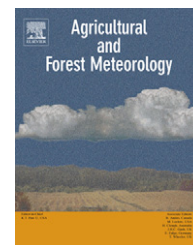


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# Decoupling structural and environmental determinants of sap velocity: Part I. Methodological development

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## ABSTRACT

This paper presents a novel theoretical framework for the study of individual tree sap flow that incorporates both spatial and temporal variability in sap velocities. In this formulation, the instantaneous sap velocity at any point in the radial profile of xylem tissue is defined as the product of a time-invariant sap velocity distribution and a time-varying term which is defined as a stem conductance. We hypothesize that the characteristic distribution of sap velocity is relatively uniform both within individual trees and between trees of the same species if location in the xylem tissue is expressed in normalized units relative to the total xylem depth (i.e. tree size). Experimental evidence confirms our hypothesis in the case of a population of sugar maples in a mixed deciduous forest and dwarf apple trees in an orchard, despite the fact that observations were drawn from a wide range of tree sizes and under varying soil moisture levels and atmospheric conditions that determines water demand. Furthermore, profiles of sap velocity and resulting integrals of total sap flow exhibit significant reduction in bias (by 30–40%) in comparison to prior methods used to extrapolate point observations of sap velocity. The method we describe exhibits the greatest improvement when only a small fraction of the total sapwood is measured, which is the typical scenario for most applications. While these results require further confirmation in order to be generalized, they nevertheless offer the basis to improve both the specific sampling strategies used to estimate whole-tree transpiration using sap velocity probes as well as methods employed to upscale water use of individual trees to larger scales for evaluation of landscape water balance.

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## 1. Introduction

Characterization of transpiration based on the water use of individual trees has the theoretical advantage of preserving vital information on plant-environment functional links and flux partitioning between species and landscape areas (Meinzer et al., 2001; Wilson et al., 2001; Wullschleger and Norby, 2001; Oren et al., 1999). However, there is a great deal of uncertainty involved in scaling up any measurements of whole-tree transpiration rates due to limitations regarding the

number of trees and species sampled (Kumagai et al., 2005; Wullschleger et al., 2001; Wullschleger and King, 2000; Loranty et al., 2008), and the sampling technique (Pausch et al., 2000; Hatton and Wu, 1995; Phillips et al., 1997). The possibility of universal scaling laws linking transpiration with morphological characteristics of the tree such as leaf area or sapwood area has been proposed by several authors (Meinzer et al., 2005; Enquist and Niklas, 2002). Generally, these relationships will only hold in conditions of abundant water supply; in the presence of water stress, scaling relationships may become

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more dependent on tree size and location (cf. Wullschleger et al., 1998).

Whole-tree transpiration has been estimated by means of sap velocity probes (Smith and Allen, 1996). In forest environments, sap velocity approaches offer the dual advantages of practicality and repeatability of measurements. However, the assumptions underlying the technique require careful verification in order to determine total sap flow from point-based estimates of sap velocity (Nadezhdina et al., 2002; Pausch et al., 2000; Clearwater et al., 1999; Grime and Sinclair, 1999; Shackel et al., 1992).

Improving whole-tree sap flow estimates critically depends on accurate descriptions of the entire profile of radial sap flow velocity ( $v_s(x)$ ). Three methods have been commonly used to extrapolate point measurements of sap velocity over the entire width of active xylem. The weighted-average method (Hatton et al., 1990), hereafter referred to as  $H_s$ , employs a step function, with each step centered on the location of each single sap velocity measurement; the final, innermost step extends to the sapwood/heartwood interface. Two modified versions of the Hatton's method were proposed by Pausch et al. (2000). In the first modification – called the zero-step method ( $Z_s$ ) – the innermost step extends only to half of the distance between the last measured point and the end of the xylem, and a null sap velocity is assigned to the remaining xylem. The second method proposed by Pausch et al. (2000) is the zero-average ( $Z_a$ ), in which an extra artificial point is located halfway between the innermost measured point and the end of the xylem. The sap velocity of this extra point is assigned a value equal to half of the innermost measured sap velocity. In addition to these three techniques, second order polynomials have been used to fit radial single-point measurements of sap velocity (e.g. Bernier et al., 2002), but with greatly reduced relative accuracy compared to the  $H_s$ ,  $Z_s$ , and  $Z_a$  methods (Pausch et al., 2000).

