REGULAR ARTICLE

Using branch and basal trunk sap flow measurements to estimate whole-plant water capacitance: a caution

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Abstract Thermometric sap flow sensors are widely used to measure water flow in roots, stems and branches of plants. Comparison of the timing of flow in branches and stems has been used to estimate water capacitance of large trees. We review studies of sap flow in branches and present our own data to show that there is wide variation in the patterns and timing of sap flow of branches in different parts of the crown, owing to the course of daily solar illuminance. In contiguous forest, east-facing and upper branches are illuminated earlier than west-facing and lower branches and most capacitance studies do not include adequate information about branch sampling regimes relative to the overall pattern of crown illuminance, raising questions about the accuracy of capacitance estimates. Measuring only upper branches and normalising these results to represent the entire crown is dangerous because flows at the stem base likely peak in response to maximum crown illuminance (and transpiration) and this will differ compared to the timing of peak flows in upper branches. We suggest that the magnitude of flow lags between branches and stems needs further study, with careful attention to branch position and method application before a robust understanding of capacitance, particularly in woody tissues of large trees, can be formed. We did not detect flow lags in the world's tallest and largest tree species *Sequoia sempervirens* and *Sequoiadendron giganteum*, despite measurement along large pathlengths (~57 and 85 m), which raises questions as to why large flow lags are often recorded for much smaller species. One conspicuous possibility is the different methods used among studies. Constant-heating methods such as the thermal dissipation probe (and also heat balance methods) include heat capacitance behaviour due to warming of wood tissues, which delays the response of the sensors to changing sap flow conditions. We argue that methods with intrinsic heat-capacitance present dangers when trying to measure water-capacitance in trees. In this respect heat pulse methods hold an advantage.

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Introduction

Thermometric methods of tracing water movement through xylem tissues have been used to study the water relations of trees and other plants for over 70 years (e.g. Huber 1928). These so-called 'sap flow methods' have proliferated over the past few decades such that there are a range of approaches to trace water movement in plants, each with their own strengths and weaknesses (Burgess et al. 2000; Smith and Allen 1996; Swanson 1994; Green et al. 2003; Lu et al. 2004). In each case, heating elements and temperature sensors are installed in or around xylem tissues typically at the base of the plant stem (although note Burgess and Bleby 2006) in order to monitor total water flux through the plant. These methods have also been employed to measure water flows in individual roots (e.g. Burgess et al. 1998; Howard et al. 1996; Hultine et al. 2004; Lott et al. 1996; Meinzer et al. 2004a; Nadezhdina and Cermak 2003; Oliveira et al. 2005; Sakuratani et al. 1999; Smith et al. 1999) and branches (e.g. Alarcon et al. 2003; Chapotin et al. 2006; Fernandez et al. 2006; Hubbard et al. 2002; Martin et al. 2001; Meinzer et al. 2004b; Phillips et al. 1999; Steinberg et al. 1990; Steppe et al. 2006; Yonemoto et al. 2004).

Sap flow has been measured in branches of trees and shrubs for a variety of reasons, including the dictates of sensor deployment (size-constrained heat balance collars are often placed preferentially on branches rather than stems, e.g. Zhang et al. 1997), but more often to answer specific questions about crown transpiration dynamics (Meinzer et al. 1997), hydraulic architecture (Alarcon et al. 2003), hydraulic limitations (Hubbard et al. 2002) and for studies of water storage in woody plants (capacitance, Goldstein et al. 1998; Chapotin et al. 2006).

The use of sap flow measurements in branches and stems (trunks) to study water storage/capacitance is the strict focus of this paper, which forms part of a special issue on sap flow measurement. Our thesis is that past investigations have used sap flow sensor types or sampling strategies that compromise estimates of capacitance. We also would like to address a minor misconception in the literature that 'delays in the onset of sap flow' are a suitable metric for identifying capacitance in trees. Because the subject of this special issue paper is the use of sap flow methods, we do not aim to review or evaluate estimates of plant capacitance that have been gathered with other methods; this

