Theory and Practical Application of Heat Pulse to Measure Sap Flow

Steve Green,* Brent Clothier, and Bryan Jardine

ABSTRACT

Heat pulse methods can be used for accurate measurements of sap flow in plant stems provided a reliable calibration procedure is used to relate the measured heat pulse velocity to the actual sap flow. This paper reviews the theory underpinning both the *compensation* and *T-max* heat pulse methods that use a linear heater and temperature probes inserted radially into the plant stem. These probes not only disrupt the sap stream, but they also alter the thermal homogeneity of the sapwood in the vicinity of the probes. The degree of disturbance depends on the size and geometry of the probes and the corresponding *wound width* of the nonconducting sapwood. A two-dimensional model of heat and water flow was used here to derive appropriate correction factors to account for the influence of both probe thermal properties and flow blockage. Wound width has a large influence on the heat pulse measurements while sensor material appears to have little or no influence. A table of correction factors is presented for both the compensation and T-max methods. These new correction factors are confirmed by comparing heat pulse measurements in the trunk of a willow (*Salix alba* L.) and a poplar (*Populus deltoides* W. Bartram ex Marsh), against actual rates of transpiration determined from measured weight loss of the trees growing in large lysimeters. On a daily basis, both heat pulse measurements were found to be within 5 to 10% of the actual transpiration. The compensation method accurately measured flows close to 2 cm/h. The T-max method had difficulty resolving any flows slower than about 10 cm/h.

HEAT PULSE TECHNIQUES can be used to measure sap flow in tree stems with minimal disruption to the sap stream (Swanson and Whitfield, 1981; Cohen et al., 1981). The measurements are reliable, use inexpensive technology, provide a good time resolution of sap flow, and are well suited to automatic data collection and storage. Sequential or simultaneous measurements on numerous trees are possible (Green and Clothier, 1988). This permits the estimation of transpiration losses from whole stands of trees (Cermak and Kucera, 1990; Giorio and Giorio, 2003). Alternative heat balance methods (Sakuratani, 1981; Ishida et al., 1991; Kjelgaard et al., 1997) have also been used to measure sap flow in the stems and roots of plants.

We have been using the compensation heat pulse technique (Marshall, 1958) to study sap flow in the orchard trees for more than 15 yr. During that time, we have developed instrumentation that is simple, probes that are robust, and measurements that are reliable and accurate (Green, 1998). The compensation method uses two temperature probes placed asymmetrically on either side of a line heater that is inserted radially into the tree stem. Following the application of a brief 1-to 2-s heat pulse, the time delay for an equal temperature rise at both sensors is used to calculate a heat pulse velocity. A theoretically derived correction factor is then used to correct the heat pulse measurements for any probe-induced effects of wounding and to calculate volumetric rates of sap flow. Without such a correction, the heat pulse measurements of sap flow are typically low by a factor of 50% or more (Green and Clothier, 1988).

We have used our heat pulse equipment in a wide variety of woody species. Examples include walnut (*Juglans ailantifolia* Carrière) (Green, 1992), olive (*Olea europaea* L.) (Moreno et al., 1996; Fernandez et al., 2001), apple (*Malus sylvestris* Miller) (Green et al., 1998), kiwifruit [*Actinidia deliciosa* (Chev.) C.F. Liang & A.R. Ferguson] (Green et al., 1989), grape (*Vitis vinifera* L.) (Green et al., 2002), pear (*Pyrus serotina*) (Caspari et al., 1993), and apricot (*Prunus armeniaca* L.) trees (Alarcon et al., 2000). In general, we have always found very good agreement between our heat pulse measurements of sap flow and independent calculations of tree water use based on water uptake from the root zone (Clothier and Green, 1994) and computer models of whole-tree transpiration (Green and McNaughton, 1997; Green et al., 2003).

Recently, we have begun to investigate the use of the T-max method (Cohen et al., 1981) in our studies on water movement in grapevines. The T-max method uses a single temperature sensor downstream of the line heater. Sap flow is determined from the time delay for a maximum temperature rise to occur at the downstream temperature sensor. To our knowledge, most users of the T-max method (e.g., Cohen et al., 1988) still rely on empirical calibration factors that depend on species and installation. This approach may, or may not, translate into a general calibration factor. The current lack of an appropriate theoretical calibration for the T-max method prompted us to develop a set of *correction factors* based on a numerical solution of the two-dimensional heat flow equation.

In this paper, we review the theory underpinning both the *compensation* and *T-max* heat pulse methods, and we present a set of theoretical correction factors that can be used to convert measured heat pulse velocities into actual sap flow rates. The new correction factors are confirmed by comparing heat pulse measurements in the trunk of a willow and a poplar against actual rates of transpiration determined from measured weight loss of the trees growing in large lysimeters.

HEAT PULSE THEORY

Heat pulse methods date back some 70 yr to the work of Huber (1932), who first conceived the idea of using heat as a

Environ. and Risk Manage. Group, HortResearch Inst., Private Bag 11-030, Palmerston North, New Zealand. Received 26 Aug. 2002. *Corresponding author (sgreen@hortresearch.co.nz).

