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Corrigendum

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The correct version of Equation (7) appears below:

$$SFD = \frac{\rho_d}{\rho_s}\left(MC + \frac{c_{dw}}{c_s}\right)V_h, \tag{7}$$

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Review

Sap-flux density measurement methods: working principles and applicability

Maurits W. Vandegehuchte[A,B] and Kathy Steppe[A]

[A]Laboratory of Plant Ecology, Faculty of Bioscience Engineering, Ghent University, Coupure links 653, 9000 Gent, Belgium.
[B]Corresponding author. Email: maurits.vandegehuchte@ugent.be

Abstract. Sap-flow measurements have become increasingly important in plant science. Since the early experiments with dyes, many methods have been developed. Most of these are based on the application of heat in the sapwood which is transported by the moving sap. By measuring changes in the temperature field around the heater, sap flow can be derived. Although these methods all have the same basis, their working principles vary widely. A first distinction can be made between those measuring the sap-flow rate ($g\,h^{-1}$) such as the stem heat balance and trunk sector heat balance method and those measuring sap-flux density ($cm^3\,cm^{-2}\,h^{-1}$). Within the latter, the thermal dissipation and heat field deformation methods are based on continuous heating, whereas the compensation heat pulse velocity, Tmax, heat ratio, calibrated average gradient and Sapflow+ methods are based on the application of heat pulses. Each of these methods has its advantages and limitations. Although the sap-flow rate methods have been adequately described in previous reviews, recent developments in sap-flux density methods prompted a synthesis of the existing but scattered literature. This paper reviews sap-flux density methods to enable users to make a well founded choice, whether for practical applications or fundamental research questions, and to encourage further improvement in sap-flux density measurement techniques.

Additional keywords: heat pulse, heat balance, transpiration, plant water relations, review, sensor.

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Introduction

Scientific interest in measuring sap flow to study plant water relations is not new. Application of dyes to trace sap flow in stems and roots has been practiced since the beginning of the previous century (Dixon 1914; James and Baker 1933; Kramer 1940). However, as this method necessitates plant cutting to follow the ascent of the dye, alternatives were sought. Huber (1932) was one of the first to report the use of heat as a tracer to determine sap flow. By measuring the time it took for a heat pulse to reach a certain distance downstream from the heater, a measure for sap flow was obtained. This method was further developed by Dixon (1936) and Huber and Schmidt (1937), adding a correction to account for conduction velocity. It was, however, Marshall (1958) who described the analytical background of heat conduction-convection, providing the theoretical basis for further development of heat-pulse based sap-flux density methods.

Besides these heat-pulse methods, techniques that apply continuous heating were also developed. Work by Vieweg and Ziegler (1960) underlay the development of heat balance methods to determine sap-flow rate (Daum 1967; Čermák *et al.* 1973; Kučera *et al.* 1977; Sakuratani 1981, 1984; Baker and Van Bavel 1987; Steinberg *et al.* 1989) and continuous heat sap-flux density methods (Ittner 1968; Balek and Pavlik 1977; Granier 1985; Nadezhdina *et al.* 1998; Nadezhdina *et al.* 2012).

Within the existing sap-flow methods, a distinction must be made between those measuring sap-flow rate ($g\,h^{-1}$), determining the total sap flow in a plant stem or stem section, and those measuring sap-flux density ($cm^3\,cm^{-2}\,h^{-1}$), assessing the amount of sap flowing through a certain surface per time. The former are very useful for estimating whole-plant water use, they are less suited to investigation of variation in sap flow within the plant, e.g. radial sap-flow profiles or hydraulic redistribution. As sap-flux density methods can discern spatial differences in sap-flux density within the plant, whether circumferentially, radially or vertically, they allow more detailed investigation of hydraulic plant traits.

Sap-flow rate can be measured by either the 'stem heat balance' (SHB) or 'trunk heat balance' (THB) method. Both methods solve the heat balance over a stem section of the plant during continuous application of heat to the tissue, applying a constant or variable power. As these methods have been clearly described by Smith and Allen (1996) and the operational principles of the methods remain unaltered, readers are referred to this work for more in-depth information on sap-flow rate methodology. The purpose of this paper is to present an updated review on recent developments in sap-flux density measurement methods. By describing the underlying theory of each method and discussing some of their most common practical and theoretical issues, we hope to encourage further improvements. This paper does not provide a complete description of all sap-flux density methods, readers are instead referred to the original methodology papers. Neither does it provide a description of the use of sap-flow methods in plant science nor of sampling or scaling problems. Abbreviations and symbols are listed in Tables 1 and 2 provides a comparison of the main features of all the sap-flux density methods included in this review.

Continuous heat sap-flux density methods

Thermal dissipation (TD) method

The 'thermal dissipation' (TD) method, often referred to as TDP (thermal dissipation probe) or 'heat dissipation' (HD) method, as developed by Granier (1985, 1987) based on the work by Vieweg and Ziegler (1960), is the most widely applied sap-flux density method because of its simplicity and low costs. It enables low, average and high sap-flux density estimations (from 0 to 80 $cm^3\ cm^{-2}\ h^{-1}$ and more) but needs zero flow conditions for its