Recently Ford et al. (2004) used a three-parameter model to fit a Gaussian curve to the radial profiles of sap velocity observed in four different pine species. Their results confirm the importance of obtaining accurate descriptions of the radial profile of sap velocity. They also propose the use of one of the parameters of the Gaussian function ( $\beta$ , in Ford et al., 2004) to link the variability of the radial profile over time and among trees with changes in atmospheric vapor pressure deficit (VPD). Though promising, this Gaussian method does not fully resolve the variability in sap velocity directly responding to environmental changes. Finally, Tang et al. (2006) use proportionality rules between measured and unknown portions of the xylem, although their method employs a thermal dissipation technique instead of the heat pulse technique we use in this study.

Clearly, the accuracy of these prior methods is strongly related to the number of radial sap velocity estimates and their co-location with respect to the entire extent of the active xylem. In particular, each method extrapolates across the entire xylem based on an absolute measure of probe depth instead of relative probe depth, so that the same method applied to trees of varying size will yield incomparable results. Because these prior methods of extrapolation are specific to the particular data sets collected and are not based any general

hypothesis regarding the shape of radial sap flow distributions, these approaches are not able to generalize sap flow across different individuals or even separate sap flow variability associated with changes in tree water availability/atmospheric water demand from variation induced by tree hydraulic architecture.

To address these shortcomings, we seek to develop an improved method of extrapolating radial velocity observations that addresses the problems identified in earlier approaches. Specifically, our goal in this work is to define a technique that allows us to (1) isolate the component of sap flow governed by the radial variation in hydraulic architecture; (2) determine the degree to which relative sap velocity profiles are consistent across different sizes of individual trees within the same species; (3) compare velocity profiles between two different species with diffuse-porous xylem (*Acer saccharum* and *Malus domestica* var. 'Royal Empire') growing under varying environmental conditions (mixed forest vs. orchard).

## 2. Analytical framework for individual tree sap flux dynamics

Usually sap velocity techniques are implemented to determine instantaneous whole-tree sap flow,  $F_s(t)$  [ $L^3 T^{-1}$ ], as the product of instantaneous spatially averaged sap velocity,  $\bar{v}_s(t)$  [ $L T^{-1}$ ], and sapwood area,  $A_s$  [ $L^2$ ] according to

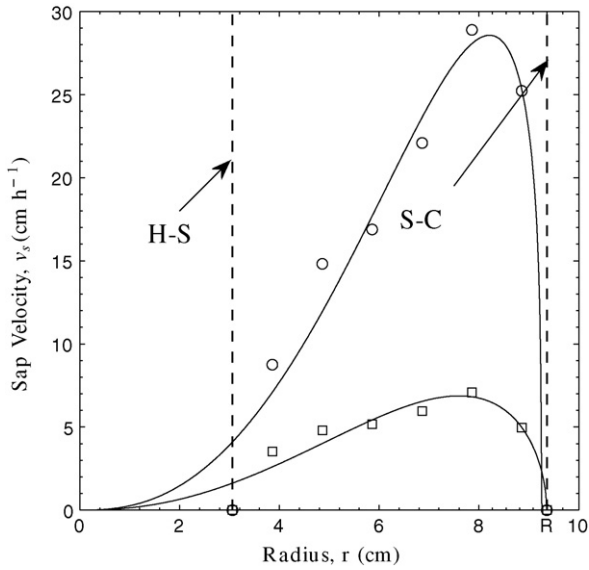
$$F_s(t) = \bar{v}_s(t)A_s. \quad (1)$$

Because both sapwood area,  $A_s$ , and the sap velocity,  $v_s$ , vary radially from the center of a tree, the use of sap velocity probes with either thermal dissipation or heat pulse techniques (Green et al., 2003; Granier, 1985) requires determining the radial distribution of sap velocity throughout the cross-sectional area of the tree. The problem is further complicated by an awareness that these radial velocity profiles often vary circumferentially around the tree. For a given tree of xylem radius  $R$ , we define a polar coordinate system with the radial coordinate described by the absolute distance from the center of the tree,  $r$ , and the angular coordinate specified as  $\theta$ . In this presentation, we define the xylem depth,  $R$ , as the distance from the center of the tree to the edge of the sapwood/cambium interface (cf. Fig. 1). It is clear that sap velocity at any point in time  $v_s(t)$  may also vary according to location in the tree,  $r$  and  $\theta$ . Considering both radial and circumferential variability in sap velocity, the instantaneous sap flow for an individual tree,  $F_s$  in Eq. (1), is now given by

