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# Thermal-dissipation sap flow sensors may not yield consistent sap-flux estimates over multiple years

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**Abstract** Sap flow techniques, such as thermal dissipation, involve an empirically derived relationship between sap flux and the temperature differential between a heated thermocouple and a nearby reference thermocouple inserted into the sapwood. This relationship has been widely tested but mostly with newly installed sensors. Increasingly, sensors are used for extended periods. After several months, tree growth, wounding, or other changes in water flow path may impair sensor performance. To quantify changes in sensor performance over time, we installed 23 sensors (one per tree) in 16-year-old Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] and red alder (*Alnus rubra* Bong.) in the western Cascades of Oregon and measured daily average sap flux ($J_s$) from April through July 2001 and 2002. We assumed the measurements from 2001 to be unimpaired and the response of $J_s$ to vapor pressure deficit ($\delta$) to be consistent under the same edaphic conditions. Differences from this assumption were attributed to "temporal sampling errors." During the study, soil moisture ($\theta$), did not differ on similar calendar dates, yet the slope of $J_s$ versus $\delta$ decreased significantly in the second year. In 2002, $J_s$ in Douglas-fir was 45% less than in 2001; in red alder, 30% less. Variations in $\delta$ could not explain the differences. A correction for temporal sampling errors improved estimates of $J_s$ from sensors used for more than one season. Differences in temporal sampling errors between the two species reveal underlying causal mechanisms. Evidence is presented that cambial growth causes errors in Douglas-fir.

**Keywords** *Alnus rubra* · *Pseudotsuga menziesii* · Sap flux · Sapwood · Temporal sampling errors

## Introduction

How accurately can sensors record xylem sap flow over long periods? The answer to that question is unknown. Yet sensor dependability for longer than one growing season is important because, depending on the research question, measurements may cover periods from a few days to a few growing seasons. Yet most sap flow studies last for less than one growing season (e.g., Granier et al. 1996; Hogg et al. 1997; Kostner et al. 2002; Moore et al. 2004). In studies that span more than one season, inserted sensors are typically replaced with new ones at new positions on the tree (e.g., Breda and Granier 1996), apparently to avoid possible inaccuracies caused by sensor deterioration (David et al. 2004). However, in other long-term studies, the same sensors are used continually in the same place for two or more growing seasons. These experiments present significant advantages because they enable understanding how extrinsic factors affect sap flux (Lambs and Muller 2002), result in time and money savings (sensors are installed only

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once), and maintain the integrity of the experimental design without using too many sensors. The advantage of this single-installation approach is that spatial variation within the tree is excluded. Otherwise, relocated sensors may not replicate the previous location on that same tree.

The study described in this paper examines potential changes in measurements made with thermal dissipation sensors used long term (Granier 1987), although similar changes may occur in other sensor types [e.g., heat pulse (Cohen et al. 1984) or heat balance (Cermak et al. 1973; Kucera et al. 1977)], especially when inserted into a sector of the stem. The thermal dissipation method for measuring sap flow has been extensively tested, and a whole body of literature has generally found the empirical relationship of sensor signal output to actual sap flux to be robust (Clearwater et al. 1999; Granier 1987; Granier et al. 1990, 1994, 1996; McCulloh et al. 2007; Saugier et al. 1997; Smith and Allen 1996; Swanson 1994); however, newly installed sensors were used in all these investigations. Because thermal dissipation sensors are increasingly used in long-term experiments in which sensor positions do not change from one growing season to the next, it is important to understand and to quantify temporal limitations caused by localized changes.

By “temporal sampling errors,” we refer to possible changes in the magnitude of sap flow under a given set of similar whole-tree and environmental conditions as measured by the same sensors over long periods. We note, however, that these changes are not necessarily caused by sensor malfunction. Instead, wounding or air embolism may alter xylem tissue around a sensor, for example, causing a localized disruption in water flow. Tree growth may cause sensors to be buried more deeply into the sapwood, where flow rates change. Because of possible data misinterpretation, it is important to differentiate reliably between actual long-term sap-flux ($J_s$) changes and temporal sampling errors.

In some cases, abrupt changes in leaf area or canopy position may lead to large shifts in $J_s$ from 1 year to the next. Fast-growing stands may have increased $J_s$ if the ratio of leaf to sapwood area increases. Furthermore, sap flux may increase or decrease depending on the position of species in closing canopies (Phillips and Oren 2001). In other cases, independent measurements of transpiration concur with long-term measurements of sap flow. For example, Schafer et al. (2002) showed a consistent relationship between sap-flux-scaled stand transpiration and eddy covariance estimate of latent heat flux in a study that spanned 3 years. Annually, however, sap-flow-based estimates of transpiration declined relative to latent heat flux.

This paper investigates possible evidence of temporal sampling errors in two tree species. We analyzed measurements of sap flux for temporal sampling errors that spanned a 17-month period in 16-year-old Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] and red alder (*Alnus rubra* Bong.). The study allowed us to contrast a softwood species growing moderately fast with a hardwood species growing faster. The xylem anatomy of these species differs (e.g., there are no vessels in Douglas-fir). Red alder is more vulnerable to drought-induced cavitation (Bond and Kavanagh 1999) and also more likely to have winter frost embolism (Sperry et al. 1994). Sap flow rates in alder are significantly higher than in Douglas-fir (Moore et al. 2004), and the optimum soil and atmospheric water conditions for maximum transpiration differ in the two species (Bond and Kavanagh 1999; Minore 1979).

