, China)

**Abstract:** Granier sap flow system is one of the most commonly used techniques for measurements of whole-tree water use in ecophysiological and forest hydrological studies. However, in the literature there is not one paper that exclusively reviews the Granier method. In this paper, we recapitulate the theoretical basis of the Granier sap flow system and review recent developments in calibration and modification of the sensor probes. Practical issues, such as the determination of the non-flow signal values, natural thermal gradient, wounding effect, reversed sap flow pattern and extrapolation of individual measurement of sap flux density to whole-tree sap flow, are discussed in detail. In the perspectives, new approaches are put forward to use the strong coupling between photosynthesis and transpiration or canopy conductance, via the measurement of <sup>13</sup>C discrimination, to estimate whole-canopy carbon assimilation.

**Key words:** Granier method; natural thermal gradient; sap flow; sap flux density; thermal dissipation probe; whole-tree water use; wounding effect

Xylem sap flow measuring systems are being increasingly used to quantify whole-plant water use, especially in woody plants (Swanson, 1994; Smith and Allen, 1996; Kostner *et al.*, 1998; Wullschleger *et al.*, 1998). Granier (1985) developed a dual-probe sap flow measuring system, which is now commonly referred to as the Granier or thermal dissipation probe (TDP) method.

The Granier method has been particularly popular among tree physiologists and forest hydrologists owing to its simplicity, high degree of accuracy and reliability, and relatively low cost. However, because the original methodological papers describing the theory and the design were in French (Granier, 1985; 1987b), there are many misunderstandings about this method. With the ever-increasing number of new users and the appearance of several commercial and “home-made” variants of the Granier sensors that more or less violate the fundamental assumption of the method, there is a need to recall the theory and discuss the specific issues with the application of the Granier method. Although several general reviews on sap flow methods discussed the Granier system (Cohen, 1994; Swanson, 1994; Smith and Allen, 1996; Kostner *et al.*, 1998), most reviewers did not have first-hand experience with the Granier method (except Kostner *et al.*, 1998) and there were often confusions on the Granier system. This paper is the first to

exclusively review the Granier system. The senior author of this paper worked for seven years with André Granier in France and has 15 years experience using the Granier system under temperate, subtropical and tropical climates and forest and orchard conditions (Lu *et al.*, 1995; 2000; Lu, 2002; Lu *et al.*, 2003). In this paper we recapitulate the theory and the original and subsequent calibrations of the Granier system for which original information was often in French and/or not-readily accessible. We then review new developments in sensor design and procedures for data processing, and finally discuss the practical issues that users of the Granier system may encounter under field conditions.

For the Granier method, as for other methods which measure only sap flow in part of the entire cross-section of a stem, e.g. the “point” measurement by the heat pulse probe (Hatton *et al.*, 1995) and the “sector” measurement by the method of Cermak *et al.* (1973), errors associated with estimating whole-tree sap flow may arise from (a) the measurement and calculation of the “point” estimates of the sap flux density and (b) the integration of these “point” estimates into a flux for a single tree (Hatton *et al.*, 1995). This review discusses these two issues. It is generally accepted that the main source of error in estimating transpiration in a forest stand is in the estimate of water use for individual trees and not in the scaling up process (Hatton

Received 26 Dec. 2003 Accepted 27 Feb. 2004

Supported by the National Natural Science Foundation of China (30270239), Provincial Natural Science Foundation of Guangdong (031265), the Knowledge Innovation Program of The Chinese Academy of Sciences (KZCX-SW-01-01B-05) and South China Institute of Botany, Knowledge Innovation Program (2002–2110).

\* Author for correspondence. Fax: +61-8-89470052; E-mail: <ping.lu@csiro.au>, new contact is Ping\_lu@yahoo.com

*et al.*, 1995; Wullschlegel *et al.*, 1998). Methods to scale up sap flow measurement from individual trees to the stand is not covered in this review and readers are referred to the publications of Hatton *et al.* (1995), Granier *et al.* (1996a) and Kostner *et al.* (1998).

## 1 Granier Sap Flow Measuring Method: Theory and Calibration

### 1.1 Measuring system

The Granier system consists of two sensor probes (Fig. 1). Each probe consists of a heating element (which also represents the effective sensing part of the probe, typically 20 mm long), wound around a steel needle containing a T-type thermocouple (copper-constantan), with the thermocouple tip located in the middle of the heating element. The constantan ends of the two thermocouples are connected to measure the temperature difference between the two probes at the ends of the copper wires. The two probes are typically inserted radially into the stem 10–15 cm apart (Granier, 1987a; 1987b; 1992), in pre-inserted heat-distributing tubes made of aluminium (Granier, 1992) or of copper (Granier, personal communication, 1994; Lu *et al.*, 2000); previously the tube was first fixed onto the probe (Granier, 1985). The downstream (upper) probe is continuously

heated at constant power (0.2 W) while the upstream (lower) probe is left unheated to measure the ambient temperature of the wood tissue and acts as a reference probe. Temperature difference between the two probes is influenced by the heat dissipation effect of sap flow in the vicinity of the heated probe.

### 1.2 Theory

Under conditions of thermal equilibrium of the system established between the sensor probe and its surroundings (wood and sap), and for a constant sap flux density, it can be assumed that input of heat by the Joule effect is equal to the quantity of heat dissipated by convection and conduction at the wall of the probe (Granier, 1985; Cabibel and Do, 1991), i.e.:

$$h S (T - T_f) = R I^2 \quad (\text{Equation 1})$$

$h$ , coefficient of heat exchange ( $\text{W} \cdot \text{m}^{-2} \cdot ^\circ\text{C}^{-1}$ )

$S$ , exchange surface area ( $\text{m}^2$ )

$T$ , temperature of the probe ( $^\circ\text{C}$ )

$T_f$ , temperature of the wood in the absence of heating ( $^\circ\text{C}$ )

$R$ , electrical resistance of the heating element ( $\Omega$ )

$I$ , intensity of the electric current (A)

It is assumed that the coefficient  $h$  is related to sap flux density (sap flow velocity) by the following equation:

$$h = h_0 (1 + \alpha F_d^\beta) \quad (\text{Equation 2})$$

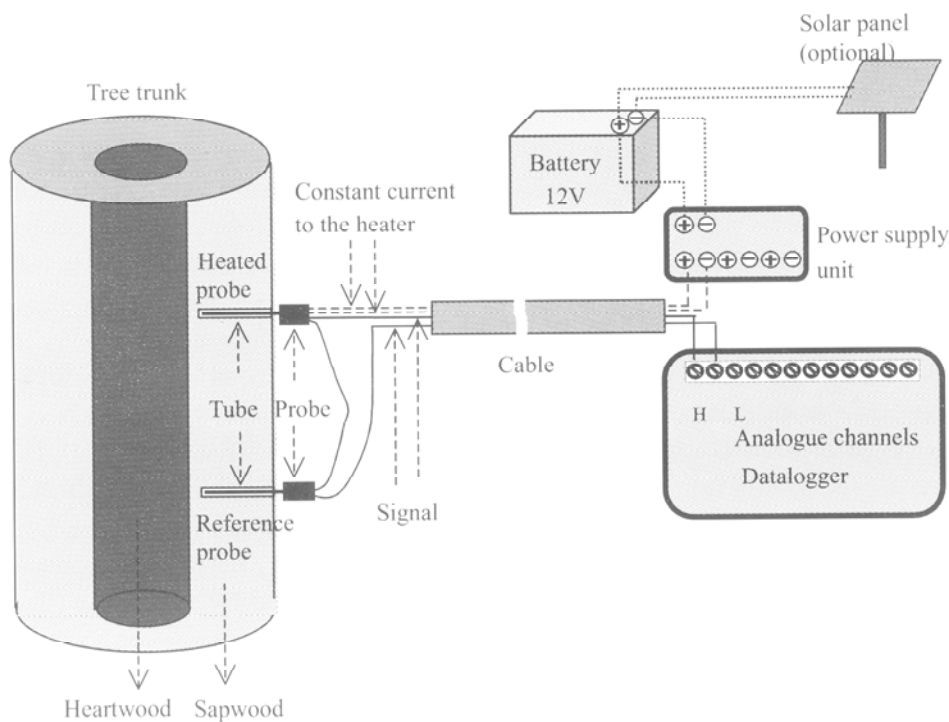


Fig.1. Configuration of the Granier system for sap flow measurement. Each probe contains a thermocouple.

$h_0$ , thermal exchange coefficient at zero flux, i.e.  $F_d = 0$

$F_d$ , sap flux density ( $\text{m}^3 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ )

$\alpha$  and  $\beta$ , coefficients depending on the quantity of heat applied.

$h_0$  is calculated from Equation 1:

$$h_0 = \frac{R F^2}{S(T_{\max} - T_f)} \quad (\text{Equation 3})$$

where  $T_{\max}$  is the temperature at zero flux ( $F_d = 0$ ), i.e. when only conductive heat loss occurs.

When  $F_d \neq 0$  and is constant, it can be described by:

$$F_d = \left[ \frac{1}{\alpha} \times \frac{h - h_0}{h_0} \right]^{1/\beta} \quad (\text{Equation 4})$$

Combining Equations 1, 3 and 4, we have:

$$\begin{aligned} F_d &= \left[ \frac{1}{\alpha} \times \frac{(T_{\max} - T_f) - (T - T_f)}{T - T_f} \right]^{1/\beta} \\ &= \left[ \frac{1}{\alpha} \times \frac{\Delta T_{\max} - \Delta T}{\Delta T} \right]^{1/\beta} \\ &= \left[ \frac{1}{\alpha} \times K \right]^{1/\beta} \end{aligned} \quad (\text{Equation 5})$$

$\Delta T_{\max}$ , maximum temperature difference established between the heated and non-heated probes at zero flux ( $F_d = 0$ );

$\Delta T$ , temperature difference between the heated and non-heated probes at a given  $F_d$ ;

$K$ , flow index (dimensionless).