Table 1. Symbols and abbreviations

Symbol/ abbreviation	Explanation	Unit
CAG	Calibrated average gradient	–
c_{dw}	Specific heat capacity of the woody matrix	$J\ kg^{-1}\ K^{-1}$
CHP	Compensation heat pulse	–
c_s	Specific heat capacity of the sap	$J\ kg^{-1}\ K^{-1}$
D_{ax}	Axial thermal diffusivity	$m^2\ s^{-1}$
D_{tg}	Tangential thermal diffusivity	$m^2\ s^{-1}$
FEM	Finite element modelling	–
HD	Heat dissipation	–
HFD	Heat field deformation	–
HPV	Heat-pulse velocity	–
HR	Heat ratio	–
K	Thermal heat conductivity	$W\ m^{-1}\ K^{-1}$
K_{ax}	Axial thermal heat conductivity	$W\ m^{-1}\ K^{-1}$
K_{tg}	Tangential thermal heat conductivity	$W\ m^{-1}\ K^{-1}$
MC	Sapwood water content	$kg\ kg^{-1}$
NTG	Natural temperature gradient	–
q	Heat liberated per length of the heater	$J\ m^{-1}$
q_t	Heat liberated per length of the heater per time	$W\ m^{-1}$
SFD	Sap-flux density	$m^3\ m^{-2}\ s^{-1}$
SHB	Stem heat balance	–
t_c	Time t_c after application of the heat pulse at which the temperature at a distance x_{up} upstream of the heater needle is equal to the temperature at a distance x_{down} downstream of the heater	s
TD	Thermal dissipation	–
TDP	Thermal dissipation probe	–
THB	Trunk heat balance	–
t_m	Time at which the temperature measured at an axial distance x downstream from the heater becomes maximal	s
t_p	Heat-pulse duration	s
t_0	Start time of the heat pulse	s
VP	Variable power	
V_h	Heat-pulse velocity	$g\ m^{-2}\ s^{-1}$
V_{h_corr}	Wound corrected heat-pulse velocity	–
x	Axial distance	m
x_{down}	Distance downstream of the heater	m
x_{up}	Distance upstream of the heater	m
y	Tangential distance from the heater	s
ΔT	Temperature difference	K
ΔT_{as}	Temperature difference between the tangential and axial upstream HFD measurement needle	K
ΔT_{down}	Increase in temperature at the distance × downstream of the heater needle	K
$\Delta T_{s\text{-}a}$	Temperature difference between the axial downstream and tangential HFD measurement needle	K
ΔT_{sym}	Temperature difference between the axial downstream and upstream HFD measurement needle	K
ΔT_{up}	Increase in temperature at the distance × upstream of the heater needle	K
ΔT_0	Temperature difference during zero flow	K
$\Delta T_{0(s\text{-}a)}$	Temperature difference between the axial downstream and tangential HFD measurement needle during zero flow	K
ρc	Volumetric heat capacity	$J\ m^{-3}\ K^{-1}$
ρ_d	Dry density of the sapwood	$kg\ m^{-3}$
ρ_s	Density of the sap	$kg\ m^{-3}$

Table 2. An overview of most common sap-flux density methods, indicating the measurement frequency, in which range they are applicable, if they are influenced by natural temperature gradients (NTG) or wounding, whether wound corrections are available and if so, which type and some important comments

Method	Frequency	Range	Zero flow needed	NTG	Wound effect	Wound correction	Comments
Empirical continuous methods							
Thermal dissipation	Continuous	Low, moderate and high flows	Yes	Yes	Yes	Not developed	Needs empirical calibration
Heat field deformation	Continuous	Reverse to high flows	No	?	Yes	Not developed	Needs empirical calibration
Theoretical heat-pulse methods							
Compensation heat pulse	Pulsed	Moderate and high flows	No	No	Yes	$V_{h\_corr} = a + bV_h + cV_h^2$	–
Tmax	Pulsed	Moderate and high flows	Depending on D_{ax} determination	No	Yes	$V_{h\_corr} = a + bV_h + cV_h^2$	Needs diffusivity determination
Heat ratio	Pulsed	Reverse, to moderate flows	Depending on D_{ax} determination	No	Yes	$V_{h\_corr} = dV_h$	Needs diffusivity determination
Calibrated average gradient	Pulsed	Zero to high flows	No	Yes	Yes	Not developed	Needs empirical calibration
Sapflow+	Pulsed	Reverse to high flows	No	No	Yes	$V_{h\_corr} = dV_h$	Allows MC estimation at low flows

calculations. The method relates 'sap-flux density' SFD ($m^3\,m^{-2}\,s^{-1}$) to a temperature difference ΔT (K), measured between a constant heated needle and an unheated needle located 10 cm lower in the xylem, based on an experimental regression for three species (*Pseutotsuga menziessii* (Mirb.) Franco, *Pinus nigra* Arnold and *Quercus pedunculata* Ahrh.) and artificial columns filled with synthetic fibre and sawdust:

$$SFD = 0.000119\left(\frac{\Delta T_0 - \Delta T}{\Delta T}\right)^{1.231}, \tag{1}$$

where ΔT_0 is the temperature difference ΔT assessed during a period of zero flow (Table 2). The method is not capable of distinguishing flow direction as reverse flow will also decrease ΔT. Moreover, the original assumption by Granier (1985) that the experimental regression coefficients as shown in Eqn 1 are species independent, has been contested by many studies. Underestimations of actual flux density, ranging between 6 and 90%, have been reported for a wide variety of species when comparing the TD to other methods (Lundblad *et al*. 2001; Bovard *et al*. 2005; Silva *et al*. 2008; Iida and Tanaka 2010) or during new calibration experiments on excised stem or branch segments (de Oliveira Reis *et al*. 2006; Taneda and Sperry 2008; Bush *et al*. 2010; Hultine *et al*. 2010; Steppe *et al*. 2010), cut trees (Lu and Chacko 1998; Uddling *et al*. 2009) or potted plants (Braun and Schmid 1999; McCulloh *et al*. 2007). Several possible reasons have been indicated for these underestimations (Lu *et al*. 2004), including deviations from the original sensor design, gradients in the radial SFD profile (Clearwater *et al*. 1999; Wullschleger *et al*. 2011) and wound effects (Wullschleger *et al*. 2011). Moreover, Clearwater *et al*. (1999) have shown that if the probe is partly installed in non-conductive tissue, large underestimations occur. Therefore, they suggested the following correction:

$$\Delta T_{sw} = \frac{\Delta T - b\Delta T_m}{a}, \tag{2}$$

with ΔT_{sw} being the corrected temperature difference for the portion of the heated probe within conductive sapwood, ΔT_m the temperature difference for the portion of the probe in inactive xylem (assumed equal to ΔT_0) and a and b the proportion of the length of the heated probe in contact with the sapwood and inactive xylem respectively. This correction, however, necessitates an accurate estimation of the position of boundaries between active and inactive xylem that are spanned by the probe, which is often difficult to obtain in practice without destructive measurements.