The specific objectives of this study are to (a) quantify potential temporal sampling errors in Douglas-fir and red alder, (b) compare and contrast the magnitude and pattern of temporal sampling degradation between the two species, and (c) develop a method to correct for the observed changes, if any. Evidence concerning the mechanistic basis of temporal sampling errors was provided in an independent investigation that compared radial profiles of $J_s$ in much older Douglas-fir measured with the same type of sensors under similar conditions in two consecutive years.

## Status of problem

Because the installation of sap flow sensors inevitably severs tracheids or vessels, xylem function may be altered in the immediate area around the sensor to the extent that water flow is increasingly diverted or restricted over time. A wound response may lead to filling of xylem elements with air, resin, or other exudates (Kramer and Boyer 1995), or it may promote tumor formation (Taiz and Zeiger 1991). Although the wounding caused by heat-pulse velocity sensors has been well documented (Barrett et al. 1995; Swanson and Whitfield 1981), the extent to which the thermal dissipation sensors cause wounding or are affected by wounding is unknown, especially over long periods. For example, Granier et al. (1994) attributed a reduction in $J_s$ to the mechanical damage of vessels when the bark was removed. Wood density is related to $J_s$ (Barbour and Whitehead 2003), which may change because of tissue injury. This wound response could be species specific, depending on wood anatomy properties. Traits unique to particular species, such as wood density and thermal properties, may amplify or dampen the effects of alterations or flow disruptions near the sensors, making some species more susceptible to temporal sampling errors.

During the winter season, freeze–thaw events cause xylem embolisms that are normally refilled in the trunk of most softwood and diffuse-porous species (Cochard et al. 2001; Wang et al. 1992). In ring-porous species, winter embolism is not repaired and results in severe reductions in older-tissue flow rates (Cochard and Tyree 1990; Granier et al. 1994; Wang et al. 1992). Drought promotes cavitation (Grace 1993). Xylem close to sap flow sensors may be less able to repair cavitation or embolism because its cell structure has been incised (Taiz and Zeiger 1991). It follows that poor embolism repair, however caused, and would reduce the exchange of heat between water in the xylem stream and the thermocouples of the sap flow sensor, leading to an apparent measured-flow-rate decline in the sensors left in trees after freezing or drought. Because sensitivity to cavitation and the ability to recover vary greatly depending on functional group (Eamus and Prior 2001) and climate (Grace 1993), the relative impact of cavitation and recovery on the sap flow measurement over time is likely to be species- and climate-dependent.

Small changes in the radial range over which sensors are positioned can result in dramatically different measured flows. In fast-growing trees, sensor position changes relative to the cambium (sensors become embedded) as the tree produces new xylem tissue. Unless compensated for, data from embedded sensors may be misinterpreted, especially when there is a pronounced radial decline in sap flux from near the cambium toward the inner sapwood (Cermak et al. 1992; Granier et al. 1994; Phillips et al. 1996). In extreme cases, as sapwood ages, sensors initially installed near the sapwood—heartwood boundary may end up partially embedded in heartwood (Clearwater et al. 1999).

## Methods

In our experiments, we used 20-mm heat-dissipation sap flow sensors (Granier 1987) produced in our laboratory according to the method of Phillips et al. (1996). Sensors were installed in the outer 20 mm of sapwood in 11 Douglas-fir and 12 red alder trees (one sensor per tree; tree age = approximately 18 years). They remained in the trees continuously between late April 2001 and early July 2002. This study spanned two 65-day measurement periods between late April and early July (days 117–182); the two periods are hereafter referred to as the first and second year. We assumed that the measurements from the first year were unimpaired by temporal errors and that the $J_s$ response to vapor pressure deficit ($\delta$) should be consistent from 1 year to the next, given the same soil moisture conditions. The trees were evenly spaced, and most trees, especially Douglas-fir, were not in a closed canopy. Their position relative to neighbors remained the same throughout the experimental period. Additionally, leaf area remained constant, or it increased in the second year. However, we did not monitor short-term phenology to assess whether leaf expansion coincided between years but assumed that it stayed the same (i.e., equal leaf area is assumed on the same calendar day).

Soil moisture ($\theta$ as volumetric water content) was monitored at 2- to 4-week intervals in June through August of each year with time domain reflectometry (Model 1502C, Tektronix, Inc., Beaverton, OR, USA, Gray and Spies 1995). The sampling positions for $\theta$ were located within 20 m of the sap flow trees at depths up to 45 cm ($n = 32$). Hourly $\delta$ was monitored at a climatic station approximately 3.5 km away with an HMP 35C temperature/humidity sensor (Vaisala, Helsinki, Finland), and it was averaged over daily time intervals. Although the true $\delta$ around experimental trees may have differed from that of the climate station, we assumed that the relationship was consistent between $\delta$ measured at the climate station and $\delta$ local to each tree in the two measurement years. During the measurement period, precipitation was recorded at the same nearby climatic station on 30/66 days in 2001 and 39/66 days in 2002. Neither solar radiation nor precipitation was considered in our model.