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Abbreviations: DOY, day of year.

tracer of sap flow. Some 50 yr later, Marshall (1958) developed a theoretical framework for heat pulse based on a set of analytical solutions to the following heat flow equation

$$\rho_w c_w \frac{dT}{dt} = \frac{d}{dx}\lambda_X \frac{dT}{dx} + \frac{d}{dy}\lambda_Y \frac{dT}{dy} - au\rho_s c_s \frac{dT}{dx} + Q \quad [1]$$

that ideally represents the two-dimensional pattern of temperature surrounding a line heater of zero dimension that is inserted into a section of sapwood of uniform physical and thermal properties. Here, ρ_w and ρ_s are the densities (kg m^{-3}) of fresh wood and sap, respectively; c_w and c_s are the specific heat capacities (J s^{-1} m^{-1} K^{-1}) of fresh wood and sap, respectively; T is the temperature departure from ambient (K); t is time (s); λ is the thermal conductivity (W m^{-1} K^{-1}) in the axial (x) and tangential (y) directions; a is the fraction of xylem cross-sectional area occupied by sap streams moving with a velocity u in the x direction; and Q is the amount of internal heat that is released from the heater (W m^{-3}). The relationship between heat pulse velocity, V (m s^{-1}), and the sap flux density, $J_S = au$ (m s^{-1}), is given by

$$V = (\rho_s c_s/\rho_w c_w)J_S \quad [2]$$

Following the application of a heat pulse, the temperature rise, T, at a distance of $r = \sqrt{(x^2 + y^2)}$ from the line heater is given by (Marshall, 1958)

$$T = \frac{Q}{4\pi\kappa t}\exp\left[-\frac{(x - Vt)^2 + y^2}{4\kappa t}\right] \quad [3]$$

where $\kappa = \lambda/\rho c$ is the thermal diffusivity (m^2 s^{-1}) of the sapwood. Swanson (1962) was one of the first to utilize Marshall's analytical solutions in his analysis of the compensation heat pulse method where two temperature sensors are placed asymmetrically on either side of a line heat source. Swanson showed that if the temperature rise is measured at distances x_U (m) upstream and x_D (m) downstream from the heater, then the heat pulse velocity can be calculated from

$$V_Z = (x_D + x_U)/2t_Z \quad [4]$$

where t_Z (s) is the time delay for the temperatures at points x_D and x_U to become equal. Equation [4] implies that the center of the heat pulse is convected downstream from the heater to reach a point midway between the two temperature sensors after a time t_Z.

Marshall's (1958) analytical theory was also used by Cohen et al. (1981) to develop an alternative *improved heat pulse method* that relies on measuring the time, t_M, for a maximum temperature rise to be recorded by a single sensor located a distance x_D downstream from a line heater. We shall refer to this as the T-max method. The heat pulse velocity, V_M (m s^{-1}), is calculated from

$$V_M = \sqrt{x_D^2 - 4\kappa t_M}/t_M \quad [5]$$

The only other factor required to determine V_M is the thermal diffusivity, κ, which is determined from the following equation

$$\kappa = x_D^2/4t_M \quad [6]$$

that is calculated at times when zero sap flow occurs. The condition $V_M = J_S = 0$ normally occurs at night when vapor pressure deficits are low, leaf stomata have closed, and transpiration losses are close to zero. We refer to the estimate of V (m s^{-1}) from Eq. [4] and [5] as the *raw* heat pulse velocity.

Calculations of V_Z and V_M assume that the heater and temperature probes have no effect on the measured heat flow. In reality, convection of the heat pulse is disturbed by the presence of the heater and temperature probes and by the disruption of xylem tissue associated with their placement. These perturbations produce a systematic underestimation in the measured heat pulse velocity (Cohen et al., 1981; Green and Clothier, 1988). Consequently, the heat pulse velocity must be corrected for any probe-induced effects of wounding. This correction can either be done empirically (e.g., Cohen et al., 1981), or it can be based on physical principals, using an equation of the form:

$$V = a_0 + a_1 V_H + a_2 V_H^2 \quad [7]$$

where V (m s^{-1}) is the corrected heat pulse velocity and V_H is the raw heat pulse velocity that has been calculated using either Eq. [4] or [5]. Swanson and Whitfield (1981) presented a set of correction factors to account for the combined influence of sensor thermal properties and the subsequent blockage of sap streams. Their correction factors were computed using a numerical solution to Eq. [1].

We have used a similar numerical approach here to derive new correction factors for both the compensation and T-max heat pulse methods. The numerical model is essentially the same as that of Swanson and Whitfield (1981), and so only the pertinent details are repeated. The model uses a finite difference form of Eq. [1] that is solved using an alternating-direction-implicit scheme in two dimensions (von Rosenberg, 1969). The numerical grid is set at 80.0 by 40.0 mm, with a spatial resolution of 0.1 mm, and the time step is set at 0.1 s. Thermal properties of the sapwood are taken from the data of Siau (1971) and Dunlap (1912), and thermal properties of the sensors are derived from data in Carslaw and Jaeger (1959). A *zero-flow* condition is assumed to occur within the wound width that exists in line with the sensors and parallel to the flow direction. The combined effect of stem moisture content, probe placement, and the wound width are simulated over a range of sap flows. A set of correction coefficients (a_i's) is then determined from the ratio of the measured heat pulse velocity to that *imposed* across the model flow domain. All other details of the model can be found in Swanson and Whitfield (1981).

A volumetric measure of the total sap flow is obtained by summing up the flow rates over the sapwood conducting area. In practice, it is necessary to sample the sap flow at several locations within the sapwood because the velocity profile is not uniform (Cohen et al., 1981; Edwards and Warrick, 1984; Green and Clothier, 1988). The heat pulse sensors that we use measure J_S at four radial depths, and so a second-order regression equation of the form

$$J_S(r) = \alpha r^2 + \beta r + \gamma \quad [8]$$

is fitted to the measurements. The fitting procedure yields an expression for the velocity profile, $J_S(r)$, as a function of stem radius, r (m). This curve is then integrated over the sapwood cross section to calculate the volume sap flux, F (L h^{-1}), as

$$F = 2\pi\int_H^R rJ_S(r)dr \quad [9]$$

for a stem of cambium radius R (m) and heartwood radius H (m). The radius H is determined from an analysis of trunk cores taken at the end of each experiment while R is derived from a measure of the stem circumference and bark depth.

