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COMMENTARY

Using branch and basal trunk sap flow measurements to estimate whole-plant water capacitance: comment on Burgess and Dawson (2008)

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Abstract Sap flow sensors are uniquely able to continuously monitor whole tree physiology. Recently, Burgess and Dawson (Burgess SSO, Dawson TE, Plant Soil 305:5–13, 2008) urged caution in using sap flow probes to estimate water storage use in trees. Here we respond to three criticisms raised there: (1) Sampling: that tree water storage, estimated from branch-bole sap flow lags, was compromised by unaccounted variation in branch position and orientation; (2) Instrumentation: that sap flow sensor response times may be sensor artefacts rather than manifestations of tree water storage; and (3) Theory: that tree water storage estimates are based on a faulty concept of lag phenomena in sap flow that persists in the literature. We agree with the need for caution in sap flow-based estimates of plant water storage, but here correct flaws in arguments and representations of studies presented in Burgess and Dawson (Burgess SSO, Dawson TE, Plant Soil 305:5–13, 2008).

Keywords Branch sap flow · Capacitance · Cohesion-tension theory · Flow lags · Heat balance gauge · Heat pulse · Heat storage · Stem water storage · Thermal dissipation probe · Water transport

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Introduction

Sap flow sensors are uniquely able to continuously monitor whole tree physiology. Recently, Burgess and Dawson (2008) urged caution in using sap flow probes to estimate water storage use in trees. Here we respond to three criticisms raised there: (1) *Sampling*: that tree water storage, estimated from branch-bole sap flow lags, was compromised by unaccounted variation in branch position and orientation; (2) *Instrumentation*: that sap flow sensor response times may be sensor artefacts rather than manifestations of tree water storage; and (3) *Theory*: that tree water storage estimates are based on a faulty concept of lag phenomena in sap flow that persists in the literature.

We agree with the need for caution in sap flow-based estimates of plant water storage, but wish to correct flaws in arguments and representations of studies presented in Burgess and Dawson (2008). Thus, we (1) describe how sap flow sensors are used to estimate tree water storage and capacitance; (2) show that the objectives of Burgess and Dawson (2008) differed diametrically from those of the studies they criticized, rendering comparisons between these studies inappropriate; (3) contend that it is premature to attribute sap flow lags to sensor artefacts before they have been demonstrated; (4) clarify that tree water storage estimates from sap flow are not predicated on the presence of "absolute" sap flow lags; and (5) demonstrate that capacitance estimates based on thermal dissipation probes (TDP) are consistent with capacitance estimates from independent techniques.

Tree water storage and its estimation using sap flow sensors

Stored water in trees can be expressed in units of volume (e.g. litres) or mass (e.g. kg). Capacitance is defined as the change in water content per unit change in water potential (e.g. kg MPa^{-1}), of a tissue, organ, or organism. While water storage and capacitance are closely related and sometimes used interchangeably, they are different quantities and carry different units. The paper by Burgess and Dawson (2008) and this paper focus specifically on tree water storage.

To the extent that trees use and refill internal stores of water on a 24-h basis, integrated crown sap flow should peak and decline earlier in the day than bole sap flow; these time series patterns form the basis for using sap flow sensors to estimate tree water storage. Simple hydraulic resistance–capacitance models of trees illustrate the expected time series (Fig. 1; Nobel 1970; Sheriff 1973; Hunt, Running and Federer 1991; Jones 1992; Phillips et al. 2004). Here all diurnal use of stored water to support transpiration is assumed to be replaced during a 24-h period, so that the integrals under the curves in Fig. 1 equal one another (although this may not always be a reasonable assumption; Waring and Running 1978; Phillips et al. 2003). When, at any point in time, crown flux exceeds bole flux, stored water is withdrawn from tissues between the two portions of the tree; conversely, when, later in the day, bole flux exceeds crown flux, net recharge of stored water occurs. The integrated difference in these two curves during either the withdrawal or recharge phases represents the amount of stored water that was used and replenished over a 24-h period of time. This value can be compared to the integrated 24-h water flux to represent the percent of daily water used that is drawn from and recharged to storage (e.g. Goldstein et al. 1998; Phillips et al. 2003).

The large size and complex architecture of real trees makes it difficult to account for all, or even most of, the instantaneous flows of water into, through, and out of the tree. Thus, studies that attempt to use sap flow to estimate tree water storage by examining