### 1.3 Calibration of the original-type Granier sensors

Experiments carried out by Granier (1985) showed that  $K$  was highly correlated with the sap flux density ( $F_d$ ). A series of calibrations of the sap flow probes on several sample stems of three different tree species (*Pseudotsuga menziesii*, *Pinus nigra* and *Quercus pedunculata* (i.e. *Q. robur*)) provided an experimental relationship between  $K$  and  $F_d$ , which was independent of the tree species studied (coniferous and ring-porous sapwood). The empiric equation proposed by Granier (1985) for the relationship between  $K$  and  $F_d$  was:

$$\begin{aligned} K &= [(\Delta T_{\max} - \Delta T) / \Delta T] \\ &= \alpha F_d^\beta = 0.0206 \times 10^{-6} F_d^{0.812} \end{aligned} \quad (\text{Equation 6})$$

Equation 6 can be rearranged as:

$$F_d = 118.99 \times 10^{-6} [(\Delta T_{\max} - \Delta T) / \Delta T]^{1.231} \quad (\text{Equation 7})$$

In fact, the Granier system directly measures the electrical potential difference ( $\Delta V$ ) between the two thermocouples. It is evident from Equation 7 that it is not necessary to convert those  $\Delta V$  measurements into  $\Delta T$  because the conversion factor (i.e., Seebeck coefficient:  $40 \mu\text{V}/^\circ\text{C}$ ) will be cancelled out in Equation 7. Therefore,  $F_d$  can be directly calculated from the voltage measurements using the following equation (Lu, 1997):

$$F_d = 118.99 \times 10^{-6} [(\Delta V_{\max} - \Delta V) / \Delta V]^{1.231} \quad (\text{Equation 8})$$

where  $\Delta V_{\max}$  is the maximum voltage difference recorded at zero flux ( $F_d = 0$ ), and  $\Delta V$  is the voltage difference recorded at a given  $F_d$ .

Granier (1985) fixed the intensity of the electric current in the heating element of the sensors to 0.140 A (for an average value of the resistance of the heating element of  $10 \Omega$ , the heating power is 0.2 W). Granier (1985) stated that this value of 0.140 A represented a compromise between the sensitivity of the sensor (which increases with the intensity applied) and the risk of unwanted heating of the reference probe. Granier (1985) found that the coefficient  $\alpha$  depended on the quantity of heat applied. Therefore, the empiric equation apparently depends on the heat field created by the probe with its particular physical properties (geometry, building materials) and the heating power used. It is evident that recalibration should be undertaken on any sensor probes that have a different geometry or heating power to the original design (i.e., Granier, 1985).

Unlike the heat pulse method, the distance between the heated and reference probes in the Granier method is not critical as long as the reference probe is not influenced by the heat propagated from the heated probe. Granier firstly used a distance of 5 cm (Granier, 1985), and then 10 cm (Granier, 1987a; 1987b) and 15 cm (Granier, 1992). The distance is now commonly set between 10 to 15 cm. The reason for these changes was to ensure that the reference measurements were not affected by the heating. It appears that the further the distance is, the less the chance for any interference. However, as discussed further, as the distance increases, the ambient thermal gradients increase too, which increases the measuring errors. Therefore, depending on the heating power used by a particular variant of the Granier system, the distance should be kept as short as possible while ensuring that the reference probe is not affected by heating. A rule of thumb is that in stems of small diameters, due to the heat storage effect during the low/zero flow periods, it is better to keep the distance larger. It is possible to assess the risk of interference by monitoring the changes of the absolute temperatures at the reference probe position while switching on and off the heating power.

Since the first publication of the method (Granier, 1985), the Granier sensors have been calibrated on several other tree species as well as on synthetic materials (Cabibel and Do, 1991; Granier, personal communication, 1992). Those calibrations confirmed that the original calibration parameters of Granier (1985) were valid for all the materials tested, which suggested that the original calibration was universal. However, we found that Cabibel and Do's (1991) calibration (Equations 9 and 10) on three broadleaf tree species

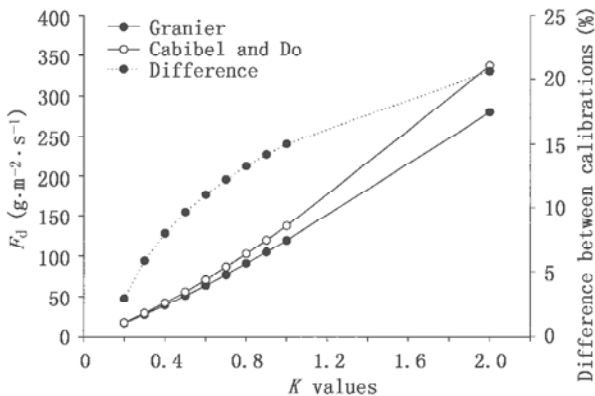
(*Malus domestica*, *Quercus robur*, *Castanea sativa*) and PVC columns filled with synthetic fibres was, in fact, somehow different from the original Granier calibration.

$$K = 0.022\ 72 \times 10^{-6} F_d^{0.769\ 4} \quad (R^2 = 0.97) \quad (\text{Equation 9})$$

$$\text{and thus } F_d = 136.835\ 6 \times 10^{-6} [(\Delta T_{\max} - \Delta T) / \Delta T]^{1.299\ 714} \quad (\text{Equation 10})$$

Figure 2 shows the values of Cabibel and Do (1991) were up to 15 % higher than those of Granier's (1985) for  $K$  values up to 1, i.e. within the normal range of the measurements.

Considering all results from various studies to date, we recommend that although the calibration coefficients are similar in diverse types of woods (coniferous, ring- and diffuse-porous trees) and even artificial medias, the early claim that Granier's original calibration is independent of tree species or wood anatomy should be considered with caution. Considering the complexity of the calibration procedure and the strict requirement of a section of the stem with homogenous sap flux density (Cabibel and Do, 1991; Goulden and Field, 1994 and Clearwater *et al.*, 1999), we do not recommend a new calibration for each new species as suggested by Smith and Allen (1996). Rather we suggest that there should be some sort of validation of the method on the species in question, for example, using gravimetric or "cut-tree" methods (Hatton *et al.*, 1995; Lu and Chacko, 1998; Lu *et al.*, 2002). Nevertheless, the spatial variability of the sap flux density in stems (Goulden and Field, 1994)



**Fig. 2.** Difference between the original calibration of Granier (1985) and that of Cabibel and Do (1991).

and the potential errors in estimation of sapwood areas should be considered while making such validations.

#### 1.4 Calibration of modified Granier sensors and new developments

Several variants of the Granier sensor probes were also calibrated (a 1-cm-long wound heating element by Granier, personal communication; a 1.5-cm-long wound heating element by Braun and Schmid, 1999; a 1-cm-long line heater by James *et al.*, 2002). All those authors claimed that their modified types of the Granier sensors adhered to Granier's original calibration equation despite Granier's (1985) suggestion that changes in the heat field around the probe may cause deviation in the calibration factors. Although there is no report of a thorough study on the heat field changes in any of those variants, James *et al.* (2002) adjusted the power input to the modified sensor such that  $\Delta T_{\max}$  remained similar to that of original-type probes (M. Clearwater, personal communication, 2003). We remain cautious about any changes in probe geometry and heating power, and recommend thorough test on any variations of the sensors.

Braun and Schmid (1999) calibrated a 1.5-cm-long Granier-type sensor probe on grapevines and extended the original calibration for a sap flux density of  $0 - 140 \times 10^{-6} m^3 \cdot m^{-2} \cdot s^{-1}$  (i.e.  $5.04 kg \cdot dm^{-2} \cdot h^{-1}$ ) to around  $225 \times 10^{-6} m^3 \cdot m^{-2} \cdot s^{-1}$  (i.e.  $8.1 kg \cdot dm^{-2} \cdot h^{-1}$ ). Under natural field conditions, observed values of sap flux density are hardly above  $4.0 kg \cdot dm^{-2} \cdot h^{-1}$  and well below  $8.1 kg \cdot dm^{-2} \cdot h^{-1}$  (Lu *et al.*, 2002).

The Granier sap flow system is commercially available from three manufacturers, UP GmbH (Germany), PlantSensors (Australia) and Dynamax (USA) (Table 1). Both UP GmbH and PlantSensors claim that their sensors are of the original Granier design. UP GmbH claims their sensor probes consume 0.2 W, but the technical data provided at their website are different. They use a current of 0.12 A for a heating resistance of  $34.5 \Omega$  which gives 0.497 W. Considering that they use a 20 gauge steel needle (observed on probes purchased in 1995 by the authors), which is thinner than Granier's original 19 gauge ones, resistance of their heating coil, can be reasonably estimated to be less than  $10 \Omega$

**Table 1** Commercial availability of the Granier sensors – claimed sensor type, heater type, contacts and published sensor price

Manufacturers	Sensor type	Heater	Web site and email address	Sensor cost
UP GmbH, Germany	original	wounded heater	<a href="http://www.upgmbh.com">http://www.upgmbh.com</a> g.kast@upgmbh.com	Contact vender
PlantSensors, Australia	original	wounded heater	<a href="http://www.plantsensors.com">http://www.plantsensors.com</a> sales@plantsensors.com	AUS\$200
Dynamax, USA	modified	line heater	<a href="http://www.dynamax.com">http://www.dynamax.com</a> admin@dynamax.com	Contact vender

that was reported by Granier (1985; 1992). Therefore, their system may only produce less than 0.15 W if they do use a current of 0.12 A. The PlantSensors' sensors use 0.13 A for a heater resistance of 12 Ω which gives 0.2 W as specified in Granier (1992). Dynamax commercializes several modified types of sensors which use a line-heater instead of a wound heater and a heating power different from the original. Although Dynamax uses the Granier's original calibration for the calculation of the sap flux density, there is no information available as to how they have calibrated their sensors. There were suspicions that those sensors with modifications in design and/or heating power may not adhere to Granier's original calibration and such modifications may have contributed to the observed substantial underestimations of  $F_d$  (Oliveras and Llorens, 2001; Wilson *et al.*, 2001; Offenthaler, 2003; Lu, unpublished data).