$$F_s(t) = \int_0^{2\pi} \int_0^R v_s(r, \theta; t) r dr d\theta. \quad (2)$$

As a temporary simplification, we adopt an assumption of circumferential homogeneity which considers the instantaneous radial profile of sap velocity,  $v_s(r; t)$  to be the same throughout the tree (i.e. does not depend on  $\theta$ ). In the circumferentially homogeneous case, the instantaneous flow reduces to

$$F_s(t) = 2\pi \int_0^R v_s(r; t) r dr. \quad (3)$$



**Fig. 1 – A example of two radial sap flux velocity profiles,  $v_s(r)$ , measured at 1 cm intervals from 4 to 9 cm in a single sugar maple tree. Open circles (upper curve) indicate velocities observed at 3 p.m. local standard time (LST), while open squares (lower curve) indicate velocities observed at 6 p.m. LST. Vertical dashed lines indicate location of the heartwood–sapwood interface (H-S) and the sapwood–cambium interface (S-C) which were estimated from tree cores. The solid lines indicate best fits to  $v_s(r)$  using Eq. (16) ( $\alpha = 3.4$ ,  $\beta = 1.5$  lower curve;  $\alpha = 3.5$ ,  $\beta = 1.3$ , upper curve).**

We further simplify the system by defining the relative radial coordinate,  $x$ , which is simply  $r/R$ , and so with substitution of  $x = r/R$  and  $dx = dr/R$  Eq. (3) becomes

$$F_s = 2\pi R^2 \int_0^1 v_s(x; t)x dx. \tag{4}$$

The quantity  $\int_0^1 v_s(x; t)x dx$  in Eq. (4) represents the instantaneous radially averaged velocity,  $\bar{v}_s(t)$ , where – as in Eq. (1) – the overbar notation represents the instantaneous spatial average across the radial profile of the tree’s xylem. However, properly specifying this average velocity is greatly complicated by the fact that measurements of  $v_s(x; t)$  include information on both the radial variation in hydraulic architecture of individual trees, as well as the time-varying component of sap velocity that is determined by resource supply and demand. Resolving these separate structural and functional determinants of  $v_s$  has been a fundamental challenge that has limited our ability to scale up short-term estimates of sap flux in individual trees to longer time scales and trees of varying sizes.

Therefore, we re-define the instantaneous sap velocity at any point in the radial profile as the product of a time-invariant sap velocity distribution  $\rho_s(x)$  [unitless] and a new time-varying term which we define as the stem conductance  $c_s(t)$  [ $LT^{-1}$ ], so that

$$v_s(x; t) = \rho_s(x)c_s(t). \tag{5}$$

In Eq. (5), the quantity  $\rho_s$  describes the relative distribution of sap velocity over the relative radial coordinate bounded by

$0 \leq x \leq 1$  such that  $\int_0^1 \rho_s(x) dx = 1$  and  $\int_0^1 \rho_s(x)x dx = \bar{\rho}_s$ . The resulting relative sap velocity profile can be easily described by a Beta distribution,  $\rho_s(x; \alpha, \beta)$ , which is a suitable candidate for approximating a distribution over a bounded support region  $x \in [0; 1]$  and is given as

$$\rho_s(x; \alpha, \beta) = \frac{1}{B(\alpha, \beta)} x^{\alpha-1}(1-x)^{\beta-1}, \tag{6}$$

where  $\alpha$  and  $\beta$  are shape parameters that together determine the distribution and  $B(\alpha, \beta)$  is the standard beta function, given as