Hence, although the original goal of the TD method was to formulate a generally applicable, species independent empirical relation between the measured temperature ratio and sap-flux density, it is now clear that species or even tree specific calibrations are necessary to obtain accurate results. Given these specific calibrations, the TD method enables measurements of low, average and high SFD if zero flow occurs to determine ΔT_0. In practice, however, zero flow is often not reached because of night-time water uptake for vegetative or reproductive growth, replenishment of internal storage (Zweifel and Hasler 2001; Steppe *et al*. 2006), Münch counterflow (De Schepper and Steppe 2010) and water loss due to a high vapour pressure deficit in combination with a high wind speed (Snyder *et al*. 2003). In these cases, ΔT_0 values will be underestimated, leading to underestimations of SFD. Therefore, it has been suggested to use the maximum ΔT_0 value reached during a measurement campaign if destructive determination of ΔT_0 by cutting the sapwood above and below the sensor is not possible (Lu *et al*. 2004). If, however, reverse flow occurs, this procedure would lead to overestimations of SFD.

Heat field deformation (HFD) method

Like the TD method, the 'heat field deformation' (HFD) method is based on temperature changes measured in a changing heat field around a continuously heated needle. However, while the TD method only measures axial temperature differences, the HFD method includes a tangential needle, making it sensitive towards the entire naturally occurring range of sap flux densities (Nadezhdina *et al*. 1998, 2012). Moreover, because of the use of symmetrical axial needles above and below the heater, zero and reverse flows can be determined (Fig. 1). Additionally, the HFD sensor needles are equipped with thermocouples at several depths, enabling radial sap-flux density profile assessment.

Basically, the HFD method is founded on an empirical temperature ratio, which has shown to be related to sap-flux density (Nadezhdina 1988, 1999; Nadezhdina *et al*. 1998, 2012):

$$SFD \propto \frac{\Delta T_{\text{s-a}} + \Delta T_{0(\text{s-a})}}{\Delta T_{\text{as}}}, \tag{3}$$

where $\Delta T_{\text{s-a}}$ is the temperature difference between the axial downstream and tangential measurement needle, $\Delta T_{0(\text{s-a})}$ the absolute value of this difference at zero flow (originally referred to as the *K*-value (Nadezhdina *et al*. 1998)) and ΔT_{as} the temperature difference between the tangential and axial upstream needle respectively. Unlike the TD method, zero flow is not necessary to determine $\Delta T_{0(\text{s-a})}$ as it can be derived by linear extrapolation of ΔT_{as} or $\Delta T_{\text{s-a}}$ versus $\Delta T_{\text{sym}}/\Delta T_{\text{as}}$ with ΔT_{sym} the temperature difference between the axial downstream and upstream needle (Steppe *et al*. 2009; Nadezhdina *et al*. 2012). Originally Eqn 3 was extended with other parameters, but Vandegehuchte and Steppe (2012*b*) have recently shown that multiplication of the temperature ratio with any parameter is an arbitrary choice. These authors also indicated that, based on 'finite element modelling' (FEM), the HFD temperature ratio is not linearly related to sap-flux density, but more as a second order polynomial and, although the temperature ratio is independent of heat input, it is influenced by axial and tangential conductivity for average to high flows (>40 $\text{cm}^3\,\text{cm}^{-2}\,\text{h}^{-1}$). Therefore, the temperature ratio should be related to SFD using empirical calibration. Given a correct calibration, the HFD method is capable of accurately determining the entire naturally occurring flow range as zero flow conditions are not required.

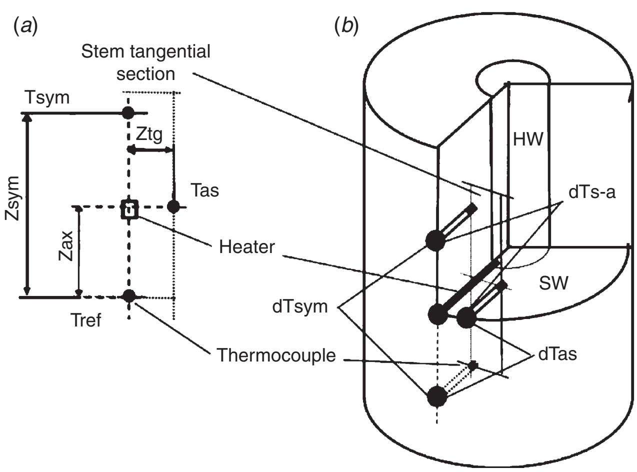

Fig. 1. (*a*) Schematic of a tangential section of the stem xylem with arrangements of the thermocouples around the heater of the HFD sensor; (*b*) schematic of the HFD sensor installed in the sapwood (SW) of a stem. Two temperature differences are measured: the symmetrical temperature difference (dT_{sym}) and the asymmetrical temperature difference (dT_{as}). The third temperature difference ($dT_{\text{s-a}}$) can be calculated as the difference between dT_{sym} and dT_{as}. After Nadezhdina *et al*. (2012).