area is worthy of a review in its own right, particularly as this science matures. Instead, we review literature on measuring sap flow in tree branches and trunks, present our own experimental data and then raise questions as to exactly what we can learn about capacitance in large trees using sap flow techniques. Our first objective is to demonstrate from the literature and our own data that there is considerable variation among branches in patterns and rates of sap flow. Our second objective is to demonstrate from the literature that when sap flow in branches has been compared to that at the base of stems in order to estimate capacitance, there has usually been little recognition of, or effort to control for, the variation among branches within the crown. Finally, we will apply (1) information on what determines patterns of branch sap flow, (2) the predictions of the cohesion-tension theory and (3) an understanding of methodological limitations to critique extant sap flow data and viewpoints on the nature of capacitance in large trees as determined from sap flow measurements.

Materials and methods

Sap flow was measured in a single 64 m *Sequoia sempervirens* (D. Don) tree in east-facing and west-facing upper crown branches (~20 cm diameter, 53 m height) and the east and west sides of the stem at breast height and at ~57 m. Sap flow was also measured in a single 88 m tall *Sequoiadendron giganteum* (Lindl.) tree in east-facing and west-facing mid-crown branches (~30 cm diameter, 54 m) and the east and west sides of the stem at the base and at ~85 m. All measurements were made during August 2006. *Sequoia sempervirens* was measured at Sonoma, CA at a site previously described by Burgess and Dawson (2004) and Burgess and Dawson (2007). *Sequoiadendron giganteum* was measured at the University of California Berkeley Whitaker Forest property, just southwest of Sequoia-Kings National Park CA (36.703°N, 118.931°W). Sap flow measurements were made every 10 min with the heat ratio method (Burgess et al. 2001) using HRM-30 sensors (ICT International, Armidale Australia) coupled to an experimental wireless sensor network (Burgess et al., unpublished manuscript) that collated data on a Zaurus SL-C3000 PDA (Sharp Corporation, Japan). Data were then averaged every 30 min. As is typical for capacitance studies, data are presented as

normalised values relative to the maximum flow rate at the measurement position in order to account for different absolute flow rates in different parts of the plant. For *Sequoiadendron giganteum*, only about 40 h of data were recorded due to technical difficulties with the experimental sensor network; weather was consistent during the period and so all data were plotted together as a function of time of day. For *Sequoia sempervirens*, 60 h of data were collected and treated in the same manner.

Results

Patterns of sap flow differed greatly between east and west-facing branches in both species, with sap flow in east-facing branches peaking much earlier than west-facing branches. Figure 1a shows sap flow in branches of *Sequoia sempervirens*. Figure 2a shows similar
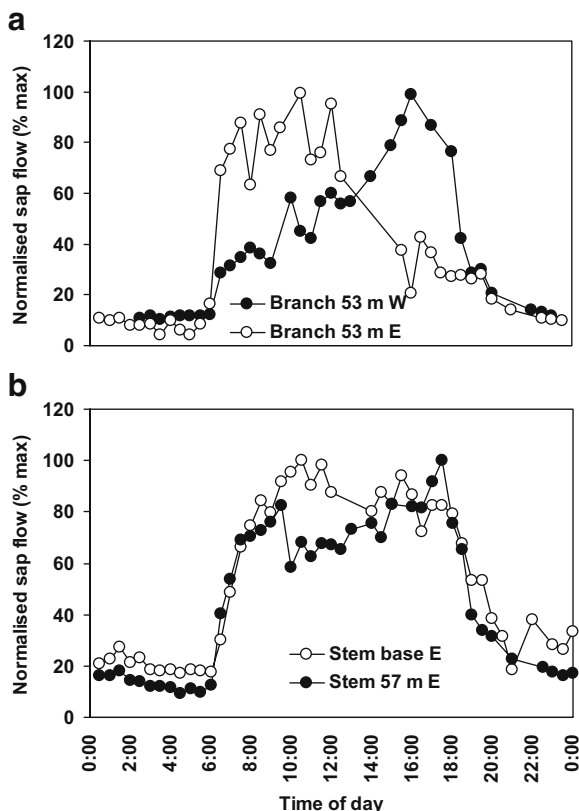