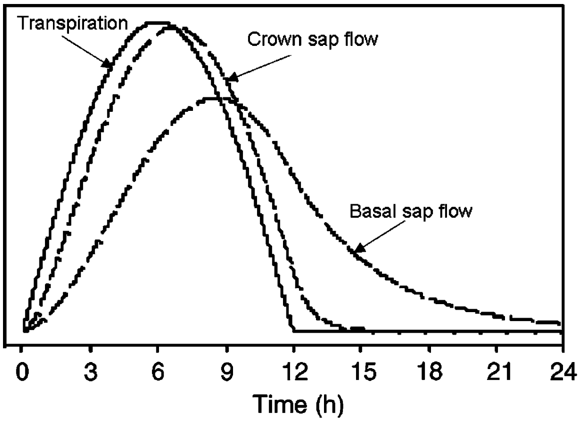

Fig. 1 Idealized time courses of transpiration (*solid curve*), crown sap flow (*dashed curve slightly to the right of transpiration*), and basal sap flow (*dashed curve farther to the right*). The time axis represents time of commencement of transpiration and sap fluxes, not time of day. Assumptions and interpretations of these curves are discussed in the text and Phillips et al. (2004)

differences in instantaneous fluxes into and out of trees identify and use branches and bole locations that are assumed to represent integrated crown or bole sap flux. One of the key concerns raised in Burgess and Dawson (2008) is that the representativity of branches used to estimate whole tree water storage has not been demonstrated or described clearly in many studies.

Sampling: branch selection/position/orientation

Burgess and Dawson (2008) suggest that studies of tree water storage based on lags between branch and bole sap flow (e.g. Goldstein et al. 1998; Phillips et al. 1999; Meinzer et al. 2003, 2004, 2008; Phillips et al. 2003; Cermak et al. 2007) are compromised by insufficient consideration of the positions and orientations of branches. They use data from two branches in each of two trees to illustrate potential errors due to variation in branch sap flow. We acknowledge that descriptions of branch position and orientation in previous studies have not been precise. However, precise specification of branch spatiality would involve far more that specified in Burgess and Dawson (2008). Indeed, it is fair to argue that we must go further than Burgess and Dawson's caution to include height and aspect when describing branch position, since the situation involves far more than these simple details. In trees with a decurrent branching structure, like those described in Goldstein et al. (1998), Phillips et al. (1999), and Meinzer et al. (2003, 2004, 2008), branches point more 'up' from a complex branch network than 'out' of a vertical bole, have an umbrella-like display, and form part of a relatively shallow upper canopy layer. Moreover, upper, exposed branches of old growth conifers, such as those studied in Phillips et al. (2003), can assume a decurrent form as a result of reiterative branching. To attempt to simply specify a branch height and direction in such cases would neither be useful nor possible, and would provide a false impression of precision.

In architecturally complex trees, precise specification of branch position and orientation, if deemed necessary for sap flow studies, would involve much more information than is implied by the simple height and direction metrics (e.g. "53 m E") described in Burgess and Dawson (2008). This would include branch order, branch path length, three dimensional coordinates of daughter–parent branch attachment (and the connectivity of the parent branches ultimately to the main bole), specification of branch "direction" (not limited to cardinal directions for branches with vertical orientation, and accounting for branch tortuosity), and the distribution and orientation of branch foliage. Commensurate with this level of detail, specification of branch microclimate—perhaps even within-branch variation in microclimate (e.g. for branches studied in Burgess and Dawson (2008) that were the size of small trees and of unspecified length)—would be needed, as well as precise positions of any neighbouring branch foliage and trees. In lieu of this precise detail, and at the expense of exact repeatability of studies, we have judged it reasonable to describe branch exposure in more general terms.

Notwithstanding that all tree branches are not as simply described as in Burgess and Dawson (2008), if a study's objective is specifically to *emphasize* branch variability, selecting the likely most different branches is a simple matter. Burgess and Dawson (2008) clearly chose branches to emphasize how the position and orientation of branches can be expected to lead to dramatically different diel time series of sap flux among branches, whereas the sampling strategy of the other studies cited was motivated by exactly the opposite goal, to choose branches that were *not* obviously prone to highly idiosyncratic or systematic direction-by-time light exposure. Ironically, while Burgess and Dawson (2008) specify the height and direction of the four branches used in their study and note their vertical positions within crowns, they do not describe in general terms how exposed the branches were to sky conditions (i.e. whether there were other branches, trees, or terrain that obscured branches from the sky during the course of the diurnal solar trajectory). The kind of descriptive language that was criticized in Burgess and Dawson (2008) would in fact have been of value in their study.

A careful reading of papers cited in Burgess and Dawson (2008) shows that in spite of limited sampling, there was recognition of and attempts to assess branch variability, to a greater degree than indicated in Burgess and Dawson (2008). For example, Goldstein et al. (1998) states that "…the crowns of the study trees were relatively shallow and well represented by the three to four upper branches…" and "previous measurements indicated…the magnitude and diurnal course of sap flow in the upper and lower crown were similar" (Goldstein et al. 1998). In another study (Phillips et al. 2003) cited in Burgess and Dawson (2008) with their comment "…*there is no record of how branches were surveyed to verify consistent patterns [in sap flow]*…", correlation coefficients close to unity were, in fact, reported for the diurnal time courses of sap flow among different branches. Finally, Phillips et al. 1999 stated clearly that variable branch microclimate likely played an important role in the diel pattern of branch sap flow, and in fact made no estimates of tree water storage based on sap flow data. Thus, this paper was grouped together with other studies in a blanket criticism, for estimates that it never made. Phillips et al. (1999, p. 122) also described the "dilution effect" that Burgess and Dawson (2008) present as an unrecognized consideration. Thus, issues of variability in branch sap flow were not ignored or unrecognized in the papers cited by Burgess and Dawson (2008), but these qualifying comments were not included in their critique.