## 2 Practical Issues of the Application of the Granier Methods

### 2.1 Determination of $\Delta T_{max}$

Estimation of  $F_d$  by the Granier method relies on the measurement of a single parameter, i.e. the temperature difference  $\Delta T$ . Determination of  $\Delta T_{max}$  is fundamental for the calculation of  $F_d$  (Equation 7). Although  $\Delta T_{max}$  can theoretically be defined as  $\Delta T$  at  $F_d = 0$  (that usually occurs predawn), many factors may prevent the occurrence of the zero flow state, such as night-time water movement for new growth (vegetative or reproductive), slow restoration of the tree's internal water storage during prolonged drought (Lu *et al.*, 1995; Goldstein *et al.*, 1998) and water loss from the canopy due to high vapour pressure deficit and high wind speed (Snyder *et al.*, 2003).

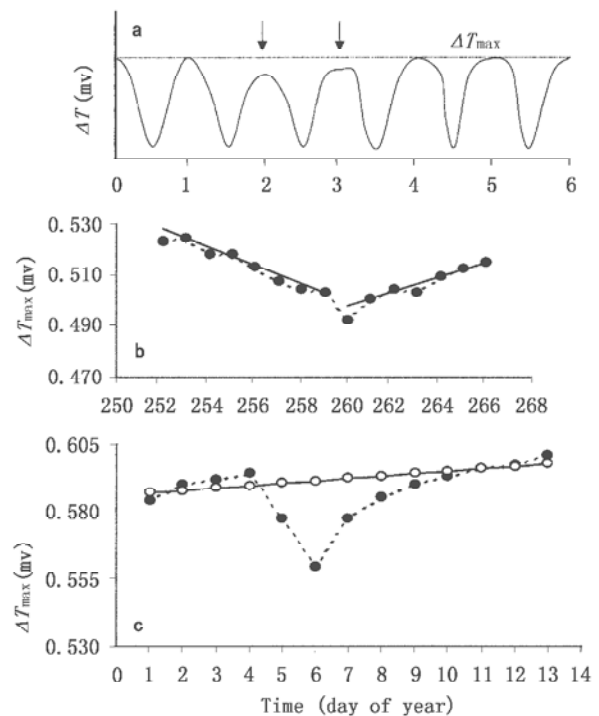
Night-time water flow: non-zero flow during the night time affect the determination of the sap flow by underestimating the true  $\Delta T_{max}$  required in calculation of the sap flux density using Equation 7, thus underestimating  $F_d$  (Fig. 3a).

Drift in  $\Delta T_{max}$ :  $\Delta T_{max}$  is influenced by the thermal properties of the wood surrounding the heated probe.  $\Delta T_{max}$  for dry wood is usually greater than for wet wood. During the development of a severe soil water deficit, there could be a drift in daily values of  $\Delta T_{max}$ . This drift in  $\Delta T_{max}$  could occur during both drying and re-wetting phases (Fig.3b).

Sometimes, there could also be a drift (increase, Fig.3c) in  $\Delta T_{max}$  over a long period from several months to years as the contact between probe and surrounding wood deteriorates and the thermal conductivity decreases. Such a drift is mostly unpredictable; and sometimes one of several

individuals of the same tree species may show such a drift while others do not. This might be linked to the quality of hole-drilling for installation of the probes. For an experienced user, this problem can be mostly overcome. In practice, when the drift exceeds a certain limit, the probe should be reinstalled to improve the quality of the measurement. It has been demonstrated that the Granier probes could produce accurate measurements over several months, and even over two growing seasons (Granier *et al.*, 1996a; Kostner *et al.*, 1998; Lu *et al.*, 2000; Oliveras and Llorens, 2001).

According to Granier (1987b),  $\Delta T_{max}$  should be determined separately for each sensor because  $\Delta T_{max}$  is a compound result of the factors mentioned above that are often probe-specific. To overcome the problem of night-time sap flow,  $\Delta T_{max}$  should be estimated over a 7–10-day period by taking the maximum value of  $\Delta T$  to avoid the underestimation



**Fig.3.** Determination of  $\Delta T_{max}$  over a period of 7–10 d, (a) when there is no drift, taking the maximum over the period. Otherwise, taking the maximum  $\Delta T$  over each 24-h cycle as  $\Delta T_{max}$  will mask the night-time flow if it does occur. Arrows indicate the nights with sap flow, (b) when there is a period of water stress,  $\Delta T_{max}$  should be determined by breaking the whole period into drying and wetting periods and applying Granier's double regression method to each of the periods (see text), and (c) when there is a period of night-time water loss and a drift in  $\Delta T_{max}$ , Granier's double regression method should be used. Closed circles represent the 24-h maximum of  $\Delta T$  and the solid lines (or opened circles) represent the regression line of the Granier estimation of  $\Delta T_{max}$ .

of the "real"  $\Delta T_{\max}$  (Fig. 3a). Otherwise, taking the maximum  $\Delta T$  over each 24 h cycle as  $\Delta T_{\max}$  (as in the calculation sheets provided by some manufacturers) will mask the night-time flow if it does occur.

In practice, to deal with the problems of both night-time flow and drift, Granier (1987b) proposed to first calculate the local maxima of  $\Delta T_{\max}$  over a 10-d period, then to calculate the new  $\Delta T_{\max}$  by a linear regression between these local maxima and time (day of year). This procedure has the advantage of not taking into account the nights during which significant transpiration or more precisely, sap movement occurs. To provide a better estimate of the true  $\Delta T_{\max}$ , especially when there are both night-time flow and drift, Granier proposed a different procedure (Granier, personal communication, 1994). Following the first linear interpolation as outlined above, the data points that were below the estimated values were eliminated, and another linear interpolation was made with the remaining data points. Figures 3a and c show the calculation of  $\Delta T_{\max}$  using Granier's procedure to overcome the problem of night-time flow during several nights. Figure 3b shows the breakup of a long time series of  $\Delta T_{\max}$  into two periods, caused by a prompt re-watering of trees undergone a prolonged water stress; a linear regression was fitted to each of the periods.

## 2.2 Calculation of whole-tree sap flow

The Granier probe only measures the sap flux density (velocity) along a  $20 \text{ mm} \times 3.14 \times 1 \text{ mm}^2$  cylinder. To extrapolate this measurement to the whole cross-sectional area of the sapwood (active water-conducting wood), total sap flow of the tree ( $F$ ) is calculated as the product of  $F_d$  and the area of the cross-section of the sapwood at the level of the heated probe ( $A_{\text{sw}}$ ).

The ideal case (Fig. 4a) is when the depth of the sapwood ( $D_{\text{sw}}$ ) is equal to the length of the probe (we assume the probe length = 20 mm), where  $A_{\text{sw}}$  is the area of the

annulus of the sapwood.

If  $D_{\text{sw}} > 20 \text{ mm}$  (Fig. 4b), the same calculation as for  $D_{\text{sw}} = 20 \text{ mm}$  can be used if  $F_d$  is assumed to be the same in the sapwood beyond the length of the probe. This assumption may not always be true as there is often substantial variation in  $F_d$  across the entire cross-section.

If  $D_{\text{sw}} < 20 \text{ mm}$  (Fig. 4c), there are several options. Granier (personal communication in 1989) assumed that the sensors integrated one section of the probe intercepting active sap flux density  $F_d$  and the other section in contact with heartwood (where  $F_d = 0$ ). Thus it could be considered that the sap moves at a mean  $F_d$  over a fictitious depth of sapwood, which is equal to 20 mm. The fictitious sapwood area corresponds to an annulus of radius of  $R$  and of the width of 20 mm.

This method assumes that the probe integrates not only temperature but also  $F_d$  along the probe length (Granier *et al.*, 1994). However, Lu (1997) showed that although the temperature could be integrated, the probe did not provide a true mean  $F_d$ , with the measured  $F_d$  always underestimating the true mean  $F_d$ . Based on a similar analysis, Clearwater *et al.* (1999) proposed an alternative method to calculate  $F_d$  in the portion of active sapwood. If a portion of the probe is inserted into non-conducting xylem while the remainder is in sapwood with uniform  $F_d$ , then it could be assumed that the measured  $\Delta T$  is a weighted mean of  $\Delta T$  in the sapwood ( $\Delta T_{\text{sw}}$ ) and  $\Delta T$  in the inactive xylem ( $\Delta T_{\max}$ , assuming that the thermal properties of inactive xylem are the same as sapwood when  $F_d = 0$ ):

$$\Delta T_{\text{sw}} = (\Delta T - b \Delta T_{\max}) / a \quad (\text{Equation 11})$$

where  $a$  and  $b$  are the proportions of the probe in the sapwood and inactive xylem ( $b = 1 - a$ ), respectively.

If the depth of sapwood is known then the corrected  $F_d$  for that portion of sapwood can be calculated by replacing  $\Delta T$  in Equation 7 with  $\Delta T_{\text{sw}}$ .

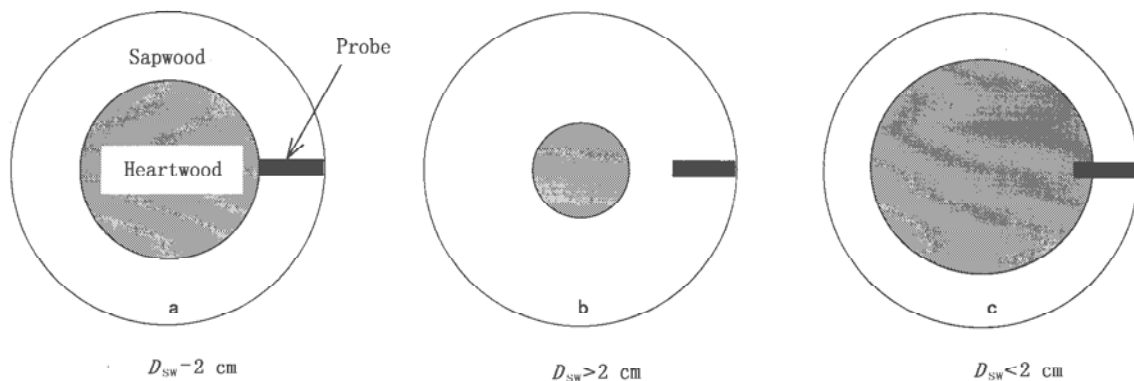


Fig. 4. Situations when the sapwood depth,  $D_{\text{sw}}$  is (a) equal to the probe length (= 2 cm), (b) > 2 cm and (c) < 2 cm.