Fig. 1 **a** Normalised sap flow (% of maximum at measurement position) in an east-facing and west facing branch of *Sequoia sempervirens* growing at Sonoma County, CA (right-hand axis, east-facing branch). **b** Normalised sap flow recorded at the stem base and the stem at ~57 m in *Sequoia sempervirens* growing at Sonoma County, CA (right-hand axis, stem base)
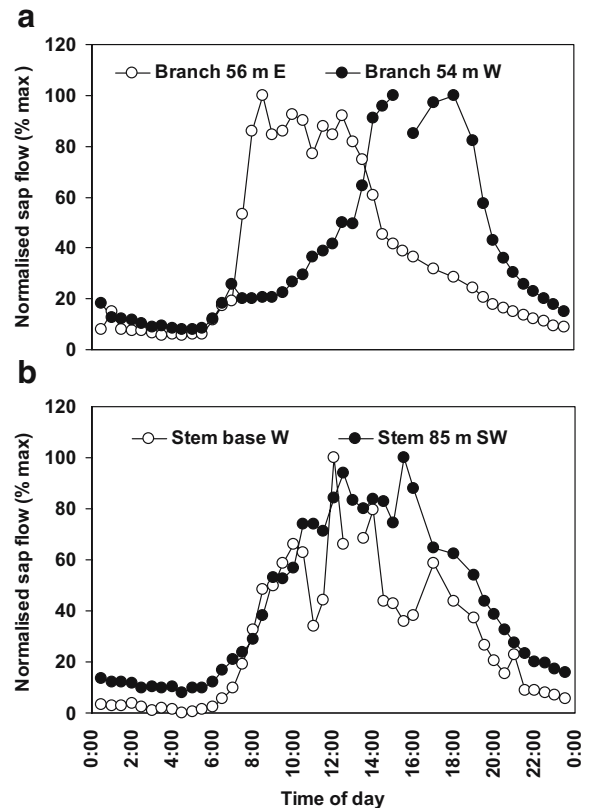

Fig. 2 **a** Normalised sap flow (% of maximum at measurement position) in an east-facing and west facing branch of *Sequoiadendron giganteum* growing at Whitaker Forest, CA. **b** Normalised sap flow at the stem base and the stem at 85 m in *Sequoiadendron giganteum* growing at Whitaker Forest, CA (right-hand axis, stem base)

patterns for east and west-facing *Sequoiadendron giganteum* branches. Patterns of flow between upper stem and stem bases did not appear to differ markedly in the timing of onset of flow or peak flow for these two species (Fig. 1b *Sequoia sempervirens* and Fig. 2b *Sequoiadendron giganteum*).

Discussion

1) Studies that demonstrate variation in sap flow among branches

There are a number of studies which have observed differences in sap flow among different branches in specific locations in the crown. For example, Steinberg et al. (1990) found that northern branches had considerably lower sap flow than southern branches of a 5-year old pecan tree (in the northern hemisphere). Akilan et al. (1994) found differences in sap flow rate

between east and west branches of the shrub Geraldton Wax (*Chamelaucium uncinatum*), which was particularly evident in the afternoons when the east branch was shaded. Alarcon et al. (2003) measured sap flow in branches and stems of apricot and found that absolute rates of sap flow in branches differed with orientation, with the greatest flows being in the better illuminated SE facing branches. Martin et al. (2001) found that each branch of *Abies amabilis* trees had its own "unique diurnal sap flow signature" resulting from the changing radiation environment as each branch moved in and out of the shade of other branches and neighbouring trees. An east-facing branch had its peak sap flow at the beginning of the day as the first sunlight of the day illuminated this side of the tree's crown before declining as it moved into the shade created by the parent tree as the sun moved west. A west-facing branch began with low rates of sap flow in the morning and then peaked in the afternoon with sun in the west.