$$B(\alpha, \beta) = \frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)}, \tag{7}$$

when  $\Gamma(x)$  is the Gamma function. While our use of a distribution function to describe the radial profile of sap velocity is most similar to the work of Ford et al. (2004), there are a number of specific differences between this earlier approach and the methods described here. These differences are described in detail in our discussion section below. If we further assume that the profile of sap velocity is unimodal (i.e. a single peak region of maximum velocity) such that  $\alpha > 1$  and  $\beta > 1$  then we can define the location of peak velocity,  $\rho_s^{\max}$ , which corresponds to the mode of the distribution of sap velocities. For the Beta distribution (Eq. (6)), the mode is given by

$$\rho_s^{\max} = \frac{\alpha - 1}{\alpha + \beta - 2}. \tag{8}$$

In addition, the radial location that contains the average value of the velocity profile,  $\bar{\rho}_s$ , is simply the average of the beta function in Eq. (6), which is given by

$$\bar{\rho}_s = \frac{\alpha}{\alpha + \beta}. \tag{9}$$

In the case of circumferentially homogeneous sap velocity, Eq. (1) is properly defined as

$$F_s(t) = \bar{\rho}_s c_s(t) A_s = 2\pi R^2 \frac{\alpha}{\alpha + \beta} c_s(t), \tag{10}$$

where now the stem conductance,  $c_s(t)$ , is the separate time-varying component of whole-tree transpiration that is independent of either the particular profile of sap velocity within the tree ( $\bar{\rho}_s$ ) or the tree’s size ( $R$ ). In this way, the value of  $c_s$  should only change due to temporal shifts in either water supplies (soil moisture) and demand (atmospheric vapor pressure deficit). The manner by which  $c_s$  varies in response to environmental forcing is the subject of Part II (Dragoni et al., 2009). We now address the methods by which  $c_s(t)$  may be determined from point observations of sap velocity before going on to test the utility of our approach for determining radial sap velocity profiles in forest and orchard-grown individual trees.

### 2.1. Determination of stem conductance from observations of sap velocity

From our earlier presentation in Section 2, it is clear that  $F_s(t)$  and  $c_s(t)$  are related via the characteristic sap velocity profile,  $\rho_s(x)$ , and the tree size,  $R$ . The question then arises as to how to

determine the value of  $c_s(t)$  from a single observation of  $v_s(x, t)$ . Inspection of Eq. (5) reveals that prior knowledge of the characteristic sap velocity profile allows for the determination of  $c_s(t)$  given an observation of sap velocity at even a single location in the xylem,  $v_s(x; t)$  such that

$$c_s(t) = \frac{v_s(x; t)}{\rho_s(x)}. \quad (11)$$

Substitution of Eq. (11) into Eq. (10) yields the following expression for determining the instantaneous total sap flow of an individual tree from a single observation of sap velocity at a single depth within the xylem:

$$F_s(t) = 2\pi R^2 \frac{\alpha}{\alpha + \beta} \frac{v_s(x; t)}{\rho_s(x)}. \quad (12)$$

Instead of measuring sap velocity at a discrete point within the xylem, some sap probes contain thermocouples that measure the average sap velocity over a finite subset of the total xylem depth,  $r' \in [r_L; r_U]$ , where  $r_L$  and  $r_U$  are the depths over which the probe is measuring sap velocity (e.g. 2–4 cm depth). As described above, we first change notation to the relative radial depth,  $x' \in [x_L; x_U]$  through division by  $R$ . Sampling the sap velocity over a range of xylem depth (as opposed to at a specific point) results in an average velocity observation,  $\overline{v_s(x'; t)}$  instead of a single point observation as in Eq. (11). In this case the determination of  $c_s(t)$  proceeds according to

$$c_s(t) = \frac{\overline{v_s(x'; t)}}{\overline{\rho_s(x')}} \quad (13)$$

where  $\overline{\rho_s(x')}$  is given by

$$\overline{\rho_s(x')} = \int_{x_U}^{x_L} \rho_s(x) x \, dx, \quad (14)$$

and

$$F_s(t) = 2\pi R^2 \frac{\alpha}{\alpha + \beta} \frac{\overline{v_s(x'; t)}}{\overline{\rho_s(x')}}. \quad (15)$$