A more common situation may be the presence of gradients in sap velocity along an individual heat dissipation probe. Lu (1997) and Clearwater *et al.* (1999) showed that the estimates of sap velocity from Granier probes were relatively insensitive to moderate radial variation in  $F_d$ , for example, in coniferous and diffuse-porous trees, as long as the probe length was within the sapwood. Lu (1997) showed that if the probe was in contact with sapwood with a two-fold differences in  $F_d$ , the error in  $F_d$  estimated from the mean  $\Delta T$  was no more than 6%. However, for some ring-porous trees with a sharply uneven radial pattern of  $F_d$ , the situation is similar to that when a probe is in partial contact with inactive xylem, i.e.  $F_d$  is high over part of the probe and close to zero over the remainder (see Fig. 7a in Clearwater *et al.*, 1999). For some species, it is almost impossible to determine the boundary between sapwood and heartwood. Use of a shorter probe to reduce the error due to non-uniformity of  $F_d$  along the length of the heated probe might be feasible to deal with the problem. However, any new design of the probes will require recalibration (James *et al.*, 2002).

Insertion of the probe tangentially into the sapwood (still perpendicular to the axis of the stem), rather than radially, to ensure the entire probe length being in contact only with active sapwood, could be another alternative when the sapwood depth is shorter (up to 50%) than the probe length. The probe should always be installed perpendicular to the stem axis to ensure the number of vessels in contact with the probe remains unchanged.

### 2.3 Determination of the sapwood area, $A_{sw}$

The portion of xylem between the cambium and the heartwood, which contains tracheary elements and living parenchyma ray cells is called sapwood. Estimation of the sapwood area,  $A_{sw}$  is critical because errors made on this parameter have a direct effect on the calculation of the total sap flow of a tree. There are several methods to measure or estimate  $A_{sw}$ .

In some cases, sapwood area can be determined on one or several incremental core(s) taken with a Pressler borer (the one used by foresters), or on a disk of the stem, by examining the natural macroscopic features (colour or density changes of the wood) or utilizing a specific chemical. For example, in eucalypts the colour generally changes from pale sapwood into reddish heartwood, and in Norway spruces the light coloured sapwood is distinctly different from the brown heartwood. Chemicals should be able to show a specific characteristic of the sapwood, such as pH or starch content. For example, bleach can stain heartwood differently from sapwood in *Pinus radiata* (Hatton *et al.*,

1990; 1991).

The colour change associated with the heartwood boundary may not be a reliable indicator of the conducting wood boundary. In a lychee tree of 16 cm diameter, both dye perfusion and Granier methods showed that the effective no flow boundary was 4 cm below the apparent heartwood boundary (Lu and Urban, unpublished data). In other species, especially tropical hardwoods, there may be no obvious indicator of the sapwood/heartwood boundary (e.g. mango), in which case other methods are required.

In most tree species, the sapwood has a much higher water content than heartwood. This is observed as an opalescent aspect or translucency of the core when it is held to diffuse light (e.g. for spruce). However, several recent studies showed that changes in relative water content of the wood in some tree species might not be a reliable indicator for determination of the boundary of the sapwood/heartwood (Cermak *et al.*, 1992; Phillips *et al.*, 1996; Lu *et al.*, 2000; Zhao, unpublished data).

For ring-porous and some diffuse-porous trees, vessels in the older xylem could be blocked by tylosis and turn into heartwood. Functional sapwood can be visually determined with a magnifying glass or the naked eye by holding up an incremental core to the light and rotating it so that the xylem vessels are aligned with the line of sight.

*In situ* staining by feeding of dye solution (e.g. Eosin) into stem through holes created under water (Granier *et al.*, 1994; Cermak *et al.*, 2002) or feeding dye solution to a "cut tree" (Lu and Chacko, 1998) provides the most accurate and direct assessment of the sapwood area, although they are more or less destructive.

Measurement of sap flux density using heat pulse probe (Hatton *et al.*, 1990; 1995; Granier *et al.*, 1994; Zang *et al.*, 1996), heat-field deformation probes (Nadezhdina *et al.*, 2002) and, to a lesser extent, the Granier probe (Phillips *et al.*, 1996; Lu *et al.*, 2000), at different depths into the sapwood should also be able to show the sapwood/heartwood boundary. Those could be used as preferred non-destructive methods.

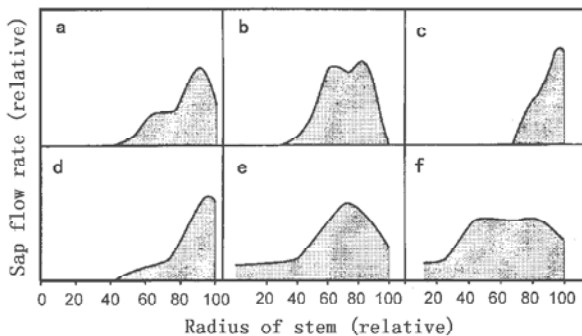
To estimate the total sapwood area of a forest stand, the sapwood area of individual trees can be estimated by taking incremental cores. Error from this procedure has been estimated to be less than 10% for trees with large and regular annual growth rings (10% for Douglas fir, Granier, 1987a; 9% for Norway spruce, Lu, unpublished). However, for trees with eccentric growth rings such as maritime pine, multiple cores per tree or even direct measurements by felling trees at the end of the experiment are required (Hatton *et al.*, 1991; 1995).

## 2.4 Spatial variation in sap flux density in stem

Substantial spatial variations (radial, circumferential and axial) in  $F_d$  in sapwood were observed in many tree species (Cermak *et al.*, 1992; Granier *et al.*, 1994; Hatton *et al.*, 1995; Phillips *et al.*, 1996; Zang *et al.*, 1996; Kostner *et al.*, 1998; Lu *et al.*, 2000; Wullschlegel and King, 2000).

When the sapwood depth is substantially larger than the length of the probe, it is necessary to determine the radial profile of  $F_d$  (Jimenez *et al.*, 2000; Lu *et al.*, 2000). Distinct patterns of radial variation in  $F_d$  along the sapwood depth were observed in tree species with different xylem structures (ring-porous, diffuse porous and coniferous, see also Phillips *et al.*, 1996; Nadezhdina *et al.*, 2002; Fig. 5). Large systematic errors of -90% to +300% arose during flow integration and scaling from single-point measurements to whole trees when it was assumed that sap flow was uniform over the sapwood depth (Lu, 1997; Nadezhdina *et al.*, 2002).

To take into account the radial variation in  $F_d$  and minimise the cost of the experiment, it is recommended to develop a point-to-area correction factor. The point-to-area correction factor can be obtained by determining first the radial  $F_d$  pattern using sensors with a 10–20-mm-long effective sensing element at multiple measuring points along a stem radius, and then establishing the correlation between the total flow of the tree and  $F_d$  measured at the depth



**Fig. 5.** Radial pattern of relative sap flow rate (in relation to depth into sapwood, 100 represents the layer immediately beneath the cambium) in trunks of trees with different wood anatomy: *Pinus sylvestris* (a), coniferous wood; *Populus-hybrid* (b), summer-green deciduous tree with diffuse-porous wood; *Quercus petraea* (c), summer-green deciduous tree with ring-porous wood; *Olea europaea* (d), evergreen sclerophyllous tree with diffuse-porous wood (narrow pores); *Ficus carica* (e), subtropical deciduous tree with diffuse-porous wood (large pores) and *Shorea sumatrana* (f), tropical rainforest tree with diffuse-porous wood without distinct annual rings (After Yoshikawa *et al.*, 1986; Cermak *et al.*, 1992; Cermak and Nadezhdina, 1998. Redrawn from "Ökophysiologie der Pflanzen" by Walter, 2001, with the permission from the publisher Verlag Eugen Ulmer, Stuttgart).

where  $F_d$  is maximal (Hatton *et al.*, 1995; Zang *et al.*, 1996; Lu *et al.*, 2000; Nadezhdina *et al.*, 2002). Long probes of 5 and 8 cm containing several thermocouples are not recommended because there is uncertainty about their measurements (Clearwater *et al.*, 1999; James *et al.*, 2002).

Because there is high temporal variation in the point-to-area correction factor along the xylem radius used for flow integration (Lu *et al.*, 2000; Nadezhdina *et al.*, 2002), the point-to-area correction factor should be calculated from the slopes of the best-fit lines between the half-hourly or hourly values of  $F_d$  at the depth where  $F_d$  is maximal and at other depths over a diurnal course (Lu *et al.*, 2000). This could minimize the influence of temporal variations on the point-to-area correction factor. Positioning a single-point sensor at a depth where  $F_d$  is maximal is advantageous because of the high sensitivity of maximum  $F_d$  to water stress conditions and changes in microclimate (Nadezhdina *et al.*, 2002). It is important to note that sap flow does not occur in the immature and differentiating tissue just inside the cambium (Swanson, 1994). Therefore, the outmost point of the sensing part of sap flow probes should be placed 1–2 mm beyond the cambium rather than immediately beneath it.

There are also substantial circumferential variations in  $F_d$ , especially where stems are short and trees are in isolation. Circumferential variation often depends on the canopy exposure in a forest stand (Granier, 1987b), but such exposure effects are often not evident in orchard trees due to horticultural practices such as grafting and training (Lu and Chacko, 1998; Lu *et al.*, 2000). Circumference variation can also be integrated into the point-to-area correction factor. However, there are also temporal changes in the circumferential patterns, particularly when the soil water status changes (Lu *et al.*, 2000). Soil water supply and drought also significantly increase circumferential variations (Lu *et al.*, 2000; Pausch *et al.*, 2000). Users should be aware of those changes when planning measurements and interpreting results.