Some studies did not show differences in sap flow patterns in different branches. For example, Fernandez et al. (2006) alternated irrigation patterns in a partial rootzone drying experiment but did not detect a change in either water taken up by main roots at each side of the trees, or in the sap flow in the trunk locations and main branches of each side. Lu and Chacko (1998) did not report differences in the patterns of sap flow in east, west and south facing branches, and east and west positions on the stem of 5-year-old mango trees. In an example involving branch height rather than aspect, Hubbard et al. (2002) found little variation in sap flux with height within the crown of *Pinus ponderosa* trees, although branches in the upper crown (at 25 m) had lower sap flux on a sapwood area basis than lower branches (at 10 m), which corresponded with lower leaf area per unit sapwood area in the upper crown. These trees were growing in a heavily thinned, open stand with "most trees receiving full sunlight throughout the day" (Hubbard et al. 2002).

Our own data for east and west-facing branches for *Sequioa sempervirens* and *Sequioadendron giganteum* in Figs. 1 and 2 agree with the findings of Akilan et al. (1994), Alarcon et al. (2003) and Martin et al. (2001): there were very large differences in the patterns of sap flow in east- versus west-facing branches corresponding to the diurnal pattern of solar radiation reaching the branches (Fig. 1a and b).

2) Studies that compare branch and basal stem sap flow to estimate capacitance

There are a number of studies that have compared patterns of sap flow in branches to flows lower in the tree, usually at the stem base, in order to estimate plant capacitance or water storage in woody tissues. Given the variation in sap flow patterns and magnitudes in branches described above, one might expect this to influence the selection of branches in studies of plant capacitance, since it may be important to the magnitude of time-lags between peak flows in branches and stems. Some studies that measured flows in upper branches and at the stem bases do describe how branches were selected: for example, Zweifel and Hasler (2001) positioned three sap flow velocity sensors at 1.5, 6 and 14 m on the south side of a tree, but did not explicitly discuss these results in the context of plant capacitance. Hubbard et al. (2002) measured flows in upper (25 m) versus lower (10 m) branches of *Pinus ponderosa* and chose branches that "received full sunlight for the longest part of the day". These authors did not find evidence of a time-lag between upper and lower branches of open and well illuminated *Pinus ponderosa* crowns (see above) but did not measure flows at the stem-base. They concluded from other studies (see references within) that capacitance "did not affect diurnal patterns of sap flux in ponderosa pine at our study site". Steinberg et al. (1990) measured northern and southern branches of a 5-year-old pecan tree (see above) and found that sap flow began simultaneously in the trunk and branches, indicating a lack of capacitance in a tree of this age. Martin et al. (2001) measured sap flow in two branches at 33 m and two branches at 25 m and although not described in their methods, from their results (see above) we can deduce that east and west-facing branches were selected. However, when it comes to comparing flows between the stem and 'branches', there is no mention of which branches, or averages of branches were used. These authors found that lagging 'branch' data by 30 min improved the correlation with flows in the stem-base, but only by 1%.

The aforementioned demonstrate that the majority of studies that do describe which branches were measured *do not* provide evidence for significant time-lags in flows between stem-base and branches resulting from capacitance. One exception is a study by Steppe et al. (2002) who measured sap flow in three branches of a 27 m tall beech tree at three

different heights (9, 16 and 22 m) and three different aspects (North, West and South, respectively). A single sensor was also placed on the north side of the stem. These authors used the opportunity afforded by a solar eclipse to detect lags in flow between stem and branches. There was a 10-min difference in the resumption of sap flow following the eclipse between the 22 m (south) branch and the stem. For reference, the eclipse was on a summer morning (10:25 A.M.), when the sun would be in the southeastern sky.

Many other studies make no mention of efforts to control for or explicitly record branch position within the crown relative to illumination patterns. Some of these studies do provide evidence of flow lags and others do not. For example, although Ewers and Oren (2000) accounted for circumferential variation in stems by measuring in north and south orientations, no mention is made of where branches were sampled from (either height or aspect, simply: "...in upper branches of 6–12 mm diameter and lower branches of 12–18 mm diameter"). These authors state, that "the use of [sap flow measurements] in branches is justified when the branches are considered to represent the entire crown and store negligible amounts of water". However, their study did not provide information on how branches might be sampled in a way that represents the entire crown. Whatever branches that were sampled did not demonstrate a time-lag between stem and branch sap flow.