To compare $J_s$ between the two periods, we used a multiple linear regression approach to estimate temporal sampling errors. To determine whether $J_s$ differed between the first and second year on the same calendar day, we used a first-order-change model to quantify the "difference in $J_s$" ($\Delta J_s$) relative to differences in the environmental drivers, $\Delta\delta$ and $\Delta\theta$. We log-transformed $\delta$ to normalize and to linearize the relationship with $J_s$ for our statistical analyses. Tree size was described by two variables, height and sapwood basal area (SBA), and it was also tested in the model. Essentially, this modeling approach is premised by the assumption that, all else being equal (e.g., leaf area dynamics and environment), $J_s$ should be equal from the first year to the next in such a way that if

| | |
|---|---|
| $J_{s,x,1}$ | apparent sap flow on day $x$ in year 2001, |
| $J_{s,x,2}$ | apparent sap flow on day $x$ in year 2002, |
| $E_{x,1}$ | environmental driver(s) on day $x$ in year 2001, |
| $E_{x,2}$ | environmental driver(s) on day $x$ in year 2002, |
| $B_0$ and $B_1$ | represent the $y$ intercept and slope. |

Then $$\Delta J_s = J_{s,x,2} - J_{s,x,1} = \mathrm{B}_0 + \mathrm{B}_1(E_{x,2} - E_{x,1}) \qquad (1)$$

Potential multiple regression model parameters are described in Table 1. The best model was found using a forward selection process from the following models:

1. $\Delta J_s \sim f\,[\Delta\ln(\delta)]$
2. $\Delta J_s \sim f\,[\Delta\ln(\delta), \text{sensor}]$
3. $\Delta J_s \sim f\,[\Delta\ln(\delta), \text{sensor}, \Delta\ln(\delta) \times \text{sensor}]$
4. $\Delta J_s \sim f\,[\Delta\ln(\delta), \text{sensor}, \Delta\ln(\delta) \times \text{sensor}, \text{sensor age}]$

**Table 1** Description of potential variables and their symbols for use in the forward selection of a suitable multiple linear regression model

| Symbol | Description |
|---|---|
| $\Delta J_s$ | The difference between apparent sap flux density (kg $m^{-2}$ $day^{-1}$) on day $x$ of 2002 and day $x$ of 2001[a] |
| Sensor | Categorical variable to allow for unique estimates by sensor |
| Species | Categorical variable to allow for unique estimates by species |
| $\Delta\ln(\delta)$ | Continuous variable of the difference between mean daily vapor-pressure deficit (mbar) that has been natural-log-transformed for linearity on day $x$ of 2002 and day $x$ of 2001 |
| $\Delta\theta$ | Continuous variable of the difference between volumetric soil moisture (%) on day $x$ of 2002 and day $x$ of 2001 |
| Height | Continuous variable of tree heights (m) for each sensor/tree |
| SBA | Continuous variable of sapwood basal areas ($m^2$) at breast height for each sensor/tree |
| Sensor age | Continuous variable of accumulated time (days) since installation |

[a] Dependent/response variable

5. $\Delta J_s \sim f\,[\Delta\ln(\delta)$, sensor, $\Delta\ln(\delta) \times$ sensor, sensor age, $\Delta\theta]$
6. $\Delta J_s \sim f\,[\Delta\ln(\delta)$, sensor, $\Delta\ln(\delta) \times$ sensor, sensor age, $\Delta\theta$, $\Delta\theta \times$ sensor]
7. $\Delta J_s \sim f\,[\Delta\ln(\delta)$, sensor, $\Delta\ln(\delta) \times$ sensor, sensor age, $\Delta\theta$, $\Delta\theta \times$ sensor, height]
8. $\Delta J_s \sim f\,[\Delta\ln(\delta)$, sensor, $\Delta\ln(\delta) \times$ sensor, sensor age, $\Delta\theta$, $\Delta\theta \times$ sensor, SBA]

(See Table 1 for a description of variables).

Our intent was to find the simplest model capable of predicting $\Delta J_s$. Additional parameters were added only if they improved the model by more than 5%, as measured by the coefficient of determination ($r$, Rawlings et al. 1989). The 5% cut-off was chosen in part because additional variables will always improve the model performance and because measurement errors are likely below that range. We used the Bayesian information criterion (BIC) to select the "best" model without bias toward large numbers of parameters; models with small BIC statistics are optimal (Ramsey and Schafer 1997).

Temporal sampling error may worsen incrementally with time (e.g., an additive or growth function) within the 65-day period of investigation. To test for an incremental temporal pattern of degradation, the term "sensor age," which could vary between 0 and 65 days, was included in the multiple regression models. If this term proved to be significant in the model, we inferred that temporal sampling integrity had declined daily as a function of the number of days that had elapsed since the sensor was first installed.