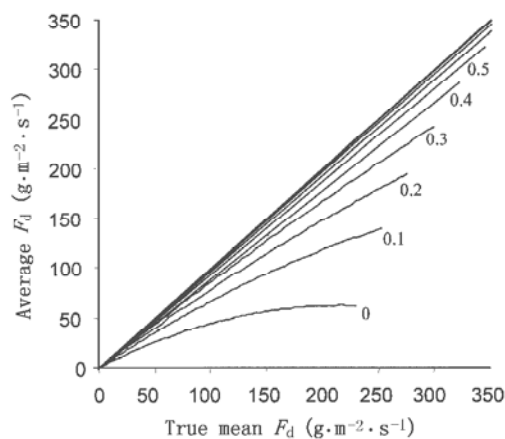
Axial variations in  $F_d$  were observed in forest trees and  $F_d$  is generally higher at higher points of the stem/trunk than at 1.3 m (Granier, 1987b; Loustau *et al.*, 1998). For the convenience of measurement and comparison of results, it is normal for trees with a tall stem/trunk to measure the sap flow at 1.3 m. In one case, Loustau *et al.* (1998) found that in a coniferous species (*Pinus pinaster*), there was significantly less circumferential variation at the height immediately beneath the lowest living whorl than at 1.3 m. However, in broadleaf trees with unevenly distributed branches, it may be the opposite (Lu *et al.*, 2000).



Sap flow sensor probes, especially the heated probes, may have been inadvertently inserted into an area of less active sapwood for pathological reasons that are not visible externally. A "bad position of the probe" is only evident when it is compared with other probes. Since there is always some degree of spatial variation in the sapwood, it is recommended to systematically examine the radial and circumferential variations for each new species.

Nevertheless, the Granier method has a clear advantage over methods based on "point" measurements (e.g. the heat pulse method). It has relatively low sensitivity to spatial variations in sap flux density caused by micro-variation in xylem structure thanks to its heat averaging property of the 2-cm-long heat distributing tube (Granier, 1987a; 1987b; Lu, 1997; Clearwater *et al.*, 1999).

Although the point-to-area method can be used to cover the spatial variations, it is certainly more desirable to monitor directly those variations, especially when the experiment extends over a long period and under varying soil water conditions (Lu *et al.*, 2000; Martinez-Vilalta *et al.*, 2003). Lu (1997; 2001) developed a method to directly measure the average  $F_d$  in a tree with important spatial variations in  $F_d$ . By using this method, the error in sap flow measurement that is usually associated with limited sampling can be substantially reduced without the need for extra datalogging facilities, the most expensive item. This method may underestimate the true mean  $F_d$  to various degrees, but under the most common situations the error is rather small (Fig.6). This method can average readily



**Fig.6.** Effect of non-conducting wood and difference in sap flux density on average sap flux density measured using the method of Lu (1997; 2001). Average  $F_d$  is the mean of  $F_d$  values measured by two sensors of equal length (2 cm) at two points in a stem or in two trees. Lu's (1997) method underestimates the true mean  $F_d$  by no more than 6% for two  $F_d$  values being different by two fold. The error of underestimation increases as the difference increases. Numbers next to the lines indicate the ratio of  $F_d$  at these two points.

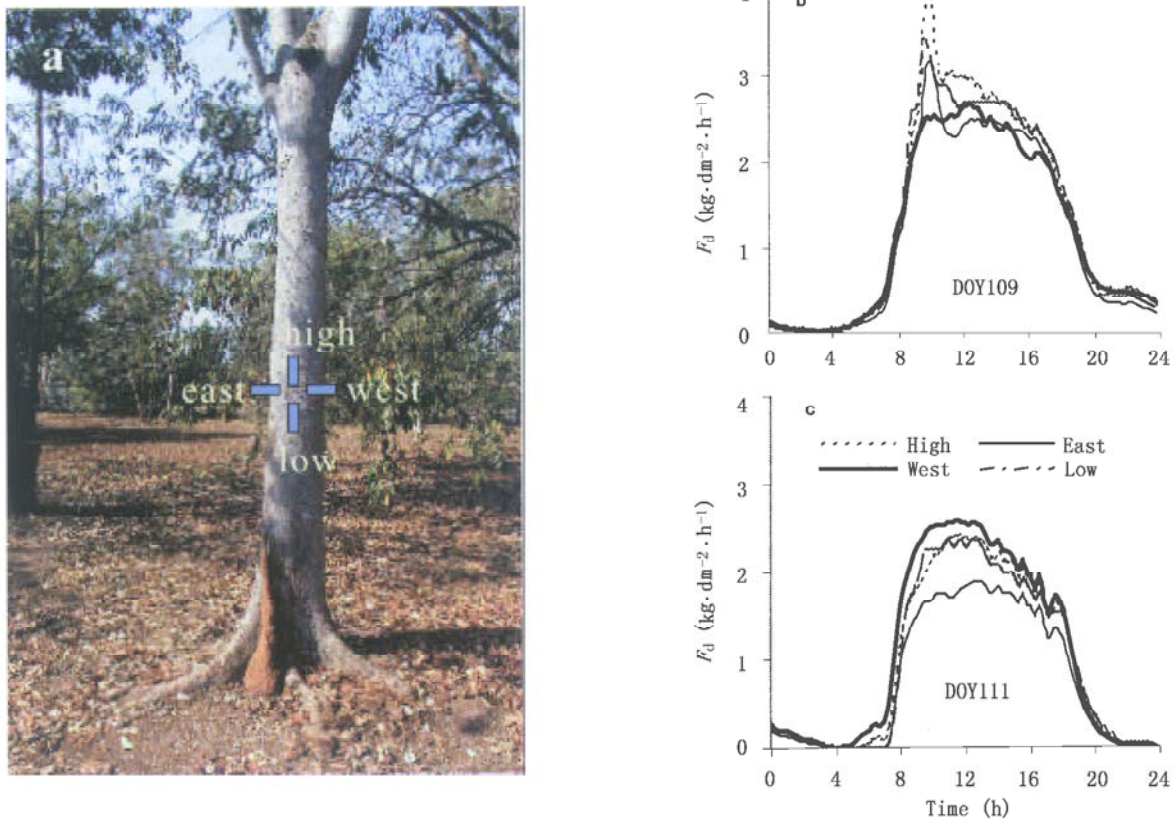
circumferentially varied  $F_d$ , and can also, without extra sampling error, average the radially varied  $F_d$  using a particular stratified sampling (i.e. each sampled sapwood annulus has equal sapwood area, Hatton *et al.*, 1990; Hatton *et al.*, 1995).

**2.5 Ambient thermal gradients, heat storage and inadequate thermal contact**

Trees are standing between soil and atmosphere, which have greatly different thermal properties. There are often thermal gradients along the trunk and such gradients are steeper near the ground and at sunrise and sunset, or near the part of stem on which direct sunlight casts. All methods based on heat balance are sensitive to external heat perturbations. Ambient thermal gradients often interfere with sap flow measurements.

A "morning peak" in sap flow refers to a rapid increase to unrealistically high sap flow rates observed soon after sunrise (Fig.7b). This is commonly observed in isolated trees, e.g., in an open forest stand or in an orchard where the lower part of the trunk is exposed to direct sun and a large area of the ground is not shaded. It also occurs when sap flow is measured very close to the ground surface. The exact cause of this problem is still unknown, but it may be associated with the natural thermal gradients between the two sap flow probes (Cermak and Kucera, 1981; Goulden and Field, 1994; Braun and Schmid, 1999; Do and Rocheteau, 2002a; 2002b) or with heat storage (build-up), especially in small stems/branches during night times (Kostner *et al.*, 1996).

Under certain conditions these "morning peaks" could be avoided or alleviated by improving thermal and radiant insulation of the area of measurement (probes, plant and soil surfaces). Figures 7b and 7c show diurnal changes in  $F_d$  measured in an open-grown mahogany tree (Fig. 7a) in tropical Darwin, Australia. "Morning peaks" (Fig.7b) were evident in those sensors on the side of the trunk, which were directly exposed to the sun (sensors named east, high and low) on DOY (day of year) 109 even though the part of the trunk into which the probes were inserted was fully insulated up to 30 cm above and 50 cm below the sensors. Note that about a 1-m-long section of the trunk below the cover and exposed root systems were still not covered. The "morning peaks" disappeared on DOY 111 after shading the exposed roots and extending the insulation to the ground surface (Fig.7c). This demonstrates that in an open forest stand or in an orchard where individual trees have isolated canopies, the type of insulation cover that is commonly used in a closed forest stand, which just covers the area of the measurement about 20–30 cm around the sensor probes, is inadequate. More extensive insulation is



**Fig. 7.** Good insulation can eliminate “morning peak” under certain situations, e.g. (a) in an open grown mahogany tree, with four sensors, named as east, west, and high and low. (b) On day of year (DOY) 109, only the trunk surface (including sensors) 30 cm above and 50 cm below the sensors was covered. (c) On DOY 111, the whole trunk below the sensors and the ground surfaces were covered.

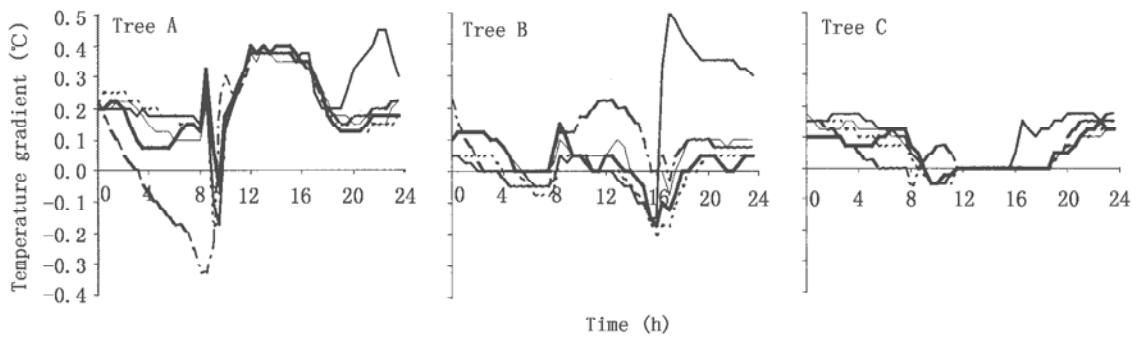
required for isolated trees. Moreover, even in closed stands, full cover of the whole trunk to the ground level will be beneficial considering the sun flecks and wind which may create thermal gradients.