In similar fashion, Chapotin et al. (2006) measured sap flow in branches and at the base of baobab trees, which are traditionally thought of as water storing trees, in order to estimate plant capacitance. Once again, selection of branches was simply "distal branches (8–13 cm in diameter)". Again these authors found no time lag between stem and branch sap flow.

Goldstein et al. (1998) made measurements on 3–4 'exposed branches' in the upper crown, but again controlled only for variation at the base of the tree by measuring sap flow on opposite sides of each tree. These authors found lags between the onset of sap flow at the base of the tree and in branches of between 0.1 and 1 h, depending on the individual. Lags between the attainment of peak flow rate in stems and branches were 1–5 h. In a study by Phillips et al. (2001), sap flow sensors were installed "in upper canopy branches in 7 of the 16 stem-measured trees". A large range in time lags was observed among the five species investigated by these authors, ranging

from no lag to a lag of 90 min. There were also large differences between individuals of the same species, e.g. 35 min versus 90 min. Interestingly, Phillips et al. (2001) found no relationship between flow lags and the distance between sensors placed in stems and branches. Once again in Phillips et al. (2003) we read "Sap flux sensors were installed in boles and upper branches of trees. Exposed upper branches were chosen to be representative of upper-crown flux." However, there is no record of how branches were surveyed to verify consistent patterns "indicating a fairly uniform temporal pattern of within-crown flux for comparison with the time series of bole flux." Because we are not told how they selected branches, this uniformity might be by proximity and not necessarily represent the whole crown. These authors did not explicitly report flow lags, but a visual appraisal of their graphed results suggests lags in peak flow of approx. 1–3 h.

We find similar limitations in the methodological description of Meinzer (2003) – "sap flow measured... in four to six branches in the crown of each tree" – and Meinzer et al. (2004b) – "mean sap flow of three to five branches". In both instances these measurements were assumed to represent crown transpiration as a whole (but see below).

One notably different study among those comparing branch and stem base sap flow was that of Steppe and Lemeur (2004), which was performed in a controlled environment growth chamber. Here, the use of static fluorescent lamps eliminated any diurnal changes to relative illuminance among branches of a 2-year-old beech tree. These authors found a 20 min lag between the time taken for sap flow measured with heat balance collars to reach 63% of daytime average in a branch versus the stem base. An anonymous reviewer has suggested that more detailed analysis of heat storage was required for this experiment and our discussion on heat storage below is cautionary. It is also worth pointing out that this experiment used a very small (1.3 m) tree, placing these results in a different category to the majority of other capacitance studies.

Why measuring lags in peak flow to estimate capacitance is dangerous

It is clear that during the morning when the sun illuminates east-facing branches, but renders west-

facing branches comparatively shaded, one could imagine, say, 80% of water flux being apportioned to east-facing branches and 20% apportioned to west-facing branches. This situation could then reverse with afternoon westerly sun, and neither the peaks in west-facing or east-facing branches would correspond with the timing of peak flux in the main stem. So whilst peak flows will occur at different times in different branches, the peak flow in the main stem will be a composite of all branches, presumably peaking when the maximum amount of foliage is lit by the maximum amount of sunlight (water stress and stomatal closure notwithstanding).

In addition to self-shading effects on sap flow patterns in branches on different sides of a tree, it also becomes apparent that 'upper' or 'distal' or 'exposed' branches within contiguous forest are illuminated by early morning sun (low solar angle) while their counterparts in the canopy remain shaded (this is not the case in the open forests such as studied by Hubbard et al. 2002). Later in the day when more branches become illuminated and compete with upper branches for water, and when crown water potential as a whole is reduced, the rate of flux through the upper branches may diminish somewhat. In other words, the timing of peak flux in upper branches may occur during a period of 'privileged' illumination and optimal water status and not match the peak flux in the stem occurring in response to the bulk of foliage being illuminated. One can see the dangers of using one set of branches to represent the entire crown and then making comparisons with flow at the stem base. Owing to a 'dilution effect' a small number of well-illuminated branches can increase to maximum transpiration rate without causing flow rates at the stem base to change by more than a few percent. To illustrate with numbers, if 10% of a crown's branches are illuminated by early morning sun such that their transpiration rate doubles, flows in the stem, which include slow flows to the remaining 90% of shaded branches, will only increase by ~10%. Consideration must be given to the pattern of illumination of the branches being measured in relation to the overall pattern of whole crown illuminance (which may also vary with season, phenology, etc). Except in the case of Steppe and Lemeur (2004) cited above, where the light source did not move, we suggest that a considerable portion of the variation in flow lags among and within species (e.g. 0.1–1 h reported by