In practice, we use an alternative expression for Eq. [2] to relate the heat pulse velocities to sap flow. This is based on the approximation of Edwards and Warwick (1984) that considers sapwood to comprise the three phases of gas, solid, and liquid with appropriate physical and thermal properties. The working equation is given by

$$J_S = (kF_M + F_L)V \quad [10]$$

where F_M and F_L are the volume fractions of wood and water, respectively. The k factor of 0.441 is related to the thermal properties of the woody matrix (Becker and Edwards, 1999) and was assumed to be constant within and between species. We have not accounted for the influence of temperature on the thermal properties of the wood.

MATERIALS AND METHODS

Heat Pulse Instrumentation

The HPV system (Green, 1998) comprises a set of probes and associated electronics connected to a data logger. Each probe set consists of a linear heater and two temperature sensors that are installed radially into the tree stem. For the compensation method, one probe is placed 5 mm upstream from the heater while the other is placed 10 mm downstream, using parallel holes that are normal to the direction of sap flow. For the T-max method, the upstream probe is simply shifted to a distance of 40 mm from the heater so that it does not *sense* the heat pulse. Rather, this second *reference* probe is used to compensate for any background changes in stem temperature that may occur during the T-max measurement.

The heater probe is made from a length of 1.63-mm-diam. stainless steel tube containing a central nichrome resistance wire (5 $\Omega\ m^{-1}$), which is insulated internally using a fine Teflon tube. The temperature sensors each have four copper-constantan thermo-couple junctions (0.1-mm-diam. wire), and are made from a length of Teflon tubing (1.70 mm diam.) that is filled with epoxy resin. The electronics consists of a heater controller and a set of linear instrumentation amplifiers that have a gain of about 5000.

A data logger (Campbell Scientific, Logan, UT) is used to activate the heater for 0.5 to 1 s. The pair of temperature sensors is then used to monitor subsequent changes in stem temperature that occur as the heat pulse is propagated through the sapwood, both by conduction through the wood and sap matrix and by convection with the moving sap streams. The logger is programmed to interpret the temperature signals and to record the subsequent *crossover* and *peak* times that are used in Eq. [4] and [5], respectively, to calculate the raw heat pulse velocity. For the T-max method, the temperature signals are also smoothed to reduce signal noise. The time for a peak temperature rise, t_M, is calculated using the convoluted least-squares procedure of Savitzky and Golay (1964). A laptop PC is later used to retrieve the t_Z and t_M data from the logger, and additional software is used to calculate the volumetric sap flow.

Practical Test of the Compensation Heat Pulse Method

A single test of the compensation method was performed in the stem of a 1-yr-old willow tree that was growing in a 800-L container of Manawatu soil inside one of the lysimeter facilities at HortResearch, Palmerston North, New Zealand. This facility includes a number of covered plastic houses (≈50% visible light transmission) that are open at both ends to allow for air ventilation. The willow tree and its container were placed on a 1000-kg load cell (±10 g resolution) that was weighed every hour. The tree was watered using drip irrigation once every 3 to 5 d, and a nutrient solution was applied several times over the summer period. The soil surface (0.3 m^2) was covered with a black plastic sheet to limit any soil evaporation. Rates of transpiration from the tree were determined from the measured weight change of the lysimeter, making an allowance for any irrigation water or drainage that occurred.

Two sets of heat pulse probes were inserted into the trunk, and sap flow rates were subsequently monitored once every 30 min over several weeks in late summer. By that stage, the trunk diameter had reached 5.5 cm, tree height was around 2.5 m, and the leaf area was about 8.0 m^2. Sap velocities were calculated by assuming a 2.4-mm wound width and using the correction factors derived for the 1.6-mm-diam. sensor probes and heater.

Practical Test of the T-max Heat Pulse Method

A single test of the T-max method was performed using a 2-yr-old poplar tree growing in an 800-L container of sawdust material. The tree was inside a shade house (≈80% visible light), and the container was sitting on top of a 2000-kg load cell that was weighed every hour. Water was supplied automatically, once every 1 to 2 d, using a drip-irrigation system that provided a maximum of 30 L during any one irrigation event. A good fraction of that water (15–20%) drained almost straightaway through the container. A balanced nutrient solution was also applied to the tree once per month over the spring and summer period. The surface of the lysimeter pot (0.4 m^2) was uncovered, but evaporation was expected to be quite low because the soil surface was never fully wetted. Furthermore, sawdust is very porous so that direct evaporation would soon be conductivity limited. Drainage water from the lysimeter was collected into a 25-L container that was sitting on a 60-kg load cell. Transpiration from the tree was determined from the measured weight change of the lysimeter, making an allowance for any irrigation water or drainage that occurred.

The poplar tree had a trunk diameter of 6.0 cm, a height of 4 m, and a total leaf area of 10 to 12.0 m^2. Two sets of heat pulse probes, each comprising a heater and temperature probe, were installed into the trunk, and heat pulse velocities were monitored every 30 min for about 6 weeks in late summer. The corresponding sap velocities were calculated assuming a 2.4-mm wound width and using the correction factors appropriate for our 1.6-mm Teflon probes located a distance of 10 mm downstream from the stainless steel heater.

RESULTS

Testing the Compensation Heat Pulse Method

Results from the numerical model are used here to illustrate the influence of stem moisture content and wound width on the measured heat pulse velocity. All other factors being equal, heat will always travel faster through dry sapwood than through wet sapwood (Fig. 1). Nevertheless, there appears to be an almost universal relationship between the actual heat pulse velocity and that measured via the compensation method. That relationship holds across a very wide range of stem moisture contents (Fig. 2). The measured heat pulse velocity, V_Z, departs significantly and systematically from the actual heat pulse velocity. The ratio between measured and actual heat pulse velocity decreases at higher sap flow rates.