Under some conditions, e.g. in a vineyard or an orchard, the main trunk/stem available for the installation of the sensor probes is usually very short (thus the probes are very close to the ground), and the natural thermal gradients seem to be inevitable despite the use of appropriate insulation. Cabibel and Do (1991) proposed a correction method which involves correlations between natural gradients for each probe and micrometeorological measurements. However, this method has been largely disregarded because it is very complicated, impractical and often ineffective (Braun and Schmid, 1999; Do and Rocheteau, 2002a; 2002b). Kostner *et al.* (1998) proposed to use measurements of natural gradients on neighbouring trees or measurements made on the same tree but at different times to correct the sap flow signals. Unfortunately, this method is not always effective. In a recent study with three young mango trees grown in an orchard in Darwin, the natural thermal gradients were

high and did not show any constant patterns during a three-day period (Fig. 8). The thermal gradients differed between trees under the same micrometeorological conditions, and between days for the same tree. This suggests that it is not appropriate to use either of the above mentioned methods.

To overcome this problem of natural thermal gradients in their heat balance sap flow system, Cermak and Kucera (1981) directly measured the natural gradients with an extra pair of thermocouples in a nearby non-heated area on the same trunk. The raw sap flow signals were then corrected by the natural thermal gradients. Goulden and Field (1994) adapted Cermak and Kucera’s compensation method for the Granier system by integrating one extra pair of thermocouples in the existing electrical circuit, therefore automatically offsetting the ambient gradients. Their system worked satisfactorily. We have further streamlined the configuration of the circuit and tested this technique on container-grown 5-year-old mango trees with satisfactory outcomes (Figs. 9a,b).

For large trees, it is also possible to place the reference probe horizontally to the heated probe if the horizontal



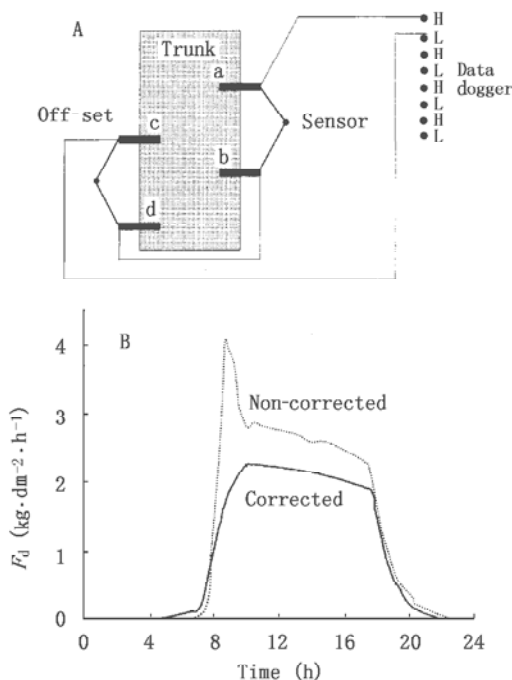
**Fig.8.** Natural temperature gradients in three orchard-grown 5-year-old mango trees over five days (represented by different line styles). Trunks were covered and the ground surface was mulched/shaded.

thermal gradients are close to zero. Evidently, the above methods require natural temperature gradients to be relatively constant along/around the trunk, and the stem to be sufficiently long or large, which may not always be true. Thus a thorough study of the natural temperature gradients is required before using these methods. In any case, good insulation is still imperative.

In recent years, two new techniques were developed to overcome the natural thermal gradients and also alleviate the problem of heat storage. Granier used a data logger to alternately switch on the power to the heater for 30 min and to record  $\Delta T$  when the system reached a thermal equilibrium,

and then to switch off the heating for another 30 min and to record  $\Delta T$  when the system again reached a thermal equilibrium (Kostner *et al.*, 1998). The advantage of this method is that the original calibration equation can still be used. The drawbacks are that under low flow situations (e.g. under water stress) the thermal equilibrium may not be achieved within 30 minutes and the measurement is discontinuous (one reading per hour).

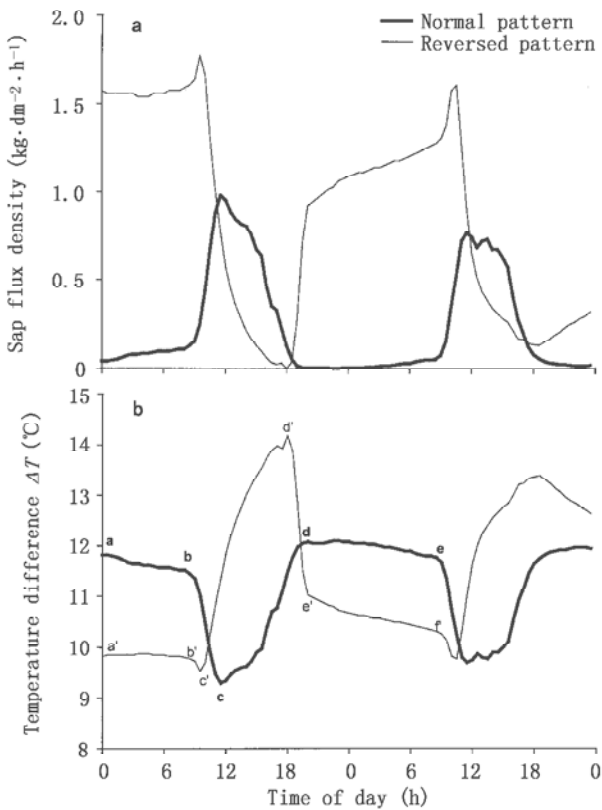
Do and Rocheteau (2002a; 2002b) further improved this technique of cyclic heating and cooling. They found that the cycle of 15 min heating on and 15 min heating off was the best option. This new cyclic TDP system is based on the same Granier probe design, but with a specific calibration to account for non-steady-state temperature regimes. Compared with the original Granier system, this new system significantly reduced the influence of the ambient temperature gradients, thus improved the accuracy of sap flow measurements under conditions where large ambient thermal gradients occurred. This system also reduces power requirements by half, which may be particularly important for field studies. However, the drawbacks are that it has a low time resolution (two sap flow measurements per hour for the recommended 15/15 cycle of heating and cooling), and increased complexity of the measuring system. It requires a datalogger with a control port and an electronic relay to provide cyclic heating. Extra electronic circuits often increase the chance of failure, especially under hot and humid field conditions. Considering the advantages and the drawbacks, we recommend using this method only when ambient thermal gradients are large, heat storage effect is evident or power supply is limited.



**Fig.9.** **A.** Configuration of the Granier probes to automatically offset the effect of natural thermal gradient (probe *a* is heated and the others are not). **B.** an example of the result of using this system on a container-grown 5-year-old mango tree.

The effect of “wounding” created by the insertion of the probes into sapwood on sap flow measurement has not been well examined for the Granier method, and it is generally believed it is not as critical as for the heat-pulse system.

However, our recent studies showed that inadequate contacts between probes (especially the heated one) and the sapwood could significantly affect sap flow measurements. A phenomenon of “reversed diurnal sap flow pattern” (Fig. 10) was observed in plant stems with soft-tissued vascular systems such as banana (Lu *et al.*, 2002) and palm plants (Ringersma *et al.*, 1996) or in trees subjected to severe soil water deficit (Wang and Ma, 2002). However, Ringersma *et al.* (1996) and Wang and Ma (2002) failed to explain such phenomena. Lu *et al.* (2002) demonstrated that this phenomenon was an artefact due to partial or full “loss of contact” between the sensor probe and the surrounding sapwood tissue. There is also evidence showing that the “wounding effect” and varying degree of the contact between the probe, covering tube and sapwood may also cause sap flow to be underestimated and alteration of the normal pattern of the diurnal changes in sap flow (Lu, unpublished data). It is, therefore, critical to ensure tight contact between the probe and sapwood tissue and install the probes with minimal disruption of the xylem (e.g. by carefully drilling the holes at predawn or under overcast



**Fig.10.** Diurnal changes in (a) sap flux density and in (b) sensor signals (temperature difference,  $\Delta T$ , redrawn from Lu *et al.*, 2002 with permission) between heated and reference probes of the Granier sensors in a potted banana plant. Two probes showing, respectively, a normal and abnormal (reversed) diurnal pattern in sap flux density and in  $\Delta T$ .

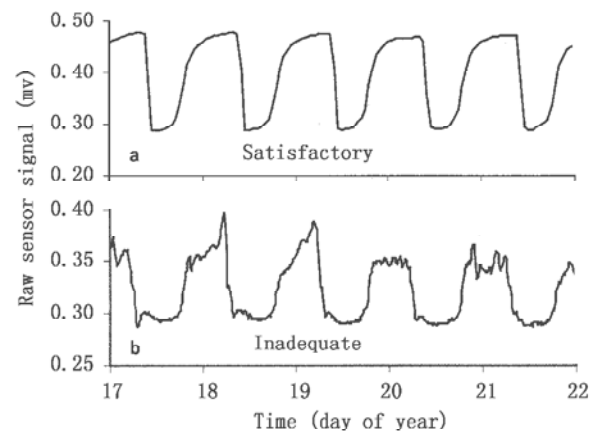
conditions).

The Granier method calculates  $F_d$  solely from  $\Delta T$ , therefore the constant power supply to the heating element is paramount. It is also desirable that the heating system is based on constant current rather than on constant voltage to avoid the effect of the variation in cable resistance. We recommend the power supply units (Fig.1) should be specially designed and made for the purpose and certainly not be bought from the shelf of an electronics shop.