To compare and contrast potential temporal sampling errors for Douglas-fir and red alder, we used a species term. If the species term proves to be significant in the model, we can conclude that sampling error differs between the two species, and separate models for each species would be justified because of a violation of statistical assumptions (i.e. homoscedasticity, Berry and Feldman 1985). Individual models for each species, if different, could provide insights into the mechanisms causing temporal sampling errors and evidence of species specificity. For example, if one species has grown more in diameter, all else being equal, the temporal sampling error might be more pronounced in that species.

To estimate the average magnitude of temporal sampling error among all the sensors combined, we used a random-slope, linear mixed-effect model (Rawlings et al. 1989 p. 579). Mixed-effect models are useful in analyzing grouped data that include both random and fixed components. Our model was

$$\Delta J_{s,ij} = B_{0j} + B_{1j} \times \Delta\ln(\delta) + \varepsilon_{ij}, \tag{2}$$

where

| | |
|---|---|
| $\Delta J_{s,ij}$ | change in $J_s$ between day $i$ of 2002 and day $i$ of 2001 of sensor $j$; |
| $i$ | day 117, 118,…,182 and $j$ = sensor 1, 2,…,11 if Douglas-fir; $j$ = 1, 2,…,12 if red alder; |
| $B_{0j}$ | temporal sampling error = average change in $J_s$ for sensor $j$ when $\Delta\ln(\delta)$ is zero; |
| $B_{1j}$ | additional discrepancy between $J_s$ on the same day of the first and second year due to the difference in vapor pressure $\Delta\ln(\delta)$ on those days; and |
| $B_{1j}$ | is normally distributed and $\varepsilon_{ij}$ is an independent, normally distributed error term with a mean of zero |

As in the multiple regression models (above), the response variable was the difference in $J_s$. As a result, the intercept term in the mixed-effect model represents the average temporal sampling error after 1 year (i.e., the average difference in $J_s$ for all measurement dates between the first and second year when all other variables are held constant). The intercept term ($B_{0j}$) represents individual temporal sampling error for each sensor, Eq. 2.

## Mechanism underlying temporal sampling errors

Because radial growth occurs in the outer xylem layers, we looked for evidence that the mechanism for temporal sampling errors was related to growth. We conducted an independent investigation during which variable-length heat dissipation sensors (James et al. 2002) were placed in two large Douglas-fir trees (1.44 and 1.0 m in diameter, respectively). Sensors were distributed radially across the active xylem at depths of 10, 25, 40, and 55 mm from the outer cambium. Six clear days during August 2002 and 2003 with maximum $\delta > 3$ kPa and mean daily $\delta = 1.74$ and 1.77 kPa for 2002 and 2003, respectively, were selected for comparisons of radial profiles of $J_s$ between years. If mean $J_s$ was higher in 2002 than 2003 in outermost radial xylem positions but not in the innermost xylem, growth could not be ruled out as a mechanism for temporal sampling errors.

## Results

The 2001 and 2002 average $J_s$ amounted to 1,187 and 612 kg m$^{-2}$ day$^{-1}$, respectively, for Douglas-fir and 1,517 and 1,007 kg m$^{-2}$ day$^{-1}$, respectively, for red alder. As expected (Moore et al. 2004), $J_s$ was generally higher in red alder than Douglas-fir (Fig. 1). Average $J_s$ was relatively constant over time throughout the study periods—see running mean, Fig. 1a, b, and c—but in the second year, it increased slightly, especially in red alder—see running mean, Fig. 1d.

More precipitation fell in early 2002 relative to 2001 (Fig. 2a). Solar radiation averaged across all sampling dates did not differ between years (228 ± 12 and 221 ± 11 W m$^{-2}$ in 2001 and 2002, respectively)—see Fig. 2b, and there were nearly equal numbers of sunny days in 2002 and 2001 (34 and 32 days, respectively). Less precipitation led to dryer atmospheric conditions in 2001 (Fig. 2c). Comparing $\theta$ between the first and second year, average soil moisture to a depth of 45 cm (Fig. 2d) did not differ. After the rainy winters of 2001 and 2002, when moisture reached field capacity, spring was the wettest period observed for the study area, with $\theta$ averaging over 28% in both years and declining consistently between years to a low of around 20% (data not shown).

Figure 3 shows daily observations of the relationship between $J_s$ and $\delta$ for the period of investigation. Maximum $J_s$ was much lower in the second year than in the first in 10 out of 11 Douglas-fir sensors as shown in Fig. 3a, b and in 11 out of 12 red alder sensors as shown in Fig. 3e, f. There was substantial variation in slopes among individual sensors in the first year—coefficient of variation (cv, %), $\text{cv}_{2001} = 33\%$—and even greater variation in the second year ($\text{cv}_{2002} = 60\%$). Based on these preliminary observations, the forward selection process proceeded with the following models:

1. $\Delta J_s \sim f\,[\Delta\ln(\delta)]$ $r^2$: DF = 0.57; RA = 0.57
2. $\Delta J_s \sim f\,[\Delta\ln(\delta), \text{sensor}]$ $r^2$: DF = 0.76; RA = 0.79
3. **$\boldsymbol{\Delta J_s \sim f\,[\Delta\ln(\delta), \text{sensor}, \Delta\ln(\delta) \times \text{sensor}]}$ $\boldsymbol{r^2}$: DF = 0.84; RA = 0.84**
4. $\Delta J_s \sim f\,[\Delta\ln(\delta), \text{sensor}, \Delta\ln(\delta) \times \text{sensor}, \text{sensor age}]$ $r^2$: DF = 0.84; RA = 0.84
5. $\Delta J_s \sim f\,[\Delta\ln(\delta), \text{sensor}, \Delta\ln(\delta) \times \text{sensor}, \text{sensor age}, \Delta\theta]$ $r^2$: DF = 0.84; RA = 0.84
6. $\Delta J_s \sim f\,[\Delta\ln(\delta), \text{sensor}, \Delta\ln(\delta) \times \text{sensor}, \text{sensor age}, \Delta\theta, \Delta\theta \times \text{sensor}]$ $r^2$: DF = 0.86; RA = 0.86
7. $\Delta J_s \sim f\,[\Delta\ln(\delta), \text{sensor}, \Delta\ln(\delta) \times \text{sensor}, \text{sensor age}, \Delta\theta, \Delta\theta \times \text{sensor}, \text{height}]$ $r^2$: DF = 0.85; RA = 0.85
8. $\Delta J_s \sim f\,[\Delta\ln(\delta), \text{sensor}, \Delta\ln(\delta) \times \text{sensor}, \text{sensor age}, \Delta\theta, \Delta\theta \times \text{sensor}, \text{SBA}]$ $r^2$: DF = 0.86; RA = 0.86

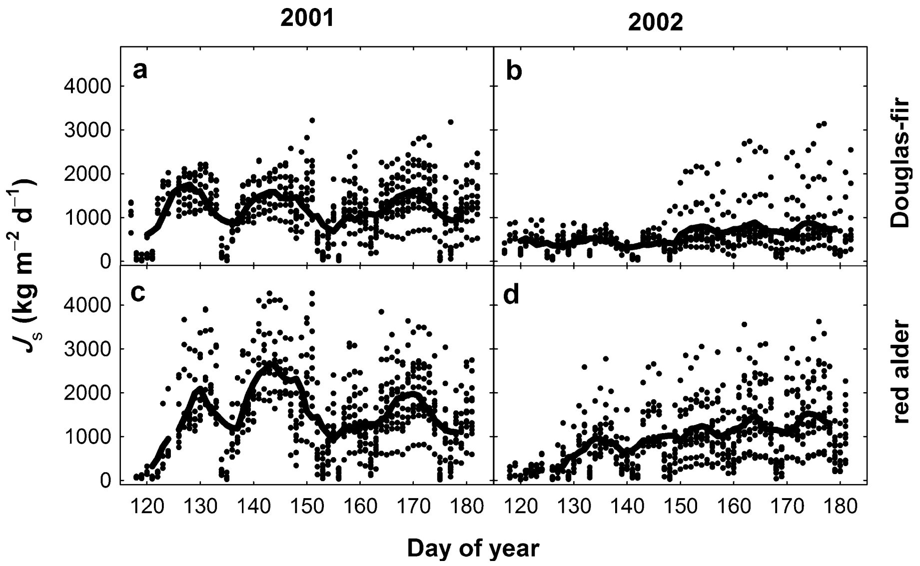

**Fig. 1** Daily sap flux ($J_s$) for 11 sensors in Douglas-fir in 2001 (**a**) and 2002 (**b**) and for 12 sensors in red alder in 2001 (**c**) and 2002 (**d**). Seven-day running means are represented by *dark lines*