Ultimately, most investigators who have published branch sap flow data, would agree that the numbers of replicate branches monitored in those studies vastly under-characterizes the full within-crown variability in sap flow and gas exchange (Leverenz et al. 1982). Moreover, all would agree that tree hydraulic systems are more complex than can be characterized by simple Ohm's law or resistance–capacitance circuit analogies (van den Honert 1948; Richter 1973, Sheriff 1973; Phillips et al. 2004). Yet, studies of additional species continue to show appreciable branch-bole sap flow lags (e.g. Fig. 6 in Meinzer et al. 2008). A relevant question is whether such large within-crown variability should preclude researchers from studying and publishing branch-bole sap flow lags altogether. We believe that, in spite of substantial sampling limitations, and not always consistent results (e.g. compare results of Goldstein et al. 1998 with those of Phillips et al. 1999) important features of tree hydraulics have been uncovered using branch-bole sap flow lags, such as relationships between tropical tree size, sapwood volume and water storage (Goldstein et al. 1998). These results would be difficult to accept as resulting from the sheer chance that idiosyncratic branch-bole sap flow lags happened to correlate with independent metrics of tree size. Moreover, as we show in further detail below, direct comparisons of independent tissue-level measures of sapwood capacitance with results obtained from branch-bole sap flow lags yield compatible conclusions concerning the impact of capacitance on whole-tree water relations (e.g. Fig. 6 in Meinzer et al. 2003).

Instrumentation: built-in sensor time lags

In describing how TDP or Tissue Heat Balance (THB) sap flow sensors contain a built-in thermal time lag, Burgess and Dawson (2008) do not present direct evidence, but rather refer to modelling results from an unpublished study. Although their explanation for a thermal time lag is plausible, reasonable, and perhaps ultimately correct, it is premature to explain apparent lags in the onset of sap flow based on an as-yet undemonstrated characteristic of TDP or THB sap flow probes. One study (Tatarinov et al. 2005) modelled the dynamics of heat pulses in TDP sensors and found that sensors approached stable temperatures in about 1 min after heat was applied to sensors, with slightly faster response at higher flow rates. However, this study did not evaluate the dynamics of sensor response to imposed changes in sap flow rate and thus its direct relevance to the assertion of Burgess and Dawson (2008) is not clear. Another study (Do and Rochetau 2002, their Fig. 1) showed that the time to "wash" the heat transferred to the tissues by TDP sensors under very low or zero flow conditions (i.e. without the contribution of substantial xylem sap flow) in natural and artificial stems is much shorter than the times suggested in Burgess and Dawson (2008). This would indicate that TDP sensors can generate an adequate temporal response to account for the rapid temperature dynamics associated with changes in xylem sap flow in the onset of sap flow at any point in a tree. The assertion of a built-in thermal lag in THB sensors is also inconsistent with fast responses of sap flux to atmospheric turbulence found in Hollinger et al. (1994). Therefore, to support a claim of a built-in sensor time lag, there is a need for these investigators or others to present the mechanistic model and experimental evidence that can be used to quantify sensor time lags independently from hydraulic time lags. Experiments should begin in a laboratory setting using artificial porous media *without* hydraulic capacitance; and then proceed to real plants wherein effects of sensor time lag can be de-convolved from genuine hydrodynamic response times.

Theory: "absolute" time lags

Burgess and Dawson (2008) imply that observed absences of "absolute" lags in their sap flow data and that of others (e.g. Chapotin et al. 2006) indicates lack of capacitance (e.g. their third conclusion). We disagree with this interpretation. Hydraulic capacitance buffers a change in flow and tension in the xylem by increasing the time required for a response to a perturbation to be completed. The onset of the response at any two points may be effectively simultaneous with the perturbation, but the capacitor dampens the rate of the response (Phillips et al. 2004). A cross-correlation analysis may show a 'lagged' response, but this does not mean that there was a lag in time of initial response.

While the theory section of Burgess and Dawson (2008, pp 10–11) appears to be compatible with our view, we are concerned with two specific inferences made in Burgess and Dawson (2008) that link apparent absolute lags, or their absence, to estimates of capacitance. First, Burgess and Dawson (2008) state that where absolute lags are observed, they are usually observed using thermal dissipation probes. Burgess and Dawson (2008) thereafter suggest that lags arise in thermal dissipation probes due to sensor artefacts, so this statement in our view sets up a contrast between theory and suggested but undocumented instrumentation problems. Second, even though we accept that Burgess and Dawson (2008) only intended 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", they nevertheless highlight the absence of such theoretically non-existent lags as evidence for lack of capacitance (their conclusion #3). Thus, Burgess and Dawson (2008) suggest that (1) absolute sap flow lags cannot exist (which, strictly speaking, we agree with), and (2) that their absence indicates lack of capacitance (their conclusion #3, with which we don't agree).