With our heat pulse system, we have the option of using either stainless-steel sensors for robustness or Teflon sensors for ease of insertion and removal. The use of different probe materials could influence the calibration factors because the thermal properties of stainless steel (a good conductor) are so very different from those of

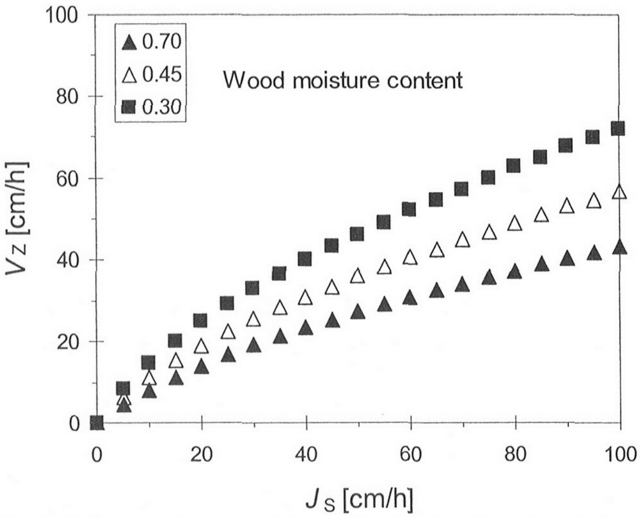

Fig. 1. Influence of wood moisture content (m^3 m^{-3}) on the relationship between measured heat pulse velocity (Vz) and sap flow (J_S). This relationship was determined using the numerical model. The temperature probes are Teflon, and the heater is stainless steel.

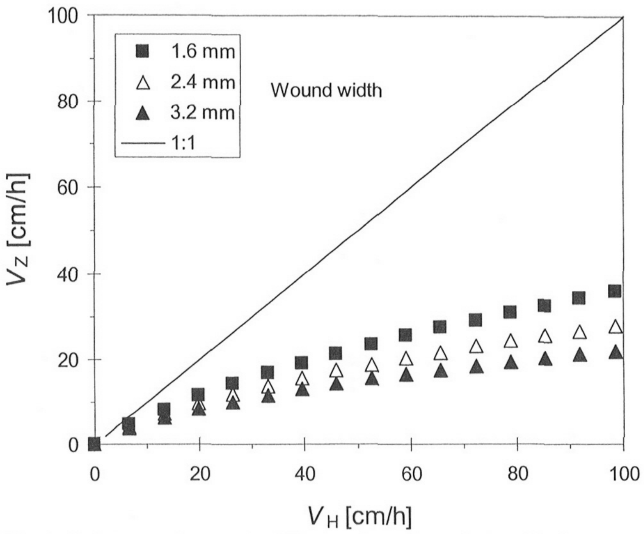

Fig. 3. Influence of wound width (mm) on the relationship between measured heat pulse velocity (Vz) and the actual heat pulse velocity (V_H). This relationship was determined using a numerical model of heat and mass flow through a 2-d slab of wet wood. The temperature probes are Teflon, and the heater is stainless steel.

Teflon (a good insulator). However, the model results for stainless steel and Teflon sensors yielded results that differed by only a few percentages (comparative data not shown). Wound width has a much larger influence on V_Z (Fig. 3) while sensor material has little or no influence. Thus, a single calibration factor for each wound width would seem adequate. We note that the calibration factors derived here for our sensors (Table 1) are very similar to those derived by Swanson and Whitfield (1981) for their glass temperature sensors and brass heater with the same probe geometries. If the probe spacing were altered, then a different set of correction factors would be required. Table 2 presents the corresponding correction factors for a probe spacing of $x_U = -5$ mm and $x_D = 15$ mm.

Flow disruptions associated with the wound width have a large and systematic influence on the flow measurements (Fig. 3). In the case of small probes (1.6 mm) at moderate flow rates (40 cm h^{-1}), the measured flow without a correction is approximately 50% of the actual sap flow. In the case of larger probes (3.2 mm) at higher flow rates (80 cm h^{-1}), the uncorrected flow measurements are just 25% of the actual flow (Table 3). To obtain reliable measurements with heat pulse, it is very important to get an accurate determination of stem moisture content and a consistent estimate of wound width. At this point, we note that a priori the wound size is not known although we might expect it to be a little larger than the size of the drill hole. This is because of additional damage that results from mechanical disruption of vessels at the edges of the drill hole, plus Péclet effects of having to *find* the nearest intact xylem vessel.

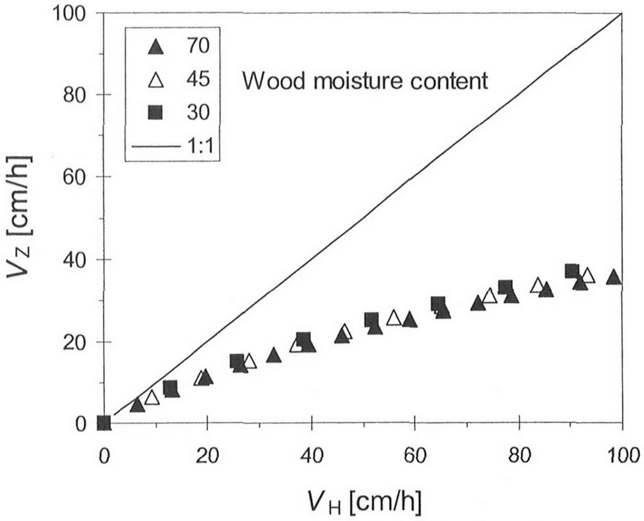

Fig. 2. Influence of wood moisture content (m^3 m^{-3}) on the relationship between measured heat pulse velocity (Vz) and the actual heat pulse velocity (V_H). This relationship was determined using the numerical model. The temperature probes are Teflon, and the heater is stainless steel.