Natural temperature gradients

Natural temperature gradients (NTG) are temperature gradients occurring in the sapwood of plants that are not caused by the intentional heating from the sap-flow measuring methods. These gradients have, amongst others, been attributed to differences in thermal heat storage in the soil, stem and root tissues resulting in temperature differences between the sap and the plant tissues (Čermák and Kučera 1981; Köstner *et al*. 1998; Do and Rocheteau 2002*a*) and to the influence of direct solar radiation (Lu *et al*. 2004). Although these influences can be minimised by shielding the gauge from radiation and locating it sufficiently high above the ground, the effect of natural gradients can never be excluded completely.

The influence of NTG on the TD method has been extensively studied and has shown to lead to errors of over 100% if not corrected for (Goulden and Field 1994; Do and Rocheteau 2002*a*, 2002*b*; Lu *et al*. 2004; Reyes-Acosta *et al*. 2012). The first attempts to correct for NTG were focussed on measuring NTG on neighbouring trees or on different positions in the tree that was being monitored (Köstner *et al*. 1998). These methods, however, require NTG to be uniform within or between trees. Therefore, more recent corrections are based on measuring the actual NTG by periodically switching the heater off. Do and Rocheteau (2002*b*) developed a cyclic TD system for which a specific calibration was developed to account for non-steady-state temperatures regimes, significantly reducing the influence of NTG. This method was updated by Ayutthaya *et al*. (2010) who improved the calibration coefficients. Recently, Reyes-Acosta *et al*. (2012) further improved this method by extrapolating the TD signal to thermal equilibrium, allowing the use of the original Granier calibration. A further improvement of this method would be the use of a single heated probe, as applied by Do *et al*. (2011) for their original cycling method, because this would reduce costs and complexity.

The influence of NTG on HFD measurements has not been reported yet. Because of the shorter distances between the needles and their closer proximity to the heater, the influence of NTG is expected to be smaller for the HFD than for the TD method.

Heat-pulse sap-flux density methods

Unlike the continuous heat methods mentioned above, heat-pulse methods are based on the fundamental heat conduction–convection equation presented by Marshall (1958), derived from Carslaw and Jaeger (1947), for an instantaneous ideal heater:

$$\Delta T = \frac{q}{4\pi K t}\exp\left(-\frac{\rho c}{4Kt}\left((x - V_{\text{h}}t)^2 + y^2\right)\right), \tag{4}$$

with ΔT the temperature difference measured at a point (x, y) away from the heater (0,0) after application of the heat pulse with heat input q ($\text{J}\,\text{m}^{-1}$). V_{h} is the heat velocity ($\text{m}\,\text{s}^{-1}$), K the thermal conductivity ($W\,m^{-1}\,K^{-1}$) and ρc the volumetric heat capacity ($J\,m^{-3}\,K^{-1}$) of the heated medium respectively. Although this equation is fit for isotropic media, sapwood is known to be anisotropic and hence the following equations for anisotropic media and a finite pulse length should be used (Vandegehuchte and Steppe 2012*c*):

$$\Delta T = \frac{q_t}{4\pi\sqrt{K_{ax}K_{tg}}}\int_0^t \frac{1}{t}\exp\left(-\frac{\rho c}{4t}\left(\frac{(x - V_h t)^2}{K_{ax}} + \frac{y^2}{K_{tg}}\right)\right) dt \text{ for } 0 < t < t_0, \tag{5}$$

$$\Delta T = \frac{q_t}{4\pi\sqrt{K_{ax}K_{tg}}}\int_{t-t_0}^t \frac{1}{t}\exp\left(-\frac{\rho c}{4t}\left(\frac{(x - V_h t)^2}{K_{ax}} + \frac{y^2}{K_{tg}}\right)\right) dt \text{ for } t_0 < t, \tag{6}$$

where ΔT is the temperature difference (K) between the measured temperature at time t (s) after application of the pulse at t_0 measured at a distance x (m) axial and y (m) tangential from the heater respectively. K_{ax} is the axial and K_{tg} the tangential thermal conductivity ($W\,m^{-1}\,K^{-1}$) of the sapwood, respectively, and q_t the energy input per unit length of the heater per unit time ($W\,m^{-1}$).

Even though most heat-pulse methods are based on the incorrect isotropic equation (Eqn 4), Vandegehuchte and Steppe (2012*e*) have shown that these methods still lead to correct results because they are derived from Eqn 4 in a way that is independent of the assumption of isotropy. However, Eqns 5 and 6 should be used when developing new methods or applying numerical models because errors may occur if alternative derivations of Eqn 4 are used. For example, the recent statistical framework developed by Chen *et al*. (2012), although promising as a tool to assess thermal sapwood properties, was based on Eqn 4. Hence, their numerical studies and derived empirical factors should be reconsidered by applying Eqns 5 and 6.

All heat-pulse methods derive heat-pulse velocity V_h from measured temperature differences at specific locations around the heater after application of a heat pulse. As the measurement procedures are based on the dissipation of the heat after application of the pulse, heat-pulse methods cannot measure continuously, with the measurement frequency depending on the time span needed to reach thermal equilibrium again after having applied the heat pulse. These heat velocities then need to be converted to sap flux densities:

$$\mathrm{SFD} = \frac{\rho_d}{\rho_s}\left(MC + \frac{c_{dw}}{c_s}V_h\right), \tag{7}$$

where SFD is the sap-flux density ($m^3\,m^{-2}\,s^{-1}$), V_h the heat velocity ($m\,s^{-1}$), *MC* the sapwood water content (weight of water over dry weight of wood), c_{dw} the specific heat capacity of the woody matrix ($1200\,J\,kg^{-1}\,K^{-1}$ at 20°C, Becker and Edwards (1999)), ρ_d the dry density of the sapwood ($kg\,m^{-3}$), ρ_s the density of the sap (assumed to be the density of water, $1000\,kg\,m^{-3}$) and c_s the specific heat capacity of the sap (assumed to be that of water, $4186\,J\,kg^{-1}\,K^{-1}$ at 20°C, Becker and Edwards (1999)). Dry wood density and water content are usually derived from wood-core measurements, implying that temporal variations in *MC* within individual stems are often not taken into account, unless other techniques are applied such as time domain reflectometry (TDR) (Wullschleger *et al*. 1996; Nadler *et al*. 2003, 2006), magnetic resonance imaging (MRI) (Van As *et al*. 2009) or vibration methods (Iki *et al*. 2010). However, these methods require additional equipment and analysis and the gravimetric method remains the reference method to determine *MC* in trees.