For example, there is little or no apparent lag in the commencement of sap flux between upper branches and boles of large or small *Psuedotsuga menziesii* or *Quercus garryana* trees shown in Phillips et al. (2003), but sap flow nevertheless peaks and declines earlier in branches or upper stems compared to boles, so that there is a lag between the two time series when they are considered in whole. Similarly, tree sap flow data presented in Goldstein et al. (1998) shows that an "absolute" lag in morning sap flow is not a required feature of trees that show sap flow dynamics consistent with the presence of substantial diel water storage extraction and recharge. Branch sap flux can have a very different characteristic response time or time constant than bole sap flux, while not exhibiting a detectable lag in commencement of sap flux.

It is not clear to what extent sap flow lags can be interpreted to indicate whole tree water storage from the lower and upper bole sap flux data shown in Burgess and Dawson (2008). This is due to at least three substantial sources of uncertainty. First, there is considerable uncertainty about circumferential and radial variation in sap flux, especially in these trees which are some of the largest in the world. Second, there is a questionable degree of hydraulic segmentation along very long bole lengths that seems to have been assumed (i.e. the eastern side of the bole at 57 m is apparently assumed to be more hydraulically linked to the eastern side of the bole at stem base than to other sides of the bole, in spite of potential spiral flow patterns and lateral integration of xylem water (Vité and Rudinsky 1959; Gartner 1995; Tyree and Zimmermann 2002)). Finally, the amounts, distribution, and activities of leaf area and evaporative demand above and below the upper bole sensor positions are not described, even in general terms. These are typical limitations of sap flow studies (including the ones cited above), but because the data in Burgess and Dawson (2008) are used to criticize the limitations of other studies, it is important to note that these data are not exempt from those criticisms either. However, to the degree that these data are used to argue for a lack of capacitance in large redwoods, the very same data could be presented to show, at least in one of the two trees, substantial capacitance. If the data shown in their Fig. 1b were normalized so that the 24-h integral of crown flux matched the 24-h integral of bole flux (Goldstein et al. 1998), these data would indicate a morning period of storage extraction and some recharge in the afternoon. Whether or not such a normalization procedure is more or less justified for the purposes of time series interpretation than the normalization procedure used in Burgess and Dawson (2008) is debatable. We do not suggest that normalizing the limited data presented in Burgess and Dawson (2008) is sufficient to estimate tree capacitance, just as we do not agree that the data they show supports their claim of lack of capacitance. We simply contend that the data presented above are too limited to make any, or preclude any, interpretations related to capacitance. In any case, whether or not there is simultaneously commencing flux in the boles and crowns of redwoods in the morning does not necessarily indicate whether or not redwoods have substantial capacitance.

It is not surprising that some large trees could have relatively small hydraulic time constants while small plants could have relatively large time constants (Hunt et al. 1991, Phillips et al. 1997). Diverse plant forms can have any combination of (a) large hydraulic resistance and large hydraulic capacitance (e.g. tall tropical trees); (b) small resistance and small capacitance (e.g. young phreatophytes); (c) large resistance and small capacitance (e.g. desert shrubs); or (d) small resistance and large capacitance (e.g. desert succulents). Because a plant's characteristic hydraulic response time is a product of effective hydraulic resistance and capacitance, plants may show a variety of hydraulic response times based on different underlying mechanisms and adaptations.

Although Burgess and Dawson (2008) question the concept of lags in the onset or peak of transpiration as a suitable metric for investigating water storage, they do not explain what *does* constitute a suitable metric for investigating water storage based on sap flow. That is, if sap flow could be measured with complete coverage and perfect accuracy in boles and crowns (or, in a simpler case, between two bole locations with no intervening leaf area), what is the appropriate lag analysis for estimating water storage? Conceptually, an answer to this question is illustrated in Fig. 1. Lags exist between entire time series, and entire time series of flow should be compared with each other throughout a time interval of interest (e.g. 24 h). Burgess and Dawson (2008) focus on lags in the onset of flux, and separately on lags in peak flow, but a suitable metric for investigating water storage is the integrated difference in sap fluxes between entire time series. When this procedure was applied to tropical trees, differences between integrated 24-h time courses of branch and bole sap flow were never significantly different from zero, consistent with no net withdrawal of water from storage over 24-h cycles (Goldstein et al. 1998; Meinzer et al. 2004).