Generally, there was a very good correspondence between the temporal patterns of measured sap flow and the actual rates of transpiration from the willow tree, as determined by lysimetry (Fig. 4). The correction factor for a 2.4-mm wound width would seem appropriate in this case. It was not possible to make a point-by-point

Table 1. Correction factors for the compensation method using 1.6-mm-diam. probes placed at a distance of $x_U = -5$ mm upstream and $x_D = 10$ mm downstream from the heater.

	Coefficients in Eq. [7]		
Wound width	a_0	a_1	a_2
mm			
1.6	−5.48E−01	1.33E+00	4.00E−02
1.8	−4.26E−01	1.31E+00	4.94E−02
2.0	−9.63E−02	1.24E+00	6.34E−02
2.2	1.31E−01	1.19E+00	7.36E−02
2.4	3.94E−01	1.12E+00	8.78E−02
2.6	8.36E−01	9.98E−01	1.07E−01
2.8	1.51E+00	7.91E−01	1.32E−01
3.0	1.79E+00	6.86E−01	1.52E−01
3.2	2.31E+00	5.02E−01	1.78E−01
3.4	2.86E+00	2.71E−01	2.11E−01

Table 2. Correction factors for the compensation method using a 1.6-mm-diam. probes placed at a distance x_U = −5 mm upstream of x_D = 15 mm downstream from the heater.

Wound width	Coefficients in Eq. [7]		
	a_0	a_1	a_2
mm			
1.6	−1.48E+00	1.38E+00	1.85E−02
1.8	−1.43E+00	1.39E+00	2.24E−02
2.0	−1.19E+00	1.37E+00	2.76E−02
2.2	−1.14E+00	1.37E+00	3.20E−02
2.4	−9.17E−01	1.35E+00	3.77E−02
2.6	−6.23E−01	1.31E+00	4.50E−02
2.8	−7.41E−02	1.22E+00	5.48E−01
3.0	1.42E−01	1.18E+00	6.27E−02
3.2	6.50E−01	1.09E+00	7.32E−01
3.4	1.44E+00	9.40E−01	8.73E−02

comparison between the measurements because of the different sampling frequencies (i.e., heat pulse at 30 min and lysimetry at 60 min). In any case, heat pulse gives the instantaneous rates of sap flow while lysimetry represents the average transpirational losses over the previous hour. Nevertheless, these results provide good support for the use of our new theoretical calibrations although this comparison cannot be considered as full validation. On a daily basis, the measure sap flow was always within 5 to 10% of that measured by lysimetry.

Peak sap flow rates on warm sunny days [e.g., day of year (DOY) 71] were up to 2.5 L h^{-1}, and this equates to a maximum sap flux density (expressed as the volume flow per unit stem cross section) of about 100 cm h^{-1}. Willows have a high water flux through a relatively small stem cross section. On cool, cloudy days (e.g., DOY 74), transpiration rates dropped to 1.0 L h^{-1}, with a maximum sap flux density of some 42 cm h^{-1}. At night, when evaporative demand was low, both the lysimeter and heat pulse measurements recorded low flows. The compensation heat pulse method was able to resolve these flows down to as low as 2 cm h^{-1}.

Theoretical Calibration of the T-max Heat Pulse Method

Our experience with the T-max method is that it usually produces very consistent measurements during the day, yet sometimes the measurements are *noisy* at night. Results from the numerical model, and an examination of some typical temperature traces, may help to provide

Table 3. Influence of wound width (ΔW), sap velocity (J_S), and stem moisture content (θ) on the *true* heat pulse velocity (V) and that measured using the compensation heat pulse method (V_Z). The results assume a 1.6-mm-diam. probe at x_D = 10 mm.

ΔW	J_S	θ	V	V_Z
mm	cm/h	m^3/m^3	cm/h	
1.6	40.0	0.525	65.4	27.9
		0.600	58.2	25.5
		0.675	52.5	23.4
1.6	80.0	0.525	130.8	44.1
		0.600	116.5	40.4
		0.675	105.0	37.4
3.2	40.0	0.525	65.4	18.1
		0.600	58.2	16.6
		0.675	52.5	15.4
3.2	80.0	0.525	130.8	26.1
		0.600	116.5	24.3
		0.675	105.0	22.7

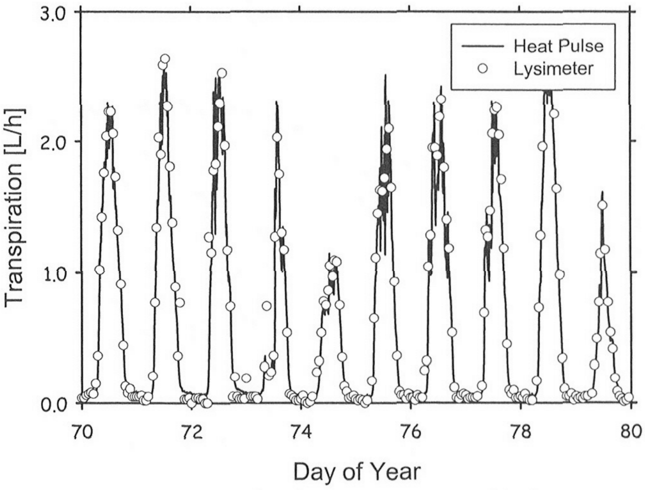

Fig. 4. Transpiration rate of a willow tree as measured by the compensation heat pulse method (black line) and calculated by the weight loss from the lysimeter (open circle).

some insight as to why this might be the case. The T-max method relies on obtaining a measure of the thermal conductivity, κ, using a value of t_M recorded during zero flow. These conditions are hard to establish in some species because nocturnal sap flows can sometimes be quite large (Green et al., 1989). The numerical model shows that the relationship between t_M and J_S is nonunique at low flow rates (i.e., <10 cm/h). This means that it is actually impossible to calculate a single value for J_S at these low flow rates if the *correct value* of t_M is used to compute κ (Fig. 5).