As heat-pulse methods are based on temporal temperature differences at the same measurement position, unlike continuous methods which apply spatial temperature differences between different positions, they are much less susceptible to NTG (with the exception of the calibrated average gradient method) (Table 2).

Compensation heat-pulse velocity (CHP) method

The 'compensation heat-pulse velocity' (CHP) method, often also referred to as the 'heat-pulse velocity' (HPV) method, is based on the time t_c after application of the heat pulse at which the temperature at a distance x_{up} upstream of the heater needle is equal to the temperature at a distance x_{down} downstream of the heater (Figs 2, 3) (Swanson 1972; Swanson and Whitfield 1981):

$$V_h = \frac{x_{down} - x_{up}}{2t_c}. \tag{8}$$

This method has the advantage that it is independent of thermal diffusivity, a sapwood characteristic that has to be determined for the Tmax and HR method. However, Eqn 8 was developed for an ideal heat pulse with an infinitely small

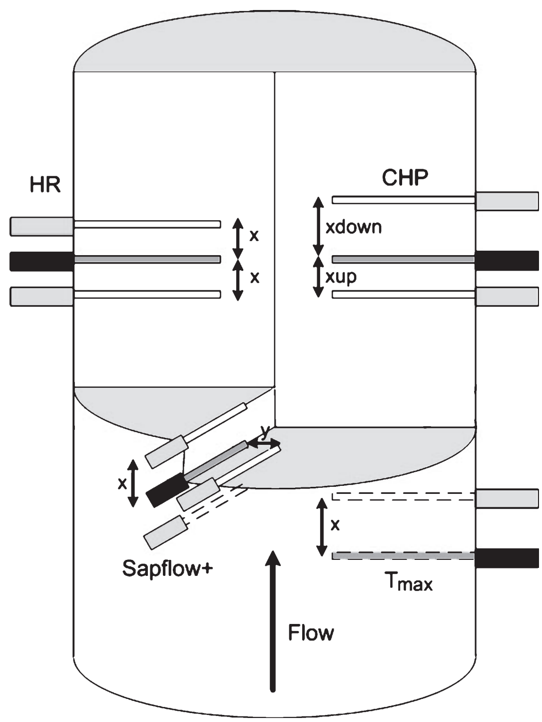

Fig. 2. A schematic representation of the most common heat-pulse methods with the heater probes in dark grey and the measurement probes in lighter grey.

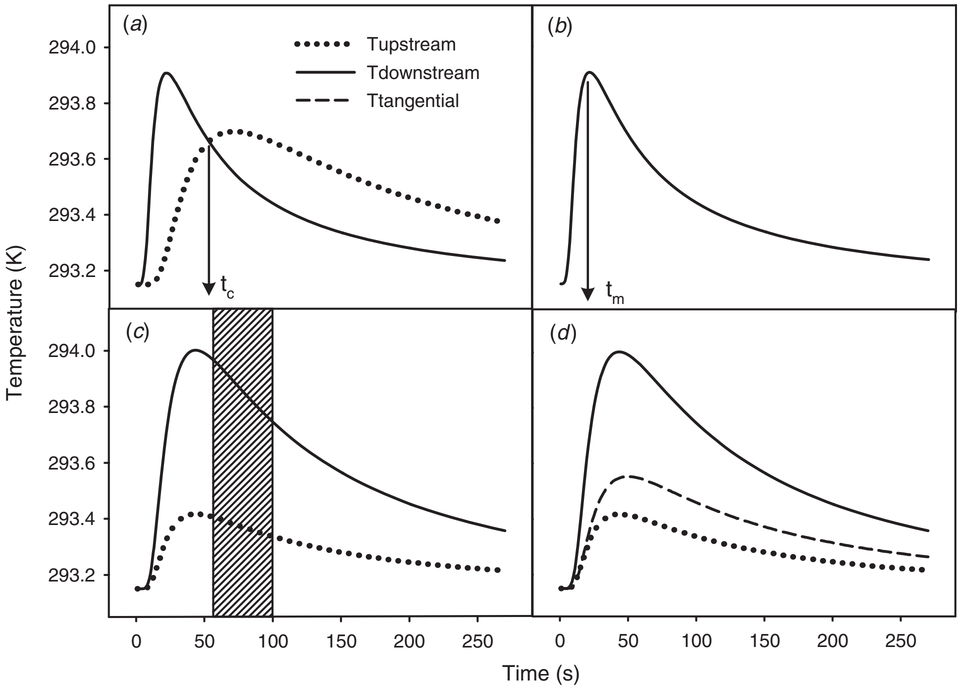

Fig. 3. A schematic representation of the measured temperature differences for the different heat-pulse methods; (*a*) compensation heat-pulse method based on the intersection of the temperature difference measured downstream and upstream from the heater; (*b*) Tmax method based on the maximal temperature difference measured downstream from the heater; (*c*) heat ratio method based on the ratio of temperature differences measured at an equal distance downstream and upstream from the heater; (*d*) Sapflow+ method based on fitting of the heat conduction-convection equations to the temperature differences measured upstream, downstream and tangentially from the heater.

length and is not theoretically correct for a step heat pulse, leading to underestimations of V_h that increase with pulse length (Vandegehuchte and Steppe 2012*c*).