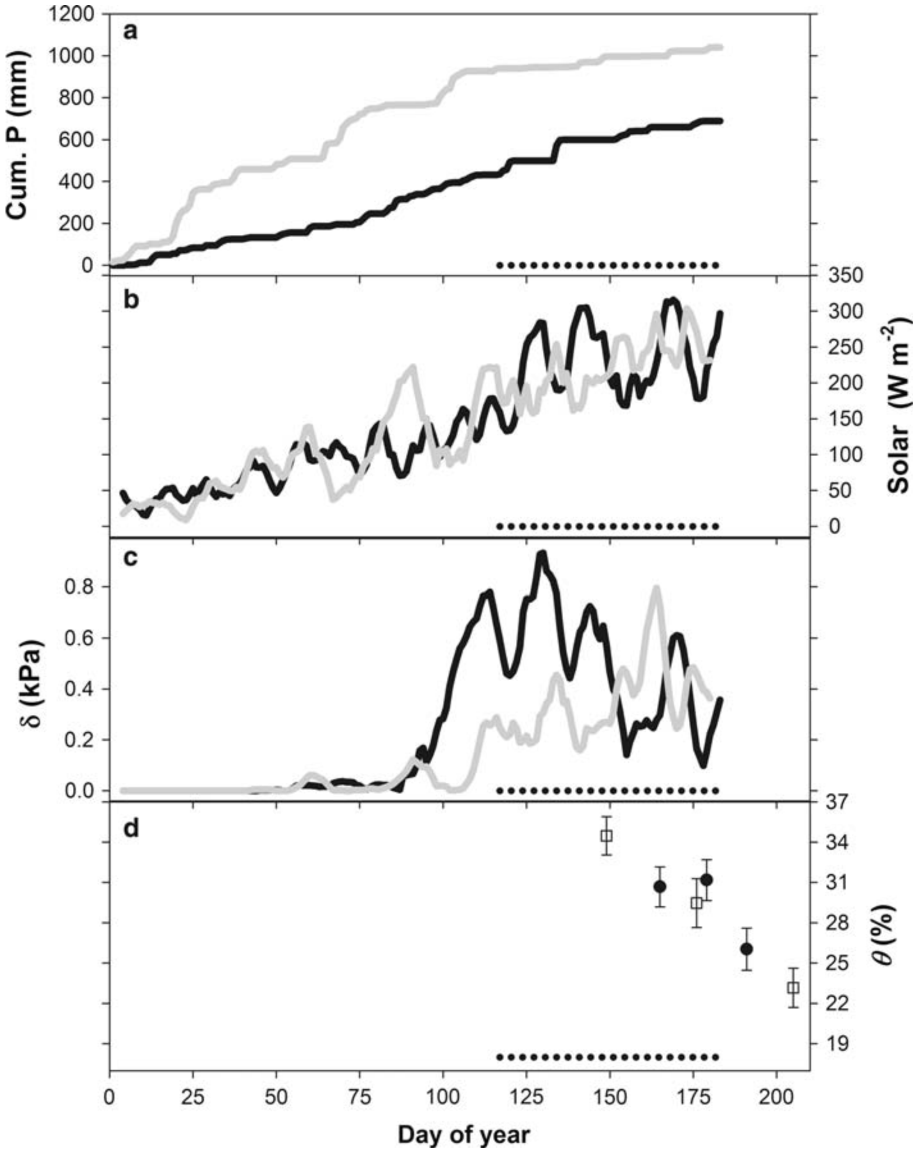

**Fig. 2** Climatic and soil moisture trends in 2001 (*black*) and 2002 (*gray*), including: **a** cumulative precipitation (mm) since January 1, **b** seven-day running means of solar radiation (W $m^{-2}$), **c** seven-day running means of vapor pressure deficit ($\delta$), and **d** volumetric soil water content ($\theta$) to a depth of 45 cm at 32 locations throughout the study area during 2001 (*solid circles*) and 2002 (*open squares*), with standard *error bars*. *Dotted lines* indicate the period of comparison

(See Table 1 for a description of variables. DF = Douglas-fir. RA = red alder).

Because the variance around $J_s$ was much greater in red alder than Douglas-fir (violates the constant variance assumption for regression, Ramsey and Schafer 1997), separate regressions were run for each species. The third model is shown in bold because it was selected as the final (or "best") model; additional parameters minimally improved the model performance, as determined by the BIC statistic. Adjusted $r^2$ values are reported by species. The final model took the general form

$$\Delta J_{s,j} = B_{0j} + B_{1j} \times \Delta \ln(\delta) \qquad (3)$$

Unique coefficients (Table 2) were estimated for each of the 11 Douglas-fir and 12 red alder sensors ($j = 1, 2, 3,\ldots,11$ if Douglas-fir; $j = 1, 2, 3,\ldots,12$ if red alder). Temporal sampling errors were apparent in most sensors, as indicated by negative $B_{0j}$. Only 2 out of the 23 trees, one Douglas-fir and one red alder, had positive $B_{0j}$ estimates, which indicates a slight increase in $J_s$ from 1 year to the next at the same level of $\delta$ (Table 2), but this increase was not statistically significant for those trees ($p > 0.05$).

The average temporal sampling error in Douglas-fir declined by 540 ± 100 kg $m^{-2}$ $day^{-1}$ ($p < 0.01$, linear mixed effects). That value amounts to a 45% decline in $J_s$ after 1 year that cannot be accounted for by changes in two of the primary environmental drivers of transpiration, $\delta$ and $\theta$. The average temporal sampling error for sensors installed in red alder was somewhat less, declining by 455 ± 152 kg $m^{-2}$ $day^{-1}$ ($p < 0.01$, linear mixed effects), which amounts to a 30% decline in average $J_s$ after about 1 year of operation. The variability in temporal sampling error among individual sensors was large, and it was greater in red alder than in Douglas-fir.

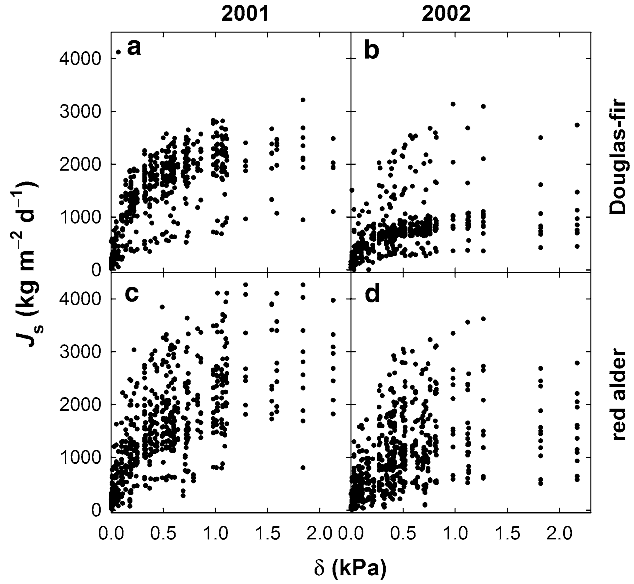

**Fig. 3** The observed relationship between sap flux ($J_s$) and vapor pressure deficit ($\delta$) for Douglas-fir (*top panels*; $n = 11$ sensors) and red alder (*bottom panels*; $n = 12$ sensors) between April 27 and July 1, 2001 (refer to **a** and **c**) and 2002 (refer to **b** and **d**)