Heat dissipation versus heat pulse and estimates of capacitance using non-sap flow-based methods

Burgess and Dawson (2008) assert that heat pulse sap flow methods hold an advantage over other sap flow methods in evaluating sap flow lags associated with tree water storage. However, measurements in trees with crown properties that are ideal for water storage estimation indicate that the heat dissipation and heat pulse methods provide comparable results (Bucci et al. 2005). Brazilian savanna (Cerrado) trees are ideal for estimating capacitance based on sap flow measurements because they are isolated; the crowns of adjacent trees do not overlap; and the leaf area index is very low, resulting in minimal self-shading. Figure 2a shows diurnal courses of sap flow in Cerrado trees measured at the end of the dry season of 2004 using a heat pulse technique (Burgess et al. 1998; Scholz et al 2002) at the base of the main stem and in terminal branches of a dominant savanna tree species. Use and recharge of stored water determined from the difference between crown and basal sap flow indicated that stored water utilization increased shortly after sunrise, peaked at about 9:00 h and ceased before midday (Fig. 2b). This daily time course of stem water utilization and recharge is similar to those obtained using heat dissipation probes (e.g. Goldstein et al. 1998; Meinzer et al. 2004).

Although Burgess and Dawson (2008) imply that reliance on internal water storage by vegetation is generally overestimated due to instrumentation artefacts, there is a large body of research demonstrating substantial plant and tree capacitance using techniques other than sap flow (e.g. Klepper et al. 1971; Molz and Klepper 1972; Hellkvist et al. 1974; Hinckley and Bruckerhoff 1975; Waring and Running 1978; Waring et al. 1978; Goldstein et al. 1984; Tyree and Yang 1990; Holbrook and Sinclair 1992; Irvine and Grace 1997; Stratton et al. 2000; Sevanto et al. 2002; Meinzer et al. 2003, 2006, 2008; Cermak et al. 2007; Scholz et al. 2007, 2008; Sevanto et al. 2008) that must be reconciled to their view.

More directly relevant to the concerns expressed in Burgess and Dawson (2008), independent techniques have increasingly been used *in conjunction with* sap flow measurements to quantify plant capacitance, and have shown mutually consistent results. One of the widest-ranging studies to date of biophysical properties of stem water storage tissue in trees found a

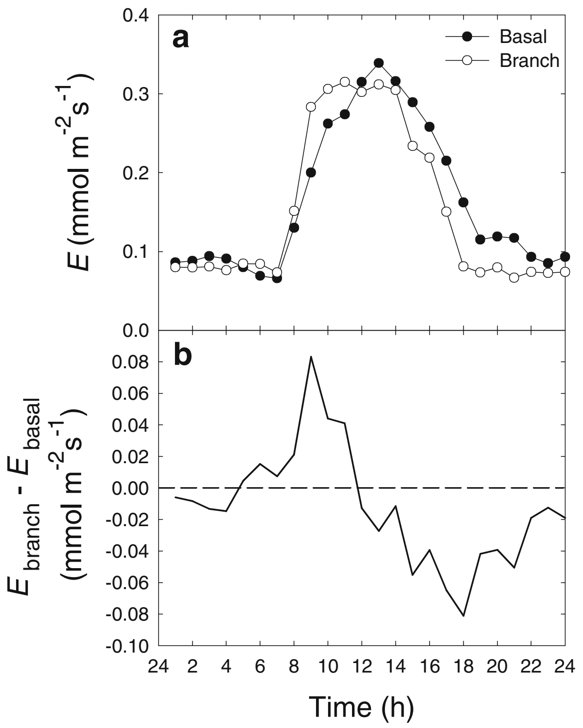

Fig. 2 **a** Representative daily courses of transpiration (*E*) estimated from terminal branch sapflow (*open circles*) and from basal sapflow (*closed circles*) measured with heat pulse probes. **b** Difference between branch and basal transpiration on the same day (August 24, 2004) as in panel **a**, in one individual of *Ouratea hexasperma*, a dominant woody species with low leaf area index of Cerrado savanna in central Brazil. Positive values indicate time periods when a fraction of transpired water was withdrawn from internal water storage, and negative values indicate time periods when water from the soil was refilling stem storage. Heat pulse systems (single point sensors) were placed at the same depth below the cambium at the base (6.1 cm basal diameter) and in a terminal branch (3.1 cm^2 sapwood area). Transpiration was obtained by dividing volumetric sap flow by the total leaf area per plant or per branch