Moreover, CHP fails to measure reverse, low or very high flux densities (<5 $cm^3 cm^{-2} h^{-1}$ and >100 $cm^3 cm^{-2} h^{-1}$) because under these conditions no equality between the upstream and downstream temperatures occurs. In addition, Green *et al*. (2009) have shown that for low sapwood water contents (from 28 to 55%), V_h decreases for increasing water contents, although this effect was not noticed for higher water content (75–105%) (Vandegehuchte and Steppe 2012*c*).

Tmax method

The Tmax method (Cohen *et al*. 1981), determines V_h based on the time t_m at which the temperature measured at an axial distance x downstream from the heater becomes maximal (Figs 2, 3):

$$V_h = \frac{\sqrt{x^2 - 4D_{ax}t_m}}{t_m}, \tag{9}$$

where D_{ax} is the axial thermal diffusivity of the sapwood ($m^2 s^{-1}$), determined during zero flow conditions:

$$D_{ax} = \frac{x^2}{4t_m}. \tag{10}$$

Note that to correctly apply this equation, the upper needle must be located directly above the heater (with x the axial distance between upper needle and heater) and, hence, cannot be shifted tangentially from the heater as implied in the original work of Cohen *et al*. (1981), where a distance $(x^2 + y^2)^{1/2}$ was applied with x and y the axial and tangential distance from the heater respectively. Given the anisotropy of wood, this would lead to incorrect results. Eqns 9 and 10 were later updated by Kluitenberg and Ham (2004) for step heat pulses instead of instantaneous heat pulses:

$$V_h = \sqrt{\frac{4D_{ax}}{t_p}\ln\left(1 - \frac{t_p}{t_m}\right) + \frac{x^2}{t_m(t_m - t_p)}}, \tag{11}$$

$$D_{ax} = \frac{x^2}{4t_m}\frac{t_p}{(t_m - t_p)}\left[\ln\left(\frac{t_m}{t_m - t_p}\right)\right]^{-1}, \tag{12}$$

where t_p is the heat-pulse duration.

Green *et al*. (2003) have shown that a curve smoothing procedure led to better results as t_m is difficult to accurately determine from the raw temperature data during low flows because of noise. However, even with curve smoothing procedures, the Tmax method cannot distinguish between zero and low flux densities (<20 $cm^3 cm^{-2} h^{-1}$) as the relationship between t_m and SFD is non-unique at these low flux densities (Fig. 4) (Becker 1998). As for the TD method, zero flow conditions are difficult to ensure, making non-destructive D_{ax} estimations impractical. Both Cohen *et al*. (1981) and Green *et al*. (2003) have, however, confirmed that a 10% error in D_{ax} only leads to errors of up to 3% in V_h and hence SFD.

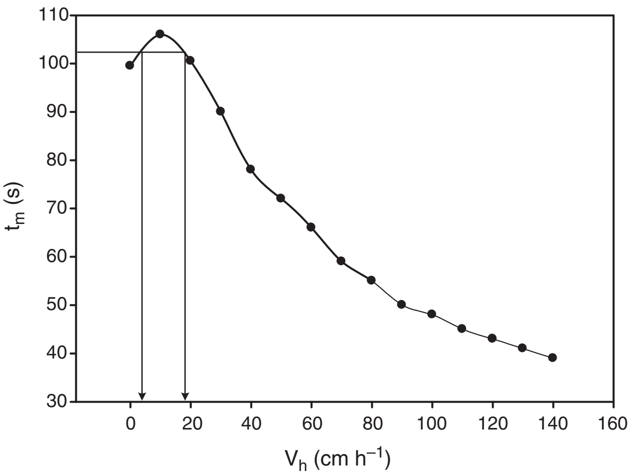

Fig. 4. Time to maximum (t_m) versus heat velocity V_h based on the 'finite element modelling' (FEM) output for a measurement probe at 1 cm downstream from the heater, a water content of 0.75, a dry wood density of 550 kg m^{-3} and an axial and tangential thermal conductivity of 0.63 and 0.42 W m^{-1} K^{-1} respectively. Wound effects were included in the model.

Heat ratio (HR) method

In an answer to the difficulties in measuring low flows with the CHP and Tmax method, Burgess *et al.* (2001*a*) developed the 'heat ratio' (HR) method, based on a suggestion presented in Marshall (1958):

$$V_h = \frac{D_{ax}}{x} \ln\left(\frac{\Delta T_{down}}{\Delta T_{up}}\right), \tag{13}$$

with ΔT_{down} and ΔT_{up} the increases in temperature at equal distances x (m) downstream and upstream from the heater needle respectively (Figs 2, 3). In practice, the temperature ratio $\Delta T_{down}/\Delta T_{up}$ does not remain constant after application of the heat pulse because of non-ideality due to wound effects. However, the rate of change in this temperature ratio becomes negligible after ~60 s. Therefore, the average temperature ratio of measurements between 60 and 100 s after application of the heat pulse are used to determine V_h.