When the radial distribution of sap velocity is uniform across the xylem, the values of  $\alpha$  and  $\beta$  in the function  $\rho_s(x; \alpha, \beta)$  are both equal to 1. In this case, the value of the mode,  $\rho_s^{\max}$ , is undefined (cf. Eq. (8)) because all locations in the xylem have the same relative velocity, and the value of  $\overline{\rho_s}$  (cf. Eq. (9)) is  $1/2$ . Therefore, for the uniform case that occurs when  $\alpha = \beta = 1$ , the value of  $\rho_s(x)$  is equal to  $1/2$  at every location in the xylem (cf. Eq. (6)) and the value of  $v_s(x; t)$  is everywhere equal to  $\overline{v_s}$ . In this case, Eqs. (12) and (15) both reduce to  $\pi R^2 \overline{v_s}$  (i.e. Eq. (1)).

A more interesting application arises when the values of  $\alpha$  and  $\beta$  are not equal, which is the most likely scenario. In this case, there is a distinct non-uniform distribution in sap velocity across the xylem, and the sample of  $v_s(x; t)$  is not representative of the radial average velocity. However, from the above discussion, it is now clear that once the species-specific relative sap velocity profile is characterized, solution of  $c_s(t)$  is trivial for sap velocity observations taken from trees of any size and over any range of xylem depths. Furthermore, analytical solutions exist to determine the value of  $F_s(t)$  from

either point-based (Eq. (11)) or radially averaged (Eq. (13)) values of sap velocity. Using this framework, the magnitude and diurnal variation of stem conductance,  $c_s$ , can be compared between individual trees of different sizes or even between different species.

A critical requirement of the method we present is that the characteristic radial profile of sap velocity,  $\rho_s(x)$ , is well-described and temporally consistent. This means that although the overall sap flow may vary greatly within a tree through time, our method assumes that the relative profile of sap velocity does not change. In addition, while we expect that different sized trees will also exhibit different rates of sap flow, our method further assumes that the relative profile of sap velocity – when expressed in normalized units across the entire depth of active xylem – is similar for all trees of the same species. Therefore, the utility of our method depends on demonstrating that the value of  $\overline{\rho_s}$  does not vary greatly during periods of active transpiration either within or between individual trees of the same species. Consistency in the value of  $\overline{\rho_s}$  would only occur if the fraction  $\alpha/(\alpha + \beta)$  that defines  $\rho_s(x; \alpha, \beta)$  is uniform spatially and temporally within individual trees, as well as between different trees of varying size. In the following section we use measured sap flow data from two different diffuse porous species (sugar maple and dwarf apple trees) growing under varying conditions (deciduous forest in the case of the sugar maples, and an orchard in the case of the dwarf apples) to explore the assumption of temporal consistency in the form of  $\rho_s(x; \alpha, \beta)$ .

### 3. Material and methods

#### 3.1. Observations of radial sap profiles

Consistency in sap velocity profiles was primarily investigated using data from an experimental campaign aimed to quantify sap flow and transpiration in sugar maple (*Acer saccharum*), during July and August of 2006. Our experimental site was located in the Morgan-Monroe State Forest (MMSF) in Indiana (USA; 39°19'N, 86°25'W). The vegetation at the site was characterized by a secondary successional broadleaf forest with 29 identified species in the immediate vicinity of an eddy covariance tower (Schmid et al., 2000); 75% of these individual trees are either sugar maple, tulip poplar (*Liriodendron tulipifera*), sassafras (*Sassafras albidum*), white oak (*Quercus alba*) or black oak (*Quercus nigra*). The estimated basal area of sugar maple at the study site was  $7.14 \text{ m}^2 \text{ ha}^{-1}$ , and the total site basal area of individual trees greater than 70 cm diameter at breast height (DBH) was approximately  $26.3 \text{ m}^2 \text{ ha}^{-1}$  (Schmid et al., 2000). The average height of the canopy was about 27 m. The leaf area index (LAI) was routinely estimated at several points in the forest and regular intervals for the entire vegetative season, using a LAI-2000 instrument (LI-COR, Lincoln, NE, USA). Observations of LAI did not vary substantially during the entire measurement period and averaged  $4.8 \text{ m}^2 \text{ m}^{-2}$ . The study landscape has ridge/ravine topography with a relative relief of less than 60 m, and an overall drop of 90 m in 4 km (Schmid et al., 2000); average elevation is about 275 m above sea level. Soils in the area are mesic typic Dystrochrepts dominated by the Berks-Weikert complex,