strong positive relationship between midday leaf water potential and species-specific sapwood capacitance, consistent with the buffering influence of internal water storage (Scholz et al. 2007). This study evaluated capacitance properties in *eight* co-occuring tree species. The slopes of the initial linear portions of water released per unit volume of xylem and outer parenchyma tissues versus sapwood water potential (measured using thermocouple psychrometer chambers) were used to estimate species-specific capacitance values over the normal physiological operating range of tissue water potential. These psychrometric estimates of capacitance were highly correlated with branch-bole sap flow lags obtained independently (Scholz et al. 2008) (Fig. 3a). Branch and bole sap flow were measured using thermal dissipation method and the time lags were calculated by finding the highest cross correlation of time series between sap flow at the base of the tree and in terminal branches (Scholz et al. 2008). Diel changes in stem expansion and contraction (measured with electronic dendrometers) and discharge and refilling of stem water storage tissues in *six* tree species (Scholz et al. 2008) also provided information on capacitance. The sapwood exhibited small relative changes in cross-sectional area per unit change in water potential but released a substantial amount of stored water for a given change in area. Cross-sectional areas of the trunk and branches (computed from temperature-corrected diameter measurements) decreased early in the morning and the rates of change in area and lags (calculated by finding the highest cross-correlation of time series between changes in cross-sectional area at the base and in the branches) were consistent with diel variations in basal sap flow and branch sap flow (Fig. 3b; data from Scholz et al. 2008). Capacitance estimates based on measurements of variation in cross-sectional area and sap flow provided similar quantitative estimates of sapwood water storage capacity, which ranged from 16 to 31% of total 24-h water loss. Despite current controversies related to tree water uptake, transport, storage and loss, evidence has accumulated over several decades indicating that (1) selective pressures have resulted in the development of internal water storage in trees; and (2) that this may help to transiently uncouple leaf water status from the hydraulic resistance of the soil to leaf water transport pathway.

Conclusions

We are aware of limitations unique to each type of sap flow sensor discussed in Burgess and Dawson (2008). In addition to their unique capabilities, they are fragile, require high maintenance, are sensitive to environmental noise, and cannot always be deployed in numbers that adequately sample the variation in sap flow within trees. These limitations have imposed themselves on the studies criticized by Burgess and Dawson (2008) as they have on any study that has used sap flow techniques. Therefore, we welcome the

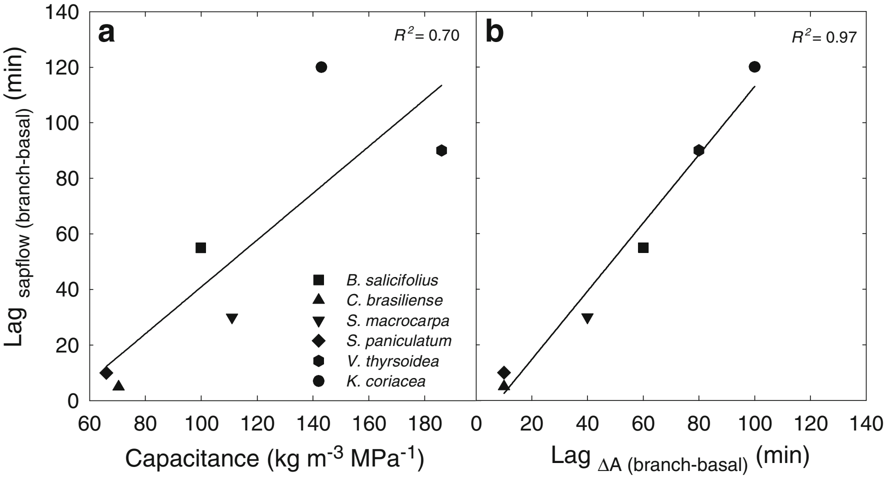

Fig. 3 The time series lag (i.e. lag corresponding to maximum correlation between time series) between branch and basal sap flow ($\mathrm{Lag}_{\mathrm{sapflow\ (branch\text{-}basal)}}$) in relation to **a** total stem capacitance (sapwood and outer parenchyma) and **b** the time series lag between branch and trunk cross-sectional area $\left(\mathrm{Lag}_{\Delta\mathrm{A(branch-basal)}}\right)$, for six dominant woody species of Neotropical savannas. Branch and bole sap flow were measured with thermal dissipation probes and branch and bole cross sectional areas (ΔA) were calculated from diameter measurements using electronic dendrometers (data from Scholz et al. 2008). Capacitance was obtained from the slopes of the initial linear portions of water released per unit volume of tissue versus tissue water potential (obtained psychrometrically) (data from Scholz et al. 2007). The lines are linear regressions fitted to the data: **a** $y=-43.4+0.8x$, $P<0.05$; **b** $y=-9.7+1.2x$, $P<0.001$. Symbols: *square Blepharocalyx salicifolius*, *triangle up Caryocar brasiliense*, *triangle down Schefflera macrocarpa*, *diamond Sclerolobium paniculatum*, *hexagon Vochysia thyrsoidea*, *circle Kielmeyera coriaceae*

note of caution advocated in Burgess and Dawson (2008), in the sense that it applies to the general use of sap flow sensors. However, we maintain that their criticism of studies of tree capacitance based on sap flow was flawed because it compared studies with very different objectives and corresponding sampling strategies. Moreover, Burgess and Dawson (2008) did not make an effective case for criticising the use of sap flow methods when they used as a basis for their arguments (1) a minimal data set of their own, with sensors that were not ‘zeroed’ (as they acknowledged); (2) suggested flaws in sensor types that were not supported with direct evidence; and (3), a mischaracterization of the role that “absolute” time lags of sap flow play in estimation of tree capacitance.