**Table 2** Estimates for intercept ($B_0$) and slope ($B_1$) for each sensor corresponding to Eq. 3. Also included are significance levels $p < 0.001$ (**), $p < 0.05$ (*), or not significant (ns)

| Species | Sensor | $B_0$[a] | $B_1$ |
|---|---|---|---|
| Douglas-fir | 1 | $-916^{**}$ | 270 |
| | 2 | $-665^{**}$ | 257 |
| | 3 | $-804^{**}$ | 152 |
| | 4 | $-954^{**}$ | 344 |
| | 5 | $-736^{**}$ | 395 |
| | 6 | $-348^{**}$ | 219 |
| | 7 | $-322^{**}$ | 162 |
| | 8 | $-116^{**}$ | 593 |
| | 9 | 77 ns | 363 |
| | 10 | $-510^{**}$ | 203 |
| | 11 | $-646^{**}$ | 245 |
| Red alder | 1 | $-314^{**}$ | 262 |
| | 2 | $-156^{*}$ | 502 |
| | 3 | $-451^{**}$ | 354 |
| | 4 | −92 ns | 465 |
| | 5 | $-164^{**}$ | 164 |
| | 6 | $-157^{*}$ | 295 |
| | 7 | $-239^{**}$ | 363 |
| | 8 | 106 ns | 651 |
| | 9 | $-1{,}613^{**}$ | 561 |
| | 10 | $-754^{**}$ | 281 |
| | 11 | $-250^{**}$ | 505 |
| | 12 | $-1{,}352^{**}$ | 438 |

[a] Temporal sampling error in kg m$^{-2}$ day$^{-1}$

There was a significant difference between species in average temporal sampling error ($p < 0.01$, multiple regression). The pattern of decline appeared to be different for the two species as well. Model results predicted an incremental pattern in red alder ($p < 0.01$, from multiple regression), which supports the hypothesis of a gradual decline in sensor function, whereas Douglas-fir models did not. This conclusion was reached because the red alder model with the "sensor age" term exhibited the smallest BIC statistic among models of its kind. For every additional day after the sensors were in place for a full year (sensor age = 1 year + 1 day), $J_s$ declined by an additional 9 kg m$^{-2}$ day$^{-1}$ in red alder. For example, when a sensor in red alder had been installed for a year, $J_s$ declined by about 450 kg m$^{-2}$ day$^{-1}$. A year and 1 week later, the estimated difference between $J_s$ measured on day $x$ of 2001 and $J_s$ measured on day $x + 7$ of 2002 was $450 + 9 \times 7$ or 513 kg m$^{-2}$ day$^{-1}$. All the changes in Douglas-fir occurred before April 27 of the second year.

Radial trends in $J_s$ are plotted in Fig. 4 for mature Douglas-fir. In the two trees investigated, differences in daily total $J_s$ between the 2 years were most pronounced near the cambium. Mean values of $J_s$ averaged higher in the first year. As the depth of the sap flow sensor increased, differences between years diminished (Fig. 4).

## Discussion

This study introduces a framework for addressing potential temporal sampling errors in long-term sap flow datasets. We attribute reduced sap flow in the second measurement year to temporal sampling errors, which occurred in both species examined. Because sensors are increasingly used in long-term research applications, this study helps researchers understand and quantify temporal limitations caused by localized changes.

Daily average vapor pressure deficit was a good predictor of sap flow variation, as has been previously demonstrated for moist environments (e.g., Oren et al. 1999). When the correction factor was applied, we achieved 74% correlation between year 1 and year 2. Daily variation in solar radiation alone could account for the remaining 26% (Fig. 2b). These simple environmental variables, $\theta$ and $\delta$, are widely available to most studies; the same framework is therefore adaptable to other experiments, provided that stand structure and leaf area are relatively stable or otherwise accounted for. In our study, it is unlikely for stand structure to have differed greatly between 2001 (age = 16 years) and 2002 (age = 17 years). It is equally unlikely that these rapidly growing young trees had lower total leaf area in the second year. Our assumption that day of year may serve as a proxy for leaf expansion from 1 year