Goldstein et al. 1998, 0–90 min reported by Phillips et al. 2001) could be due to variable illumination patterns of the individual branches, or cohorts of branches measured.

Lags in the onset of transpiration: a suitable metric for investigating capacitance?

We have theoretical objections to the idea that capacitance can cause absolute lags in onset of transpirational flow between the stem base and upper branches of a tree: these are based on our understanding of the cohesion-tension model. Any capacitor along the root-leaf tip continuum is hydraulically coupled to the transport pathway. Indeed there is a continuum of 'capacitors' spanning the length of the xylem transport pathway and all are connected to the main transport pathway by cohesion–tension – if they were not, they could neither be filled nor depleted. At steady state – following refilling and before the onset of transpiration – these capacitors are in hydraulic equilibrium with the rest of the water column. As transpiration starts in the upper crown, water may be sourced either from the main (axial) water column or the capacitors located along it, depending upon the resistance to flow from these two water sources and the way their water potential changes with depletion. If any water is extracted from a capacitor, its water potential will be lowered. Two things follow: (1) there will be an immediate tendency for this capacitor to be refilled from the main water column and (2) until this occurs, the 'competitiveness' of this source relative to the main water column is reduced. Water may now be extracted preferentially from the water column and, as flow induces frictional losses to water potential along this transport gradient, the competitiveness of this source will be reduced. Our simplification here has these water sources being arbitrated in binary fashion, but in reality, these processes occur simultaneously in a dynamic equilibrium-competition between sources and sinks, all inescapably coupled by cohesion-tension. The main point in this is that any depletion of a capacitor within a plant will instantaneously initiate water movement from the soil either by commencing refilling of the capacitor or becoming a competitive source for water. Even if there is a cascade of capacitors along the water column acting in this way, the idea of continuity among sources and sinks holds true. Ideas of 'threshold resistances' that

would lead to a binary or sequential arbitration of water sources are in our view beyond the cohesion-tension model; the closest we have perhaps are the asymptotic water release functions of sapwood described by Meinzer (2003), but here the threshold is to further depletion rather than at its commencement. We believe, based on theory, that there are no absolute flow lags within a plant, even if some of the corresponding flows are below the scrutiny of our observations. Although reporting of absolute flow lags is a limited practice in the literature, we can see that the idea has nevertheless taken root from the study of Chapotin et al. (2006) which opens with the report "We found no lag in the daily onset of sap flow between the base and the crown of the tree".

Where absolute lags in the onset of transpirational flow between upper branches have been reported, it is usually using the thermal dissipation sap flow technique. Given the difficulties in determining zero flow with this technique (Lu et al. 2004), we believe that the cohesion-tension model would predict that more careful determination of zero flow would demonstrate small flows at the stem base commencing simultaneously with flows in the branches. Although these flows may be small owing to the 'dilution effect' we mentioned above, or due to capacitance, they should be recognised for the sake of consistency with the cohesion-tension theory.

Our own limited data comparing flow rates in stems in the upper crown and at the stem base do not suggest significant lags in onset of flow between these parts of the transport pathway, some 60-80 m apart. However, we did not cut the xylem to establish an accurate zero reference for our data as suggested by Burgess et al. (2001). Careful calibration of zero flow and an assessment of night-time transpiration dynamics (Dawson et al. 2007) will be needed to confirm that flows indeed start simultaneously within the continuous water transport-storage system. For the thermal dissipation method, values for δT_{max} (zero reference) can vary nightly and seasonally depending on thermal contact between the probe and wood, wood moisture content and night-time transpiration (Do and Rocheteau 2002).