It is unfortunate that a legitimate question raised by Burgess and Dawson (2008) was diminished by a misdirected focus on sampling, instrumentation, and conceptual flaws in other studies, and an insufficient data set to support their conclusions. The authors’ central, unanswered question is how trees can utilize stored water and yet show little to no internal lags in sap flow. We have noted above how size alone is not necessarily a good predictor of tree water storage and internal sap flow lags. More fundamentally, “textbook” portrayals of trees as parallel resistance–capacitance circuits (e.g. Nobel 1970; Jones 1992) will benefit from revisions that include the realism of tension flow in porous media (e.g. Aumann and Ford 2002; Chuang et al. 2005; Perämäki et al. 2005). These models may better apply to trees cited in Burgess and Dawson (2008) that show little to no internal sap flow lags. Thus, in this clarification we do not suggest that understanding of tree hydraulic capacitance is complete. For example, we still do not understand how cavitated xylem elements can be refilled under tension, which constitutes a form of capacitive recharge.

To improve understanding of hydraulic capacitance and how it is detected, we believe that Burgess and Dawson (2008) would support us in calling for further studies of tree water storage that compare sap flow measurements with independent measures of capacitance, as in the data shown here and in other recent studies (e.g. Meinzer et al. 2006; Cermak et al. 2007; Sevanto et al. 2008). As part of these efforts, sap flow sensor inter-comparisons should be performed, backed by detailed physical models of sensor-sapwood thermodynamics. Coordinated observational and modelling studies should be targeted toward tree species that have shown substantial internal flow lags in comparison to those that have shown little to no apparent internal flow lags. Complementary research should investigate how the nature and distribution of capacitive elements in trees differs in trees showing different degrees of internal flow lags when exposed to similar environmental conditions. Trees with ideal structure for water storage study, like open grown columnar palms or the isolated, open crowns of Cerrado trees discussed here can be further targets of intensive study. If the paper by Burgess and Dawson (2008) and this clarification stimulate those efforts, our contributions may be considered constructive steps toward a firmer understanding of the nature of tree hydraulic capacitance.

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References

Aumann CA, Ford ED (2002) Modeling tree water flow as an unsaturated flow through a porous medium. J Theor Biol 219:415–429

Bucci SJ, Goldstein G, Meinzer FC, Franco AC, Campanello P, Scholz FG (2005) Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plants in Neotropical savanna trees. Trees 19:296–304

Burgess SSO, Adams MA, Turner NC, Ong CK (1998) The redistribution of soil water by tree root systems. Oecologia 115:306–311

Burgess SSO, Dawson TE (2008) Using branch and basal trunk sap flow measurements to estimate whole-plant water capacitance: a caution. Plant Soil 305:5–13

Cermak J, Kucera J, Bauerle WL, Phillips N, Hinckley TM (2007) Tree water storage and its diurnal dynamics related to sap flow and changes of stem volume in old-growth Douglas-fir trees. Tree Physiol 27:181–198

Chapotin SM, Razanameharizaka JH, Holbrook NM (2006) Water relations of baobab trees (Adansonia spp. L.) during the rainy season: does stem water buffer daily water deficits? Plant Cell Environ 29:1021–1032

Chuang YL, Oren R, Bertozzi AL, Phillips N, Katul GG (2005) The porous media model for the hydraulic system of a conifer tree: linking sap flux data to transpiration rate. Ecol Model 191:447–468

Do F, Rocheteau A (2002) Influence of natural temperature gradients on measurements of xylem sap flow with thermal dissipation probes. 2. Advantages and calibration of a noncontinuous heating system. Tree Physiol 22: 649–654

Gartner BL (1995) Patterns of xylem variation within a tree and their hydraulic and mechanical consequences Ch 6. In: Gartner BL (ed) Plant stems, physiology and functional morphology. Academic, San Diego, pp 125–148

Goldstein G, Andrade JL, Meinzer FC, Holbrook NM, Cavelier J, Jackson P, Celis A (1998) Stem water storage and diurnal patterns of water use in tropical forest canopy trees. Plant Cell Environ 21:397–406

Hellkvist J, Richards GP, Jarvis PG (1974) Vertical gradients of water potential and tissue water relations in sitka spruce trees measured with the pressure chamber. J Appl Ecol 11:637–667

Hinckley TM, Bruckerhoff DN (1975) The effects of drought on water relations and stem shrinkage of Quercus alba. Can J Bot 53:62–72

Holbrook NM, Sinclair TR (1992) Water balance in the arborescent palm, Sabal palmetto. II. Transpiration and stem water storage. Plant Cell Environ 15:401–409

Hollinger DY, Kelliher FM, Schulze E-D, Köstner BMM (1994) Coupling of tree transpiration to atmospheric turbulence. Nature 371:60–62

Hunt ER, Running SW, Federer CA (1991) Extrapolating plant water flow resistances and capacitances to regional scales. Agric For Meteorol 54:169–195