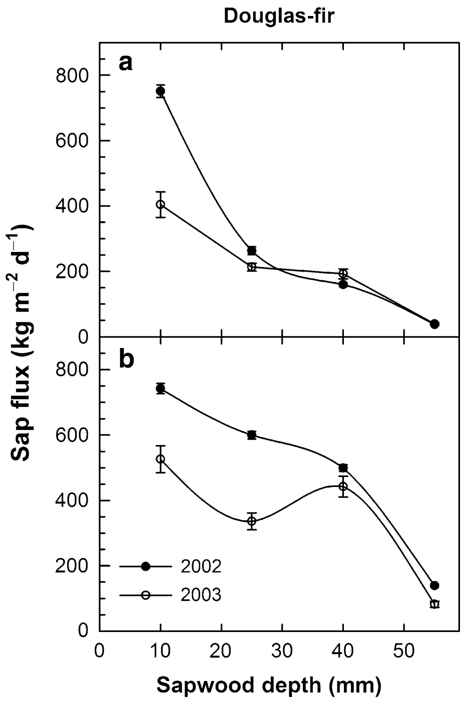

**Fig. 4** Radial profiles of mean daily total sap flux in two large Douglas-fir trees (see **a** and **b**) for six comparable paired days in August 2002 and 2003. Mean daytime vapor pressure deficit ($\delta$) was 1.74 (0.17) and 1.77 (0.09) kPa, mean daytime photosynthetic photon flux was 923 (20) and 861 (26) μmol m$^{-2}$ s$^{-1}$, and mean daily soil volumetric water content at 60 cm was 21% (0.4) and 21.8% (0.9) in 2002 and 2003, respectively. *Standard errors* denoted in parentheses above and in the figure are based on $n = 6$ days

to the next warrants further investigation; however, it is unlikely that phenological differences alone could explain the large reductions in $J_s$ the following year.

Furthermore, belowground factors—for example, seasonal root growth responses to drought or hypoxia, fungal damage to roots or other diseases, and deep access to groundwater—may also partially explain the observed differences. It is often difficult to assess root dynamics in mature forest stands; yet any of these factors might change significantly from 1 year to the next, even if only for a few weeks. The reduced $J_s$ during the second year was not likely due to less soil–water availability, as has been found previously (Bovard et al. 2005; Oren and Pataki 2001). Precipitation within the study area during winter and spring is in excess (Fig. 2a). Trees were located in gravelly clay loam soils known to be well drained (Gray and Spies 1995). Soil water supply was comparable on the same dates in 2001 and 2002 (Fig. 2d) and remained high enough within the top 45 cm (>20%) that drought-related reductions in transpiration are unlikely. Nearby observations indicate field capacity is between 30 and 35% (Czarnomski et al. 2005).

Our two study species, Douglas-fir and red alder, demonstrated that the magnitude and pattern of temporal sampling errors may be species-specific. A greater decline occurred in Douglas-fir compared with red alder. Further, the year-to-year difference in red alder appeared to worsen as the second spring progressed. Variability in temporal sampling error among individual sensors was large, and it was greater in red alder than in Douglas-fir. An alternative explanation for species differences may be that seasonal leaf area dynamics played a greater role in red alder.

## Evidence for a growth-related mechanism for temporal sampling errors

Insights about potential causes of temporal sampling errors (i.e., growth, tissue injury, or xylem embolism) can be inferred from patterns in the observed trends. Temporal sampling errors in Douglas-fir apparently occurred before April 2002 and remained constant during the second study period. It is possible that tissue near the sensor will have been unable to recover from winter frost embolism. By contrast, the worsening trend for red alder suggests a small incremental change may have occurred during the second year. It is possible that radial growth and/or a gradual wound response may explain this pattern, but further investigations are needed.

Red alder may have grown much faster than Douglas-fir during the period of investigation; growth-related changes between April and July 2002 in Douglas-fir were too small to detect. However, our field observations indicate that growth should be a factor in both species. Many trees of both species had grown substantially over the 17-month period of our study, and consequently embedded sensors were often extremely difficult to remove from the tree after the experiment ended. Radial variation in flow occurs in both of these species (Moore et al. 2004), and thus the relative flow rate changes substantially with depth, but red alder has a steeper radial decline in sap flux with depth, whereby tiny growth increments could measurably reduce $J_s$ over time.

An additional set of measurements provided independent evidence that growth was the primary mechanism for temporal sampling errors in Douglas-fir. In the two mature trees investigated, differences in daily total $J_s$ were most pronounced near the cambium; differences lessened or disappeared in deeper sections of sapwood (Fig. 4). These data suggest that lower flows measured on comparable days in the second season are a result of the most active zone of flow having moved outward as the cambium adds wood and as the somewhat deeper sapwood becomes less conductive. Others have found temporal changes in radial patterns of sap flow attributed to declining $\theta$ (Ford et al. 2004) and xylem freezing (Schafer et al. 2002).

## Conclusions

This paper calls to attention the need for caution when using sap flow sensors for more than one growing season; however, we demonstrated a means of testing for and correcting potential temporal sampling errors, based on two environmental drivers for transpiration, soil water supply ($\theta$) and atmospheric vapor pressure deficit ($\delta$). After accounting for differences due to $\theta$ and $\delta$, $J_s$ had declined by 45% in Douglas-fir and 30% in red alder after 1 year of sensor use. Although further investigation is needed to verify the precise mechanisms that lead to temporal sampling errors, our results provide guidance for decisions to reinstall sensors in subsequent growing seasons.

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