It is recommended to regularly check the quality of the measurement by examining the raw sap flow signals. Operators should carefully consider practical suggestions stated above and follow the installation procedures provided by the supplier of the system. A pattern similar to the one shown in Fig.11a will produce satisfactory measurements of sap flow. Signals like that in Fig.11b, which could not reach a stable  $\Delta T_{\text{max}}$  during the night and appear erratic, clearly demonstrate a major problem with the measuring system (e.g., unstable heating, varying contact or inadequate insulation against wind or rainwater).

### 3 Perspectives

The Granier method is based on heat balance of an undelimited volume around the heated probe and so far sap flux density is calculated using empiric calibrations. Theoretic calibration and numeric simulation such as that made for the heat-pulse sensors (Green *et al.*, 2003) should be of great value for improving the reliability and accuracy of the Granier method, and assessing impacts of many unexplored effects, such as “wound-width” of the non-conducting sapwood, different heating power, size and geometry of the probes, hole size and water content of the sapwood. With the commercialization of the true original design of the Granier system at an affordable price, this



**Fig.11.** The sap flow sensors should reach a good thermal balance at the night as shown by raw signals in (a). Problems with thermal balance in the system are evident as shown in (b).

method will become more popular. Less sensitive to natural thermal gradients and consuming less power, the new cyclic heating TDP system (Do and Rocheteau, 2002a) should render this method more reliable and attractive for sap flow measurements under conditions where large ambient thermal gradients occur.

Use of sap flow measuring techniques in studies of tree physiology, orchard/vineyard irrigation and forest hydrology has been rapidly expanding and has been reviewed by Cohen (1994) and Wullschleger *et al.* (1998). The sap flow method can be used in research on hydrology of irrigated areas and ground-water pollution by fertilizers, pesticides (Cohen, 1994) and other industrial pollutants. Drainage of irrigation water (in irrigated areas) and rainwater (in bioremediation projects) into the ground water can be controlled by accurately estimating plant water requirement. The importance of this aspect is gradually increasing in many regions in the world where good water quality sources are declining (Cohen, 1994). Actual knowledge of whole-tree water use and transpiration from forests, woodland and plantation would improve our ability to assess the hydrologic impact of changes in vegetation types, thus manage local ecosystem.

With the increasing concerns about the global warming, carbon budgeting of forest stands is becoming particularly important in the greenhouse gas studies. We believe that whole-tree sap flow measurements will play a unique and important role in the forest carbon budgeting. Use of coupling between canopy photosynthesis and whole-tree transpiration estimated from sap flow measurements to assess forest stand carbon assimilation seems particularly promising. Both leaf and branch gas exchanges methods were used to derive the coupling factors (instantaneous water use efficiency) between transpiration and carbon assimilation (Moren *et al.*, 2001). A promising approach, we put forward here, is to use the long-term water use efficiency derived from  $^{13}\text{C}$  discrimination (Farquhar *et al.*, 1989). However, such coupling factors may be affected by the vapour pressure deficit of air and/or phenology (Condon *et al.*, 1993; Moren *et al.*, 2001). In our studies on improvement of mango productivity, we found strong coupling between stomatal conductance and net leaf photosynthesis in evergreen mango trees, which is apparently independent of the changes in vapour pressure deficit of air and largely unaffected by phenology (Urban *et al.*, 2003; Lu, unpublished data). We are currently using this coupling factor and the canopy stomatal conductance calculated from the Penman-Monteith equation and sap flow measurements (Granier *et al.*, 1996b; Kostner *et al.*, 1996; Wullschleger *et*

*al.*, 2000; Oren *et al.*, 2001; Lu *et al.*, 2003) to estimate mango canopy photosynthesis. Recently Catovsky *et al.* (2002) and Schafer *et al.* (2003) successfully used this approach in forest trees that display strong coupling between stomatal conductance and photosynthesis.

Another very promising approach, which we put forward here, is to express the net photosynthesis as a function of the stomatal conductance, ambient air  $\text{CO}_2$  concentration and  $^{13}\text{C}$  discrimination (Farquhar *et al.*, 1989). As a result, the problem of the vapour pressure deficit can be overcome. We can then use the coupling factor between net photosynthesis and stomatal conductance derived from  $^{13}\text{C}$  discrimination together with the canopy conductance derived from sap flow to estimate the long-term canopy carbon assimilation. This approach combines the advantages of two of the most powerful tools in modern plant ecophysiology: sap flow and stable isotope techniques. Continuous canopy conductance can be readily and reliably simulated from weather data and physical characteristics of the canopy (Granier *et al.*, 1996b) and the highly representative, intrinsic photosynthesis-stomatal conductance coupling can be derived from easily measurable  $^{13}\text{C}$  discrimination of well-mixed leaf samples.

Similarly, the above mentioned approaches using whole-tree sap flow measurements would make a great contribution to plant growth dynamic modelling. To link structure and function, models generally rely on the Penman-Monteith transpiration model and on the assumption that water use efficiency (biomass per water use) is constant, at least over extended periods of time, to calculate biomass acquisition (de Reffye and Hu, 2003).

**Acknowledgements** We thank Anna Padovan (CSIRO) for the correction of the text.

## References:

- Braun P, Schmid J. 1999. Sap flow measurements in grapevines (*Vitis vinifera* L.). 2. Granier measurements. *Plant Soil*, **215**: 47–55.
- Cabibel B, Do F. 1991. Mesures thermiques des flux de sève dans les troncs et les racines et fonctionnement hydrique des arbres. I. Analyse théorique des erreurs sur la mesure des flux et validation des mesures en présence de gradients thermiques extérieurs. *Agronomie*, **11**: 669–678.
- Catovsky S, Holbrook N M, Bazzaz F A. 2002. Coupling whole-tree transpiration and canopy photosynthesis in coniferous and broad-leaved tree species. *Can J Forest Res*, **32**: 295–309.
- Cermak J, Cienciala E, Kucera J, Hallgren J E. 1992. Radial velocity profiles of water flow in trunks of Norway spruce and oak

- and the response of spruce to severing. *Tree Physiol*, **10**: 367–380.
- Cermak J, Deml M, Penka J M. 1973. A new method of sap flow rate determination in trees. *Biol Plant*, **15**: 171–178.
- Cermak J, Jimenez M S, Gonzalez-Rodriguez A M, Morales D. 2002. Laurel forests in Tenerife, canary islands. II. Efficiency of the water conducting system in *Laurus azorica* trees. *Trees*, **16**: 538–546.
- Cermak J, Kucera J. 1981. The compensation of natural temperature gradient at the measuring point during the sap flow rate determination in trees. *Biol Plantarum*, **23**: 469–471.
- Cermak J, Nadezhdina N. 1998. Sapwood as the scaling parameter – defining according to xylem water content or radial pattern of sap flow? *Ann Sci Forest*, **55**: 509–521.
- Clearwater M J, Meinzer F C, Andrade J L, Goldstein G, Holbrook N M. 1999. Potential errors in measurement of non-uniform sap flow using heat dissipation probes. *Tree Physiol*, **19**: 681–687.
- Cohen Y. 1994. Thermoelectric methods for measurement of sap flow in plants. Stanhill G. *Advances in Bioclimatology*. Vol 3. New York: Springer-Verlag. 63–89.
- Condon A G, Richards R A, Farquhar G D. 1993. Relationships between carbon-isotope discrimination, water-use efficiency and transpiration efficiency for dryland wheat. *Aust J Agr Res*, **44**: 1693–1711.
- de Reffye P, Hu B G. 2003. Relevant qualitative and quantitative choices for building an efficient dynamic plant growth model: Greenlab case. Hu B G, Jaeger M. *Plant Growth Modeling and Applications*. 2003' International Symposium on Plant Growth Modeling, Simulation, Visualization and Their Applications. Berlin: Springer-Verlag. 87–107.
- Do F, Rocheteau A. 2002a. Influence of natural temperature gradients on measurements of xylem sap flow with thermal dissipation probes. 1. Field observations and possible remedies. *Tree Physiol*, **22**: 641–648.
- Do F, Rocheteau A. 2002b. Influence of natural temperature gradients on measurements of xylem sap flow with thermal dissipation probes. 2. Advantages and calibration of a non-continuous heating system. *Tree Physiol*, **22**: 649–654.
- Farquhar G D, Ehleringer J R, Hubick K T. 1989. Carbon isotope discrimination and photosynthesis. *Annu Rev Plant Phys*, **40**: 503–537.
- Goldstein G G, Andrade J L, Meinzer F C, Holbrook N M, Cavellier J, Jackson P, Celis A. 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant Cell Environ*, **21**: 397–406.
- Goulden M L, Field C B. 1994. Three methods for monitoring the gas exchange of individual tree canopies: ventilated-chamber, sap-flow and Penman-Monteith measurements on evergreen oaks. *Function Ecol*, **8**: 125–135.
- Granier A. 1985. Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Ann Sci Forest*, **42**: 193–200.
- Granier A. 1987a. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol*, **3**: 309–320.
- Granier A. 1987b. Mesure du flux de sève brute dans le tronc du Douglas par une nouvelle méthode thermique. *Ann Sci Forest*, **44**: 1–14.
- Granier A. 1992. Principle and fabrication of the sap flow probes (new series with Teflon isolated heater wire). INRA-Nancy: Internal publication. (in French)
- Granier A, Anfodillo T, Sabattin, Cochard H, Dreyer E, Tomasi M, Valentini R, Breda N. 1994. Axial and radial water-flow in the trunks of oak trees — a quantitative and qualitative analysis. *Tree Physiol*, **14**: 1383–1396.
- Granier A, Biron P, Breda N, Pontailler J Y, Saugier B. 1996a. Transpiration of trees and forest stands: short and long term monitoring using sapflow methods. *Global Change Biol*, **2**: 265–274.
- Granier A, Biron P, Kostner B, Gay L W, Najjar G. 1996b. Comparisons of xylem sap flow and water vapour flux at the stand level and derivation of canopy conductance for scots pine. *Theor Appl Climatol*, **53**: 115–122.
- Green S R, Clothier B E, Jardine B J. 2003. Theory and practical application of heat-pulse to measure sap flow. *Agron J*, **95**: 1371–1379.
- Hatton T J, Catchpole E A, Vertessy R A. 1990. Integration of sap flow velocity to estimate plant water use. *Tree Physiol*, **6**: 201–209.
- Hatton T J, Greenslade D, Dawes W R. 1991. Integration of sap flow velocity in elliptical stems. *Tree Physiol*, **11**: 185–196.
- Hatton T J, Moore S J, Reece P H. 1995. Estimation stand transpiration in *Eucalyptus populnea* woodland with the heat pulse method: measurement errors and sampling strategies. *Tree Physiol*, **15**: 219–227.
- James S A, Clearwater M J, Meinzer F C, Goldstein G. 2002. Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiol*, **22**: 277–283.
- Jimenez M S, Nadezhdina N, Cermak J, Morales D. 2000. Radial variation in sap flow in five laurel forest tree species in Tenerife, Canary Islands. *Tree Physiol*, **20**: 1149–1156.
- Kostner B, Biron P, Siegwolf R, Granier A. 1996. Estimates of water vapor flux and canopy conductance of Scots pine at the tree level utilizing different xylem sap flow methods. *Theor Appl Climatol*, **53**: 105–113.
- Kostner B, Granier A, Cermak J. 1998. Sapflow measurements in