As for the Tmax method, D_{ax} needs to be determined. Burgess *et al.* (2001*a*) based this determination on previous work of Swanson (1983) who applied an empirical equation to determine K_{ax} deducted by Siau (1971) and corrected by Vandegehuchte and Steppe (2012*a*), only necessitating a wood core sample to determine MC and ρ_d:

$$K_{ax} = K_w(MC - MC_{FSP})\frac{\rho_d}{\rho_w} + 0.04186 \left[21.0 - 20.0\left(1 - G\left(\frac{\rho_w}{\rho_{cw}} + MC_{FSP}\right)\right)\right], \tag{14}$$

where K_w is the thermal conductivity of water (0.5984 W m^{-1} K^{-1}), G the specific gravity of wood (dry mass per fresh volume divided by the density of water), MC the water content of the sapwood (water per DW), MC_{FSP} the water content at the fibre saturation point (generally taken as 30%), ρ_{cw} the cell wall density (1530 kg m^{-3}, (Kollmann and Côté 1968)) and ρ_d and ρ_w the density of dry wood and water respectively. As thermal diffusivity is the ratio between thermal conductivity and volumetric heat capacity, only ρc now needs to be determined, based on measurements of volume and weight of the same wood sample (Skaar 1988):

$$\rho c = \frac{w_d c_d + c_w(w_f - w_d)}{V}, \tag{15}$$

where w_f is the fresh and w_d the oven-dried weight of the wood sample (kg), V the volume of the wood sample (m^3) and c_w and c_d the specific heat capacity of water and dry wood as mentioned by Becker and Edwards (1999).

This method for determining thermal diffusivity can also be used for the Tmax method, making zero flow conditions redundant. Note that if Eqn 10 is used to determine D_{ax} for the HR method, a 10% error in D_{ax} will lead to an equal error in V_h, making this a less favourable approach because zero flow conditions can be difficult to ensure.

Given a good estimation of $D_{ax,}$ the HR method has proven its value for measuring low and reverse flows. It is, however, limited for high flux densities (>45 cm^3 cm^{-2} h^{-1}) (Bleby *et al.* 2008) because for these flows, the ΔT_{up} signal decreases, reducing the sensitivity of Eqn 13.

Recently, Clearwater *et al.* (2009) developed an external HR method enabling sap-flux density measurements for small diameter stems (<5 mm). D_{ax} is derived based on Eqn 10 and was found to be dependent on both the stem and the cork material applied to fix the sensor. Promising results were obtained for low and reverse flows (–7.5 cm h^{-1} < V_h <7.5 cm h^{-1}).

Calibrated average gradient (CAG) method

Another promising heat-pulse method, the 'calibrated average gradient' (CAG) method, has been proposed by Testi and Villalobos (2009). These authors extended the CHP method to enable low and even zero flow measurements. Results from both FEM and field experiments confirmed that for low flows (V_h <30 cm h^{-1}), V_h was linearly correlated with ΔT_a, the average temperature difference between the downstream and upstream temperature sensors during the 180 s after application of the heat pulse (Fig. 5). By extrapolating this linear relationship, which is only dependent on sensor characteristics and thermal properties of the sapwood, low and zero flows can be measured based on ΔT_a, although for high flows, the original CHP method is applied. The use of the average temperature gradient, however, implies that the CAG method is likely to be influenced by NTG. Although for the other methods, only the temperatures before and after application of the heat pulse are of importance, here the temperature difference between downstream and upstream positions is needed during the entire 180 s. Hence, although for the other methods the relative temperature changes are not influenced by a shift in absolute temperature, this will likely affect the CAG method, reducing the ΔT_a signal for positive gradients from roots to crown and *vice versa* and, hence, influencing the linear relationship between V_h and ΔT_a. Therefore, the effects of NTG on the CAG method should be further investigated. Moreover, if the thermal properties of the sapwood change significantly during the measurement period, a new linear relationship might need to be established.

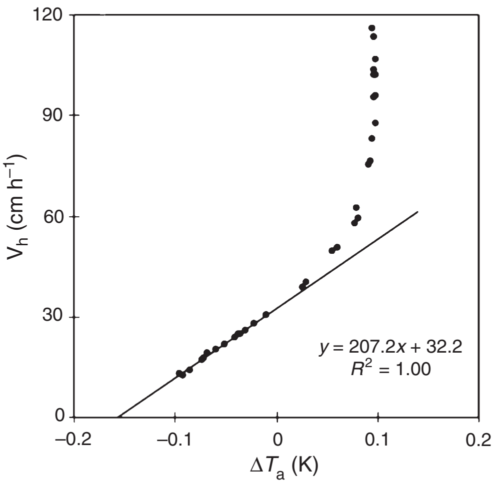

Fig. 5. Extrapolation of the relationship between V_h and ΔT_a for *Olea europaea* and the 'calibrated average gradient' (CAG) method. The line is the regression of V_h on ΔT_a obtained with the data pairs where $\Delta T_a < 0$ K, recorded over a period of 24 h (adapted from Testi and Villalobos (2009)).

Sapflow+ method

The latest developed method to determine sap-flux density, the 'Sapflow+' method, is based on both axial and tangential measurements of the changing heat field after application of a heat pulse (Figs 2, 3) (Vandegehuchte and Steppe 2012*c*, 2012*d*). The anisotropic equations for heat conduction-convection (Eqns 5, 6) are fitted to the measured temperature curves by a calibration procedure from which V_h, K_{ax}, K_{tg} and ρc are estimated. From these parameters, D_{ax}, D_{tg} and *MC* can be calculated.

As with this method changes in *MC* are measured over time, SFD can be more accurately determined from V_h (Eqn 7). Moreover, monitoring *MC* can provide information on plant stress and relates plant water potential to capacitance. Another advantage is that the Sapflow+ method allows measurements of the entire naturally occurring sap-flux density range, independently of thermal diffusivity.