Irvine J, Grace J (1997) Continuous measurements of water tensions in the xylem of trees based on the elastic properties of wood. Planta 202:455–461

Jones HG (1992) Plants and microclimate, 2nd edn. Cambridge University Press, Cambridge, p 428

Klepper B, Browning VD, Taylor HM (1971) Stem diameter in relation to plant water status. Plant Physiol 48:683–685

Leverenz J, Deans JD, Ford ED, Jarvis PG, Milen RS, Whitehead D (1982) Systematic spatial variation of stomatal conductance in a Sitka spruce plantation. J Appl Ecol 19:835–851

Meinzer FC, James SA, Goldstein G, Woodruff D (2003) Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. Plant Cell Environ 26:1147–1155

Meinzer FC, James SA, Goldstein G (2004) Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees. Tree Physiol 24:901–909

Meinzer FC, Brooks JR, Domec JC, Gartner BL, Warren JL, Woodruff D, Bible K, Shaw DC (2006) Dynamics of water transport and storage in conifers studied with deuterium and heat tracing techniques. Plant Cell Environ 29: 105–114

Meinzer FC, Woodruff DR, Domec J C, Goldstein G, Campanello PI, Gatti MG, Villalobos-Vega R (2008) Coordination of leaf and stem water transport properties in tropical forest trees. Oecologia 156:31–41

Molz FJ, Klepper B (1972) Radial propagation of water potential in stems. Agron J 64:469–473

Nobel PS (1970) Introduction to biophysical plant physiology. Freeman, San Francisco, p 488

Perämäki M, Vesala T, Nikinmaa E (2005) Modeling the dynamics of pressure propagation and diameter variation in tree sapwood. Tree Physiol 25:1091–1099

Phillips N, Nagchaudhuri A, Oren R, Katul G (1997) Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. Trees 11:412–419

Phillips N, Oren R, Zimmermann R, Wright SJ (1999) Temporal patterns of water flux in trees and lianas in a Panamanian moist forest. Trees 14:116–123

Phillips NG, Ryan MG, Bond BJ, McDowell NG, Hinckley TM, Cermak J (2003) Reliance on stored water increases with tree size in three species in the Pacific Northwest. Tree Physiol 23:237–245

Phillips NG, Oren R, Licata J, Linder S (2004) Time series diagnosis of tree hydraulic characteristics. Tree Physiol 24:879–890

Richter H (1973) Frictional potential losses and total water potential in plants: a re-evaluation. J Exp Bot 24:983–994

Scholz FG, Bucci SJ, Goldstein G, Meinzer FC, Franco AC (2002) Hydraulic redistribution of soil water by neotropical savanna trees. Tree Physiol 22:660–612

Scholz FB, Bucci SJ, Goldstein G, Meinzer FC, Franco AC, Miralles-Wilhelm F (2007) Biophysical properties and functional significance of stem water storage tissues in Neotropical savanna trees. Plant Cell Environ 30:236–248

Scholz FG, Bucci SJ, Goldstein G, Meinzer FC, Franco AC, Miralles-Wilhelm F (2008) Temporal dynamics of stem expansion and contraction in savanna trees: withdrawal and recharge of stored water. Tree Physiol 28:469–480

Sevanto S, Vesela T, Perämäki M, Nikinmaa E (2002) Time lags for xylem and stem diameter variations in a Scots pine tree. Plant Cell Environ 25:1071–1077

Sevanto S, Nikinmaa E, Riikonen A, Daley M, Pettijohn JC, Mikkelsen TN, Phillips N, Holbrook NM (2008) Linking xylem diameter variations with sap flow measurements. Plant Soil 305:77–90

Sheriff DW (1973) Significance of the occurrence of time lags in the transmission of hydraulic shock waves through plant stems. J Exp Bot 24:796–803

Stratton L, Goldstein G, Meinzer FC (2000) Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. Plant Cell Environ 23:99–106

Tatarinov FA, Kucera J, Cienciala E (2005) The analysis of physical background of tree sap flow measurement based on thermal methods. Meas Sci Technol. 16: 1157–1169

Tyree MT, Yang S (1990) Water storage capacity of Thuja, Tsuga and Acer stems measured by dehydration isotherms: the contribution of capillary water and cavitation. Planta 182:420–426

Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap, 2nd edn. Berlin Heidelberg, New York, p 48

Van den Honert TH (1948) Water transport in plants as a catenary process. Disc Faraday Soc 3:146–153

Vité JP, Rudinsky JA (1959) The water-conducting systems in conifers and their importance to the distribution of trunk injected chemicals. Contr. Boyce Thompson Inst. 20:27–38

Waring RH, Running SW (1978) Sapwood water storage: its contribution to transpiration and effects upon the water conductance through the stems of old-growth Douglas fir. Plant Cell Environ 1:131–140

Waring RH, Whitehead D, Jarvis PJ (1978) The contribution of stored water to transpiration in Scots pine. Plant Cell Environ 2:309–317