defined as moderately deep and shallow (0.5–1.5 m in the experiment area), steep and very steep, well drained soils formed in residuum from sandstone, siltstone, and shale. This soil association is characteristic of upland areas in this region (Wayson et al., 2006).

Seventeen sugar maples were selected along a south-facing topographic transect approximately 140 m long and with a relative relief of about 20 m. The selection of the trees was mostly driven by the necessity to uniformly represent the range of tree sizes observed in the forest. For this reason, the selected trees were spatially distributed over approximately 80 m in the east-west direction. The topographic transect extended from the top of a hill down to the bottom of the ravine. The DBH range of selected trees was between 11.4 and 31.2 cm. The selected trees did not present any obvious peculiarity in stem and canopy structure (i.e. crown asymmetry, branching patterns, split or tortuous trunks). However, four of the smallest trees had canopies located completely within the understory. These smaller understory trees were not excluded from the methodological analysis presented here, but were excluded from the environmental forcing analysis presented in Part II. Throughout the study period air temperature, relative humidity (HMP35C, Vaisala, Woburn MA), and precipitation (TE525, Texas Electronics, Dallas, TX, USA) were measured at the top of an eddy-covariance tower (i.e. about 20 m above the canopy) located within 100 m of the sugar maple experiment (Schmid et al., 2000). Volumetric water content in the first 30 cm of soil depth (CS615, Campbell Scientific Inc., Logan, UT) was measured in proximity of each maple (i.e. no further than 2–3 m from the tree) during sap flow measurement periods (Dragoni et al., 2009).

Sap flow velocity in each tree was estimated using the compensation heat pulse technique (Green and Clothier, 1988; Green et al., 2003) and gauges specifically manufactured for the experiment (Tranzflo NZ LTD, New Zealand). Sap velocity probes use heat pulses to estimate the velocity of heat transfer, which is converted to sap velocity using the bulk volumetric water content of xylem tissue (Becker and Edwards, 1999). This method of relating a heat velocity to a sap velocity assumes that the structural component of xylem does not contribute significantly to heat transfer (Green and Clothier, 1988). Three different sets of four gauges each were used: the first set had probes of 2 cm length and the second set had probes of 4 cm length. Both the first and second sets measured sap velocity at four different radial points. The first set of probes measured at depths from the cambium of 0.5, 1.0, 1.5, and 2.0 cm, while the second set of probes measured at depths from the cambium of 0.5, 1.2, 2.1, and 3.2 cm. These two sets of probes were used on the smallest and medium-size trees (less than 20 cm DBH). The third set of probes had 6 cm-long needles that measured sap velocity at six radial points: 0.5, 1.5, 2.0, 2.5, 3.5, 4.5 and 5.5 cm. These longer probes were used for the largest trees ( $\geq 20$  cm DBH). Four probes were inserted into each one of the selected trees at breast height, with the four gauges oriented along the magnetic North, East, South and West axes. Following the approach adopted in Green et al. (2003), the upstream and downstream probe needles with thermocouples were vertically placed 20 mm apart; one probe needle was located 5 mm below the heater probe and the other probe needle was located 15 mm above

the heater probe. Each probe measured sap velocity in either four or six radial points in the xylem, providing enough samples to extrapolate the radial profile of sap velocity. Because only three sets of four probes each were used, the heat pulse gauges were left in place for 5–7 days and then moved to a different tree; thus, only three trees at a time were measured simultaneously. Details of probe placement and timing of observations in each tree are provided in the accompanying manuscript (Dragoni et al., 2009). Trunk diameter and bark thickness were measured at the location of the gauge installations, and incremental cores extracted from each tree at the end of the measurement period were used to determine the volume fractions of wood and water (Becker and Edwards, 1999). Cores were also used to visually determine the depth of the active xylem and sapwood area; when this was not possible or uncertain, the allometric relation between DBH and sapwood area proposed by Wullschleger et al. (2001) for sugar maple was used. Heat pulses were released every 15 min. Sap velocities were estimated as described by Green et al. (2003) and Green and Clothier (1988). A wound size of 2.4 mm was assumed as suggested by the manufacturer.