Sensor spacing

All sap-flux density methods are based on the insertion of measurement and heater needles into the sapwood. With exception of the TD method, all methods have probe spacing directly incorporated in their sap-flux density equations. So although for the TD method exact spacing is less important as long as the reference probe is not influenced by the heated probe, for the other methods correct spacing is crucial (Cohen *et al*. 1981; Swanson 1983; Burgess *et al*. 2001*a*; Steppe *et al*. 2010; Vandegehuchte and Steppe 2012*b*). Probe misplacement can be assessed by placing over-length probes in the drill holes, enabling measurement of the spacing and angle between the probes (Hatton *et al*. 1995). Moreover, for the HR method, Burgess *et al*. (2001*a*) measured probe placement *in situ*, based on zero flow conditions. However, parallel placement of the needles remains crucial for accurate results and is often difficult to ensure, especially at large sapwood depths. If probes are installed parallel, but needles are tangentially displaced, this cannot be taken into account in the HFD, CHP, Tmax, HRM or CAG methods. In the Sapflow+ method both the axial and tangential distances are included in the equations, and tangential displacements can also be corrected for if they are measured after installation. Generally, applying a specific drill-bit template for each heat-pulse method can improve probe positioning during sensor installation.

Wounding

When inserting probes in the sapwood, flow is locally obstructed with the obstructed zone dependent on sensor geometry and probe size and, to a lesser extent, probe material (Swanson and Whitfield 1981; Barrett *et al*. 1995; Green *et al*. 2003). Barrett *et al*. (1995) have shown that wounding also effects wood density and fibre direction, especially in the axial direction. Besides these direct wound effects, probe insertion also induces the formation of wound tissue which alters wood properties and, hence, heat dissipation in this wood in the longer term (Moore *et al*. 2010). This long-term effect can be avoided by regularly reinstalling sensors during long-term experiments, although little research has been done on the required frequency of reinstallation (Moore *et al*. 2010).

Short-term wounding, in contrast, has been assessed to be an important error-inducing factor for the TD method (Wullschleger *et al*. 2011). These authors developed a numerical heat flow model to assess TD performance, allowing investigation of error inducing factors both separately and combined. They determined that physical disruption of the xylem due to wounding was a significant cause of error, besides gradients in the radial sap-flux density profile.

Moreover, Wullschleger *et al*. (2011) have shown that the TD method is sensitive to changes in thermal conductivity and, hence, is dependent on sapwood characteristics. This implies that for a specific tree species, the calibration could change due to varying dry wood density of the sapwood and, even for a single tree, could change due to variations in sapwood water content as wounding progresses. According to their modelling results, a combination of these error inducing factors can lead to both under- and overestimations of sap-flux density when using the original calibration coefficients. These authors justly warn users of the TD method to interpret their results with caution and plead for an approach where numerical modelling is combined with updated calibration coefficients to improve TD method accuracy. Unlike for the TD method, wounding has not been thoroughly assessed for the HFD method, although it is expected to have a similar influence on the results.

Next to the continuous heat methods, flow path obstruction due to wounding also greatly influences the sap-flux density results for heat-pulse methods. Based on FEM, it has been shown that wounding partially interrupts sap flow, leading to underestimations of V_h and hence SFD of up to 50% and more (Swanson 1983; Burgess *et al*. 2001*a*; Green *et al*. 2009). Therefore, wound correction equations were developed for the existing heat-pulse systems based on FEM. Wound width has been shown to have a much larger effect than probe material, calibration factors based only on wound width therefore seem sufficient for a given sensor configuration (Swanson and Whitfield 1981; Green *et al*. 2003). For the

CHP method, Swanson and Whitfield (1981) developed readily applicable wound correction coefficients a, b and c for the correction equation $V_{h\_corr} = a + bV_h + cV_h^2$, where V_{h_corr} is the heat velocity corrected for wound effects (Table 2). Cohen *et al*. (1981) derived correction factors for the Tmax method empirically, whereas Green *et al*. (2003) presented similar wound corrections for the Tmax method as those developed by Swanson and Whitfield (1981) for the CHP method. For the HR and Sapflow+ method, Burgess *et al*. (2001*b*) and Vandegehuchte and Steppe (2012*c*) have shown that a linear correction equation is sufficient. For the Sapflow+ method, wounding does not only affect V_h, but also the other estimated parameters. Based on FEM, correction equations for these parameters can be established (Vandegehuchte and Steppe 2012*c*).

For hardwood species with a markedly non-uniform distribution of sap-conducting vessels, however, an additional correction factor besides the wound correction may be necessary. This type of wood diverges more from the assumption of thermal homogeneity, on which the heat conduction-convection equations are based, than for softwoods or hardwoods with closely-spaced and more uniform xylem elements (Green and Clothier 1988; Swanson 1994). This correction factor can be empirically determined or derived from enhanced FEM that includes vessel anatomy.

In the various models used to assess wounding, flow obstruction is implemented as a region of zero flow starting from the most upstream sensor needle and stretching on downstream with a width slightly larger than the sensor needles. The effect of different wound widths and sapwood water contents have been simulated, but the axial length of the zero flow region has never been mentioned (Swanson and Whitfield 1981; Burgess *et al*. 2001*a*; Green *et al*. 2003). Nevertheless, it is likely that this length will differ depending on wood anatomy. In addition, apart from flow obstruction, wood properties also can be locally altered due to installation. Further investigations are needed to determine wound effects for different sapwood types and assess possible differences in wound correction factors. Also, FEM could be improved by including differences in vessel anatomy. In this way, the accuracy of heat-pulse based sap-flux density estimates might be enhanced.

General conclusions

Many sap-flow methods have been developed, each with their advantages and disadvantages. Heat-balance methods integrate flow in the entire stem or in a large stem section of the plant, giving a good indication of whole-plant water use. Sap-flux density methods, in contrast, give more precise information on flow directions and spatial flow distribution. Within this group, the heat-pulse methods seem to outperform the continuous methods as they do not require specific calibrations and they are less susceptible to NTG. For many methods, wounding influences sap-flow results. Despite the existing wound corrections for the heat-pulse methods, a more thorough insight in wound effects, including long-term experiments combining sap-flow methods with FEM and more advanced techniques such as magnetic resonance imaging, will likely further improve sap-flow methodology.

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