A note on method selection for capacitance studies

Finally we come to the question of which methods are most suited to studies of capacitance. We desire to make our critique of current practice constructive, motivated by a desire for increasing clarity in our understanding of plant function. We certainly do not wish to throw stones at other researcher's methods, when we ourselves are currently back in the glasshouse improving the shortcomings of our own techniques at higher flow rates. But we would like to make two important points concerning constant heating methods such as the thermal dissipation technique or heat balance technique. First, thermal gradients can potentially alter the diurnal pattern of sap flow by augmenting or reducing apparent flow rates depending on the direction of the thermal gradient (Do and Rocheteau 2002). Determining and correcting thermal gradients that underlie constantly heated tissue requires considerable rigor, but which is likely to bear fruit in improving our estimates of plant capacitance; the differences in thermal regimes of branches and stems may also warrant investigation. Secondly, and more seriously, constant heating methods suffer the effects of heat storage or capacitance that delays the response of the sensor. Constant heating causes heat to build up in wood tissues and it takes a considerable amount of time for xylem sap flow to "wash" the heat from tissues such that the sensor can respond with the correct quasi-steady state reading for the particular flow rate. Where flow rates are calculated from running 30-min averages, the earlier samples in this period will suffer considerable carry-over or 'memory effect' as sensor temperatures re-equilibrate. The result is serious time lags in changes to sensor output in response to changes in sap flow rate. Ongoing work using a numerical model originally written by CR Beverly to study heat pulse sensors (based on the work of Swanson and Whitfield 1981) and modified to study thermal dissipation probes shows considerable lags (sometimes >1 h during slow flows, unpublished data) in correct sensor response following changes to imposed sap flow rate. Heated probes surrounded by heated tissue simply take considerable time to cool down or reheat again as flow rates alter the amount of heat transported away from the sensor. For this reason we suggest that results from constant heating methods that include heat capacitance behaviour should be given careful scrutiny. Further modeled and experimental investigation of the thermal lag-behaviour of constant-heating methods is warranted before estimates of water capacitance-induced lags made with these

methods are made definitive. There may be further methodological refinement from such work including adoption of cyclic heating regimes (Do and Rocheteau 2002) or reductions in heater power settings to minimise heat buildup.

Conclusions

1) Patterns of branch sap flow vary widely within tree crowns, largely due to the timing of illumination of foliage as the sun moves from the east, to overhead, and then to the west over the course of a day. This can have a confounding effect on measurement of lags in peak flow between branches and stems, and this has generally not been accounted for in studies of plant capacitance to date.

2) The cohesion-tension theory predicts that flows will commence in all parts of a plant simultaneously at the onset of transpiration. Absolute lags in the onset of flow between branches and stems should not occur because there is no 'threshold resistance' in the arbitration of different water sources. Careful determination of zero flow (e.g. by cutting xylem) is needed to detect the immediate response at the stem base to capacitor discharge higher in the tree. Although such flows may be small, their documentation will lend support to the cohesion-tension theory of water transport in plants and avoid propagation of inaccurate descriptions of internal competition for water within large plants.

3) The fact that studies on some trees, including one of the most likely candidates for significant capacitance (baobab), and some of the largest trees (*Sequioa sempervirens* and *Sequioadendron giganteum*), have not recorded flow lags with sap flow techniques raises the possibility of plausible doubt concerning the magnitudes of some of the flow lags so far recorded in this field of study; if not, then there are interesting questions as to why lags are found in some trees and not others. Studies in controlled conditions such as that of Steppe and Lemeur (2004) or strategies to account for the differences in flow patterns in different crown positions under field conditions are required. In addition, added rigor in the application of sap flow techniques is needed, with caution in using methods that themselves exhibit 'flow lags'

due to heat storage effects. Given that estimates stored water usage can range from 2–25% (e.g. Phillips et al. 2003), an analysis of the relative errors from sources such as radial variation, heat storage, etc. will be a useful inclusion. We believe these approaches will help build a better grounding for our understanding of how capacitance functions in large plants: it is perhaps not quite time to write the textbooks yet.

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