The low-flow resolution could be improved somewhat if the probe spacing is increased from x_D = 10 mm to x_D = 15 mm (Fig. 5). This is the spacing adopted by Cohen et al. (1981). A wider spacing helps to improve the measurement sensitivity (dt_M/dJ_S). The trade-off will be a smaller temperature rise, for the same heat input, and this could reduce the signal/noise ratio measured at the temperature sensor. There may also be practical

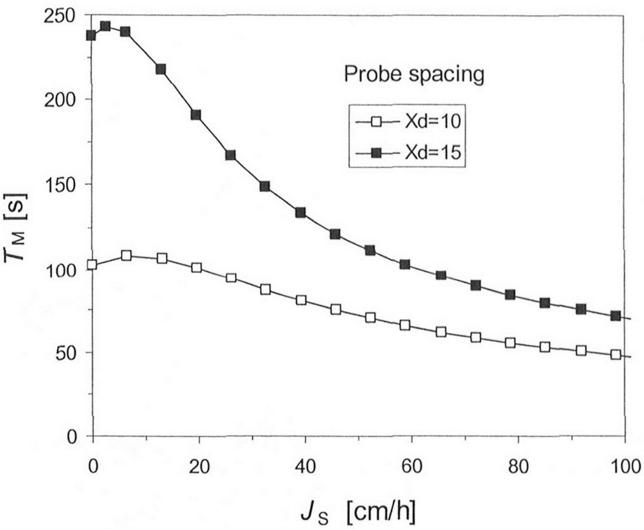

Fig. 5. The influence of sap velocity, J_S, on the time for a peak temperature rise to occur, T_M, at a distance of x_D = 10 mm and 15 mm downstream from the heater probe.

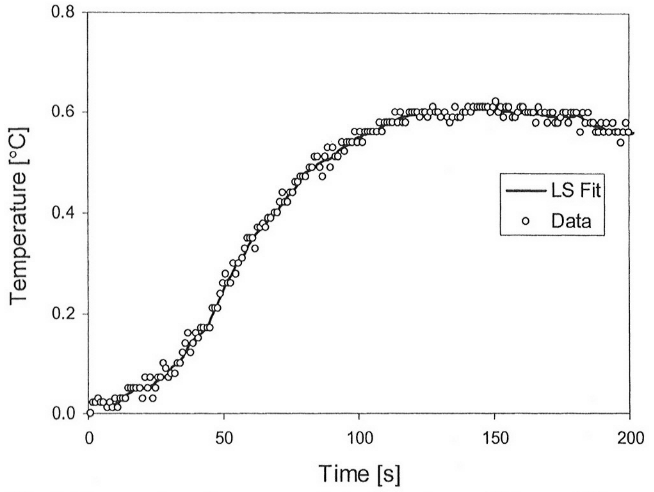

Fig. 6. Temperature rise measured at a downstream distance of 10 mm (data) following the application of a 1-s heat pulse. The measurements are smoothed (LS Fit) to reduce signal noise, and the time for a maximum temperature rise to occur is calculated using the convoluted least-squares procedure of Savitzky and Golay (1964). These are predawn measurements (zero flow) in a mature grape vine.

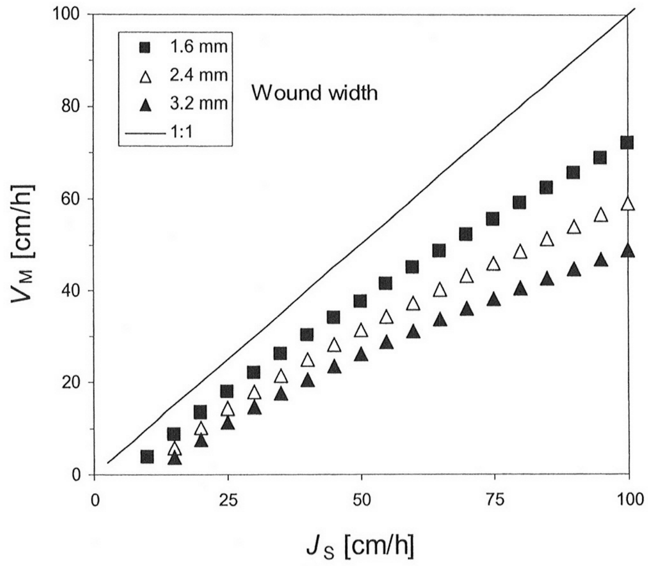

Fig. 8. Influence of wound width (mm) on the relationship between measured heat pulse velocity (V_M) and the imposed sap flow (J_S). The temperature probes are Teflon, and the heater is stainless steel.

difficulties in measuring t_M at low flow rates. The measured temperature trace has a much broader peak that is less easy to identify (c.f. Fig. 6 and 7), and the measurements of t_M are prone to error resulting from signal noise. A 15-point convoluted least-squares procedure (Savitzky and Golay, 1964) was used here to reduce the signal noise and better identify the temperature peaks. In addition, a second *reference probe* was used upstream of the heater to accommodate any other drifts in stem temperature. At a probe spacing of x_D = 10 mm, the T-max method cannot distinguish the difference between zero flow and 10 cm/h (Fig. 8). Tables 4 and 5 present the wound-dependent correction factors for the T-max method.