A second set of sap flow observations taken from dwarf apple trees (*Malus domestica*) from June to September of 2002 was also used to provide further evidence for the utility of our approach. Measurements were conducted on four 8-year-old dwarf Royal Empire apple trees on M9 rootstock. The orchard is located at Cornell University's New York State Agricultural Experimental Station in Geneva, NY (USA; 42°N, 77°W). Sap flow in each tree was estimated using the compensation heat pulse technique and gauges specifically manufactured for the experiment (Tranzflo NZ LTD, New Zealand). The methodology used to estimate sap flows was similar to the one adopted for sugar maples described above, except that only one measurement per tree was taken and gauges were all inserted on the south site of the trunk. For complete details on the experimental design of our dwarf apple tree data see Dragoni et al. (2005).

We obtained maximum likelihood estimates of the parameters  $\alpha$ ,  $\beta$ , and  $c_s$  (Eq. (10)) for each radial sap velocity profile using the least-square method (Press et al., 2002) and the following equation that relates observed sap velocity ( $v_s$ ) to the three unknown parameters ( $\alpha$ ,  $\beta$ , and  $c_s$ ):

$$v_s(r/R) = c_s \frac{1}{B(\alpha, \beta)} \left(\frac{r}{R}\right)^{\alpha-1} \left(1 - \frac{r}{R}\right)^{\beta-1}. \quad (16)$$

Two points were arbitrarily added to the set of measured sap velocities corresponding to the cambium–sapwood and sapwood–heartwood interfaces, which were assumed to have a sap velocity of zero (Fig. 1). These additional points were added to increase the constraint for the fit of Eq. (16), but without necessarily forcing the curve through zero at the two points, since there is obviously some uncertainty regarding the location of these two interfaces within the radial profile of the tree.

Finally, to assess the utility of our approach in comparison to past empirical estimates of radial sap velocity profiles, we compared our profiles of sap velocity and their integrals to those computed using the methods of Hatton and Wu (1995) (referred to as  $H_a$ ), and the zero-step ( $Z_s$ ) and zero-average ( $Z_a$ ) methods proposed by Pausch et al. (2000). Hourly estimates of sap flow obtained using the  $H_a$ ,  $Z_s$  and  $Z_a$  methods were