- forest stands: methods and uncertainties. *Ann Forest Sci*, **55**: 13–27.
- Loustau D, Domec J C, Bosc A. 1998. Interpreting the variations in xylem sap flux density within the trunk of maritime pine (*Pinus pinaster* Ait.): application of a model for evaluating water flows at tree and stand levels. *Ann Forest Sci*, **55**: 29–46.
- Lu P. 1997. A direct method for estimating the average sap flux density using a modified Granier measuring system. *Aust J Plant Physiol*, **24**: 701–705.
- Lu P. 2001. A direct method for estimating the average sap flux density using a modified Granier measuring system (Vol 24, pg 701, 1997). *Aust J Plant Physiol*, **28**: 85.
- Lu P. 2002. Measurement of whole-tree water use of some tropical and subtropical tree crops and its application in irrigation management. *Acta Horticult*, **575**: 781–789.
- Lu P, Chacko E K. 1998. Evaluation of Granier's sap flow meter in mango (*Mangifera indica* L.) trees. *Agronomie*, **18**: 461–471.
- Lu P, Biron P, Breda N, Granier A. 1995. Water relations of Norway Spruce (*Picea abies* (L.) Karst) under soil drought in the Vosges mountains: water potential, stomatal conductance and transpiration. *Ann Sci Forest*, **52**: 117–129.
- Lu P, Muller W, Chacko E K. 2000. Spatial variations in xylem sap flux density in the trunk of orchard-grown, mature mango trees under changing soil water conditions. *Tree Physiol*, **20**: 683–692.
- Lu P, Woo K C, Liu Z T. 2002. Estimation of whole-plant transpiration of bananas using sap flow measurements. *J Exp Bot*, **53**: 1771–1779.
- Lu P, Yunusa I A M, Walker R R, Muller W I. 2003. Regulation of canopy conductance and transpiration and their modelling in irrigated grapevines. *Function Plant Biol*, **30**: 689–698.
- Martinez-Vilalta J, Mangiron M, Ogaya R, Sauret M, Serrano L, Penuelas J, Pinol J. 2003. Sap flow of three co-occurring Mediterranean woody species under varying atmospheric and soil water conditions. *Tree Physiol*, **23**: 747–758.
- Moren A S, Lindroth A, Grelle A. 2001. Water-use efficiency as a means of modelling net assimilation in boreal forests. *Trees*, **15**: 67–74.
- Nadezhdina N, Cermak J, Ceulemans R. 2002. Radial patterns of sap flow in woody stems of dominant and understory species: scaling errors associated with positioning of sensors. *Tree Physiol*, **22**: 907–918.
- Offenthaler I. 2003. Water Status of Norway Spruce as affected by climate, stand characteristic and pathogens. Ph D Dissertation, University of Agricultural Sciences, Vienna.
- Oliveras I, Llorens P. 2001. Medium-term sap flux monitoring in a Scots pine stand: analysis of the operability of the heat dissipation method for hydrological purposes. *Tree Physiol*, **21**: 473–480.
- Oren R, Sperry J S, Ewers B E, Pataki D E, Phillips N, Megonigal J P. 2001. Sensitivity of mean canopy stomatal conductance to vapour pressure deficit in a flooded *Taxodium distichum* L. forest: hydraulic and non-hydraulic effects. *Oecologia*, **126**: 21–29.
- Pausch R C, Grote E E, Dawson T E. 2000. Estimating water use by sugar maple trees: considerations when using heat-pulse methods in trees with deep functional sapwood. *Tree Physiol*, **20**: 217–227.
- Phillips N, Oren R, Zimmermann R. 1996. Radial patterns of xylem sap flow in non-, diffuse- and ring porous tree species. *Plant Cell Environ*, **19**: 983–990.
- Ringersma J, Mecherghi M, Pijnenburg S. 1996. Transpiration Measurements in Date Palms using the Granier Method. American Society of Ag Engineers, Proceedings of the International Conference. 141–146.
- Schafer K V R, Oren R, Ellsworth D S, Lai C T, Herrick J D, Finzi A C, Richter D D, Katul G G. 2003. Exposure to an enriched CO<sub>2</sub> atmosphere alters carbon assimilation and allocation in a pine forest ecosystem. *Global Change Biol*, **9**: 1378–1400.
- Smith D M, Allen S J. 1996. Measurement of sap flow in plant stems. *J Exp Bot*, **47**: 1833–1844.
- Snyder K A, Richards J H, Donovan L A. 2003. Night-time conductance in C<sub>3</sub> and C<sub>4</sub> species: do plants lose water at night? *J Exp Bot*, **54**: 861–865.
- Swanson R H. 1994. Significant historical developments in thermal methods for measuring sap flow in trees. *Agr Forest Meteorol*, **72**: 113–132.
- Urban I, Lechaudel M, Liu P. 2003. Modelling mango leaf photosynthesis: phenology effects. Hu B G, Jaeger M. Plant Growth Modeling and Applications. 2003<sup>rd</sup> International Symposium on Plant Growth Modeling, Simulation, Visualization and Their Applications. Berlin: Springer-Verlag. 67–75.
- Walter L. 2001. Ökophysiologie der Pflanzen. Leben, Leistung und Stressbewältigung der Pflanzen in ihrer Umwelt. 6th ed. Stuttgart: Verlag Eugen Ulmer. 216.
- Wang H T, Ma L Y. 2002. Measurement of whole-tree's water consumption with thermal dissipation sap flow probe (TDP). *Acta Phytoecol Sin*, **26**: 661–667.
- Wilson K B, Hanson P J, Mulholland P J, Baldocchi D D, Wullschlegel S D. 2001. A comparison of methods for determining forest evapotranspiration and its components: sap-flow, soil water budget, eddy covariance and catchment water balance. *Agr Forest Meteorol*, **106**: 153–168.
- Wullschlegel S D, Meinzer F C, Vertessy R A. 1998. A review of whole-plant water use studies in trees. *Tree Physiol*, **18**: 499–512.

- Wullschlegel S D, King A W. 2000. Radial variation in sap velocity as a function of stem diameter and sapwood thickness in yellow-poplar trees. *Tree Physiol*, **20**: 511–518
- Wullschlegel S D, Wilson K B, Hanson P J. 2000. Environmental control of whole-plant transpiration, canopy conductance and estimates of the decoupling coefficient for large red maple trees. *Agr Forest Meteorol*, **104**: 157–168.
- Yoshikawa K, Ogino K, Maiyus M. 1986. Some aspects of sap

flow rate of tree species in a tropical rain forest in West Sumatra. Hotta M. Diversity and Dynamics of Plant Life in Sumatra. Report and Coll. Papers, Part 1. Kyoto: Kyoto University, Sumatra Nature Study. 45–59.

- Zang D Q, Beadle C L, White D A. 1996. Variation of sap flow velocity in *Eucalyptus globulus* with position in sapwood and use of a correction coefficient. *Tree Physiol*, **16**: 697–703.

(Managing editor: HAN Ya-Qin)

## 应用 Granier 热消散探针(TDP)法测定树木的 木质部液流: 理论与实践

陆平<sup>1\*</sup> Laurent URBAN<sup>2</sup> 赵平<sup>3</sup>

(1. CSIRO Plant Industry, Darwin Laboratory, PMB 44, Winnellie, NT 0822, Australia;

2. INRA/CIRAD-Flhor, Station de Bassin-Martin, BP 180, 97455 Saint-Pierre, La Réunion, France;

3. 中国科学院华南植物研究所, 广州 510650)

**摘要:** Granier热消散探针法是目前研究树木生理生态和森林水文最常用的测定整树水分利用的方法之一。然而, 已有的相关综述文献中, 还没有专门介绍利用Granier热消散探针研究木质部液流的综述文章。本文重点介绍了Granier热消散探针测定系统的理论基础, 对有关该探针的校准和改进的最新研究进展进行了综述, 并还深入探讨了零液流信号值的确定、自然热梯度、损伤效应、液流的逆格型和将木质部液流密度外推至整树蒸腾耗水量等重要的实际问题。

**关键词:** Granier方法; 自然热梯度; 树干液流; 液流密度; 热消散式木质部液流探针; 整树水分利用; 损伤效应

**中图分类号:** Q948.1 **文献标识码:** A **文章编号:** 1672-6650(2004)06-0631-16

收稿日期: 2003-12-26 接受日期: 2004-02-27

基金项目: 国家自然科学基金(30270239); 广东省自然科学基金(031265); 中国科学院知识创新工程重大项目(KZCX-SW-01-01B-05); 中国科学院华南植物研究所所长基金(2002-2110)。

\* 通讯作者。Fax: +61-8-89470052; E-mail: <ping.lu@csiro.au>。

(责任编辑: 韩亚琴)