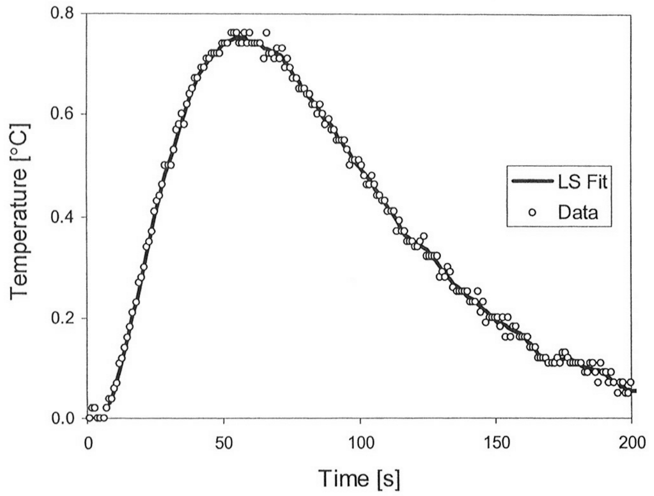

Fig. 7. Temperature rise measured at a downstream distance of 10 mm (data) following the application of a 1-s heat pulse. The measurements are smoothed (LS Fit) to reduce signal noise, and the time for a maximum temperature rise to occur is calculated using the convoluted least-squares procedure of Savitzky and Golay (1964). These are midday measurements (high flow rate) from a mature grape vine.

Practical Test of the T-max Heat Pulse Method

A comparison between measured sap flow and the actual transpiration rates from the poplar tree, as determined by lysimetry, is shown in Fig. 9. During the daytime, the heat pulse measurements were always in very good agreement with the actual transpiration losses. Peak flow rates on warm sunny days (e.g., DOY 71) were between 1.5 and 1.8 L h^{-1}. This equates to a maximum sap flux density of ≈75 to 90 cm h^{-1} when expressed as a sap flow volume per unit cross section. On cool, cloudy days (e.g., DOY 79), transpiration dropped to about 0.5 L h^{-1}. The maximum sap flux density on those days declined to ≈25 cm h^{-1}. By comparison, we note that the water flux through the stem of the poplar tree was less than that through the willow tree under a similar evaporative demand, yet the poplar tree had almost twice the leaf area.

When evaporative demand dropped at night, the lysimeter still recorded a small evaporative loss. A small part of that water loss was probably associated with some evaporation from the sawdust because it was not

Table 4. Correction factors for the T-max method using 1.6-mm-diam. probes placed at a distance of x_D = 10 mm downstream from the heater.

	Coefficients in Eq. [7]		
Wound width	a_0	a_1	a_2
mm			
1.6	7.53E+00	1.32E+00	5.56E−03
1.8	8.70E+00	1.33E+00	6.80E−03
2.0	9.05E+00	1.39E+00	7.55E−03
2.2	9.74E+00	1.40E+00	9.07E−03
2.4	1.04E+01	1.43E+00	1.06E−02
2.6	1.11E+01	1.45E+00	1.23E−02
2.8	1.19E+01	1.46E+00	1.43E−02
3.0	1.28E+01	1.46E+00	1.66E−02
3.2	1.36E+01	1.48E+00	1.91E−02
3.4	1.47E+01	1.47E+00	2.21E−02

Table 5. Correction factors for the T-max method using 1.6-mm-diam. probes placed at a distance of x_D = 15 mm downstream from the heater.

Wound width	Coefficients in Eq. [7] a_0	a_1	a_2
mm			
1.6	2.14E+00	1.93E+00	8.10E−03
1.8	2.89E+00	1.95E+00	9.78E−03
2.0	3.12E+00	1.99E+00	1.12E−02
2.2	3.46E+00	2.01E+00	1.33E−02
2.4	3.78E+00	2.03E+00	1.55E−02
2.6	4.12E+00	2.05E+00	1.79E−02
2.8	4.43E+00	2.07E+00	2.05E−02
3.0	4.84E+00	2.09E+00	2.34E−02
3.2	5.36E+00	2.08E+00	2.72E−02
3.4	5.80E+00	2.09E+00	3.09E−02

covered. Intermittent *spikes* of sap flow at night clearly did not reflect the actual transpiration losses (e.g., DOY 74). The T-max method does not seem to be well suited to measuring these low flow rates, at least in the case of a temperature sensor located just 10 mm from the heater. These problems at low flows still present a practical challenge that needs to be resolved.

The average predawn values of t_M varied between about 120 s, when the probes were first installed, and increased to about 140 s beyond a period of 6 to 8 wk. Most of that change occurred in the first 2 wk when, presumably, the tree was still reacting to the new wound. So how important are these differences in t_M? That question can be answered simply by examining the influence of κ on the volumetric sap flow. A value of t_M = 120 implies that κ = 2.1×10^{-3} cm^2 s^{-1} while a value of t_M = 140 s implies that κ = 1.8×10^{-3} cm^2 s^{-1}. These two κ values have a moderate influence (<10%) on calculated flow during the middle of the day. T-max measurements are much more sensitive to κ when the flow rates are very small (see Fig. 5, Cohen et al., 1981). Using a lower value of κ consistently yielded *apparent* nighttime flows of 0.2 to 0.4 L h^{-1} that were not realized by the lysimeter measurements. Using a higher value of κ consistently yielded many more failed readings of J_S at night. For practical purposes, we have adopted the 7-d average predawn value of t_M, as measured between the hours of 0300 and 0500. This approach yields daytime values of sap flow that closely match the measured transpiration rates of the poplar tree (Fig. 9).

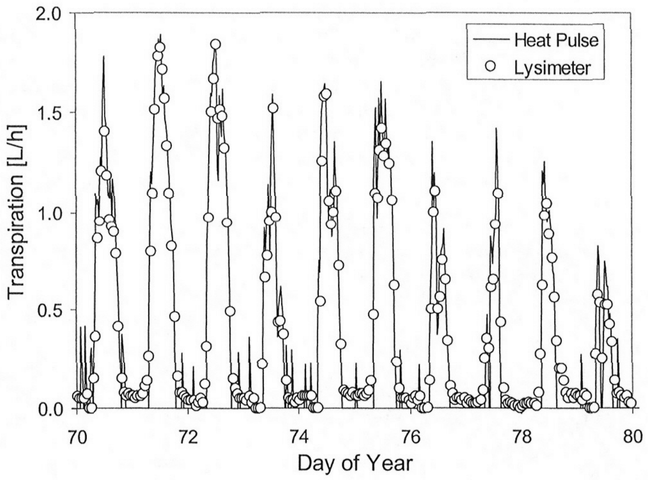

Fig. 9. Transpiration rate of a poplar tree as measured by the T-max method (black line) and calculated by the weight loss from the lysimeter (open circle).

DISCUSSION AND CONCLUSIONS

Heat pulse methods can produce accurate measurements of sap flow in plant stems provided a reliable procedure is adopted to relate the measured heat pulse velocity to the actual sap flow. For the T-max method, the use of a convoluted least-squares procedure (Savitzky and Golay, 1964) to reduce signal noise and better identify t_M, has greatly improved the reliability of our measurements at low flows. The step of converting consistent measurements of t_M into reliable measurements of J_S was achieved by deriving new calibration factors via the numerical model (Fig. 8). These correction factors are based on physical principals rather than simple empirical adjustments. Burgess et al. (2001) used a similar modeling approach to develop a wound-dependent calibration factor for their heat-ratio method that can resolve both low flows and flows that are reversed.

The ability to measure low flow rates is important in studies of root sap flow, nocturnal transpiration, and when measuring transpiration from shaded understory trees. Recent work by Becker (1998) has suggested some limitations to the compensation method at low rates of flow. However, he also noted that some of their measurement problems were associated with poor thermal contact of their hollow stainless probes. Here we have successfully measured quite low flow rates ($J_S \approx$ 1–2 cm h^{-1}) with the compensation method in a willow tree (Fig. 5). Small nocturnal flows were in good agreement with actual transpiration losses at night. Like Burgess et al. (2001), we believe the compensation method can resolve quite low flows, but not flow reversal, provided the cutoff time for t_Z is extended beyond 300 s and that the calibration factors are recalculated close to zero flow. Our new calibration factors generate values of $V \approx$ 2 cm h^{-1} if the cutoff time for t_Z is set at 500 s. The same is not true for the T-max method. There are theoretical reasons why T-max cannot resolve the low flows (Fig. 5), and there are practical difficulties in measurement that are associated with the broad temperature peaks and any small drifts in temperature (Fig. 6).

From our model calculations, and the calibration work of others (Swanson and Whitfield, 1981; Cohen et al., 1981; Burgess et al., 2001), wound width is identified as an important physical factor affecting the accuracy of the heat pulse measurements. Providing the wound width is known, or can be estimated, it should be possible to use a wound-dependent correction factor for most woody-stemmed species where the sapwood is homogeneous and the interstitial distances between the xylem vessels is small (<0.4 mm). In that case, either heat pulse method can be used with confidence and without any additional empirical calibration. The question remains as to what is the most appropriate wound width.

Anatomical investigations by Barrett et al. (1995) indicated the total wound width (from drilling) is likely to extend about 0.3 mm on either side of the drill hole. Thus, a wound correction of $(1.8 + 2 \times 0.3)$ mm seems appropriate for a drill hole of 1.8 mm diameter. For both heat pulse methods presented here—using poplar and willow trees that have small, closely spaced xylem vessels—we have used exactly this wound width. However, in other heat pulse work in kiwifruit, we found a larger wound correction of some 3.2 mm was required for kiwifruit vines to bring the heat pulse measurement into line with actual flow rates (Green and Clothier, 1988). Kiwifruit has very large xylem vessels and a substantial interstitial area of woody matrix that affects the thermal homogeneity of the sapwood. These large vessels affect the transmission and measurement of heat pulse in kiwifruit. The act of drilling into kiwifruit cuts the xylem vessels, leaving the next closest active xylem vessels some 0.2 to 0.5 mm further away. We expect similar discrepancies to occur with heat pulse measurements in grape vines because the sapwood also has very large xylem vessels. A validation test on grapes is planned in the near future.

Our kiwifruit results (Green and Clothier, 1988), and the observations of Barrett et al. (1995), show the importance of checking the heat pulse method to determine an appropriate wound factor for species that have large xylem vessels. It is also very important to measure the stem moisture content since this has a large influence on the measured rates of sap flow (Fig. 1). A negative relationship exists between changes in stem moisture content and the sensitivity of the heat pulse measurements. This is because heat travels faster in dry sapwood. Our previous observations in apple trees revealed that the moisture content of the stem sapwood typically varies between 50 and 60% (L/L) over the course of a growing season (unpublished). Such large seasonal changes would result in an apparent 6 to 9% increase in measured heat pulse velocity for the same sap flow (Table 5). While these are significant *errors*, they can easily be accounted for by routinely monitoring the stem moisture content.

The computer model that we developed here for heat pulse is available from the authors on request. With small changes to the FORTRAN code, it should be possible to simulate other heat pulse and heat balance methodologies, such as the thermal dissipation technique of Granier (1985) and the heat-ratio method of Burgess et al. (2001), and thereby determine the corresponding theoretical correction factors for them.

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