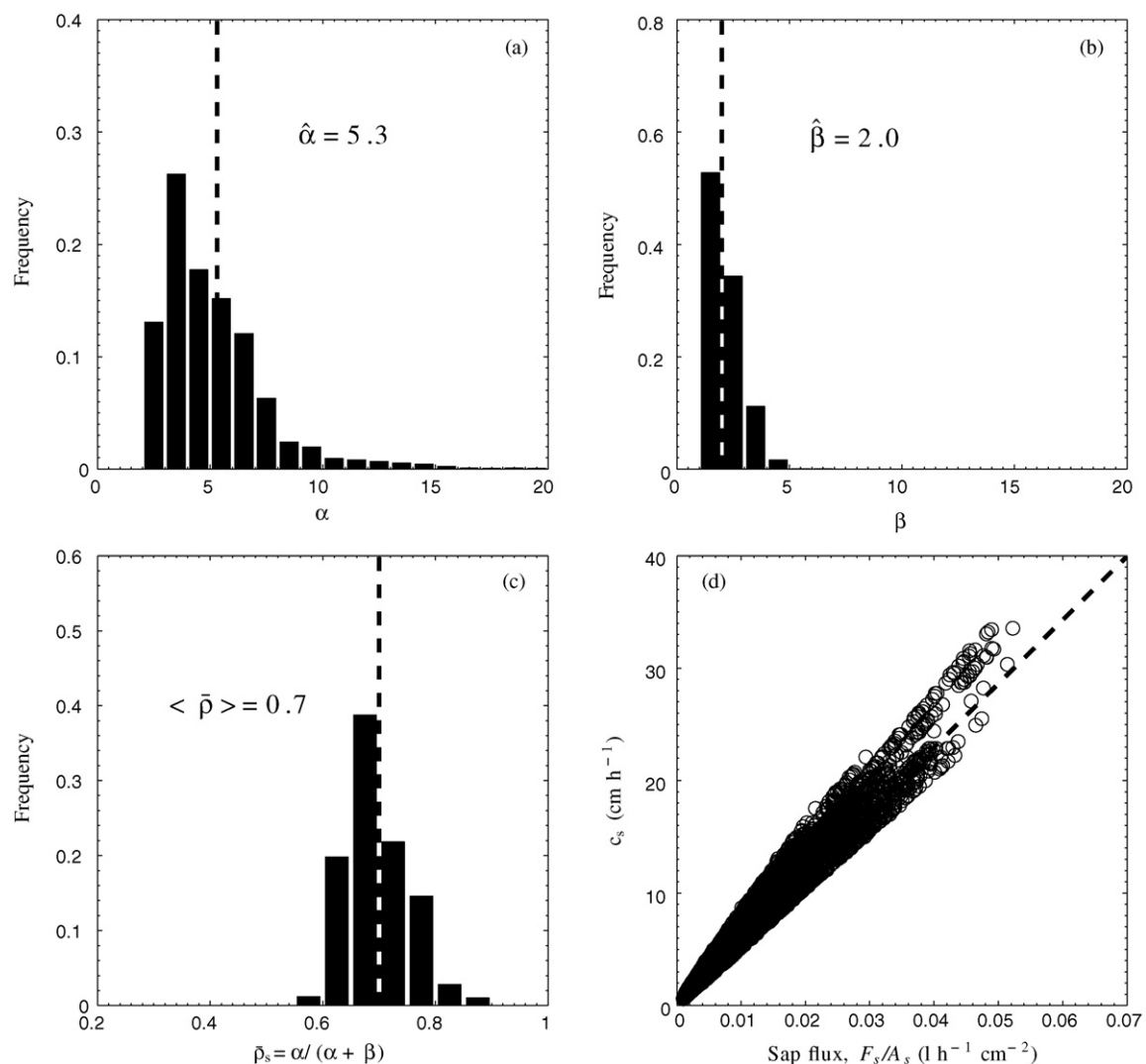
regressed against those obtained using our Beta distribution function approach, and slopes were taken as a measure of the difference between each of the three prior methods and the one presented here. We also analyzed all of our sugar maple data using the method presented in Ford et al. (2004) in order to directly compare our approach to this prior work, and to evaluate the degree to which each method is capable of characterizing the profiles of sap velocity which we observed.

#### 4. Results

The final datasets contain 18,392 radial profiles of daytime sap velocity for apple trees and 19,926 radial profiles of daytime sap velocities for sugar maples. Fits with the Beta distribution function yielded coefficients of determination greater than 0.9 in most of the cases (97% for apple trees and 85% for sugar maples). For the sugar maple data, only 5.4% of all profiles

yielded coefficients of determination less than 0.8. These poorly fitting profiles corresponded to daytime periods with sap velocities close to zero; these times occurred mostly in the early morning, late evening, or during rain events.

Environmental conditions during both the 2006 and 2002 field experiments were somewhat similar. In the humid climate characteristic of the northeastern US where the apple tree data was collected (Dragoni et al., 2005), daytime atmospheric VPD is generally low, and averaged 1.12 kPa (standard deviation of 0.73 kPa) during the 4-month observation period. However, a period of high temperature and irradiance that lasted for 2–3 weeks during August resulted in daily VPD peaks of about 4 kPa. These higher VPD values caused the onset of brief but intense drought conditions (Dragoni et al., 2005). The concurrent lack of irrigation lead to conditions of water and heat stress in the apple trees, which was characterized by a reduction in transpiration promptly recorded by the sap flow gauges (Dragoni et al., 2005).

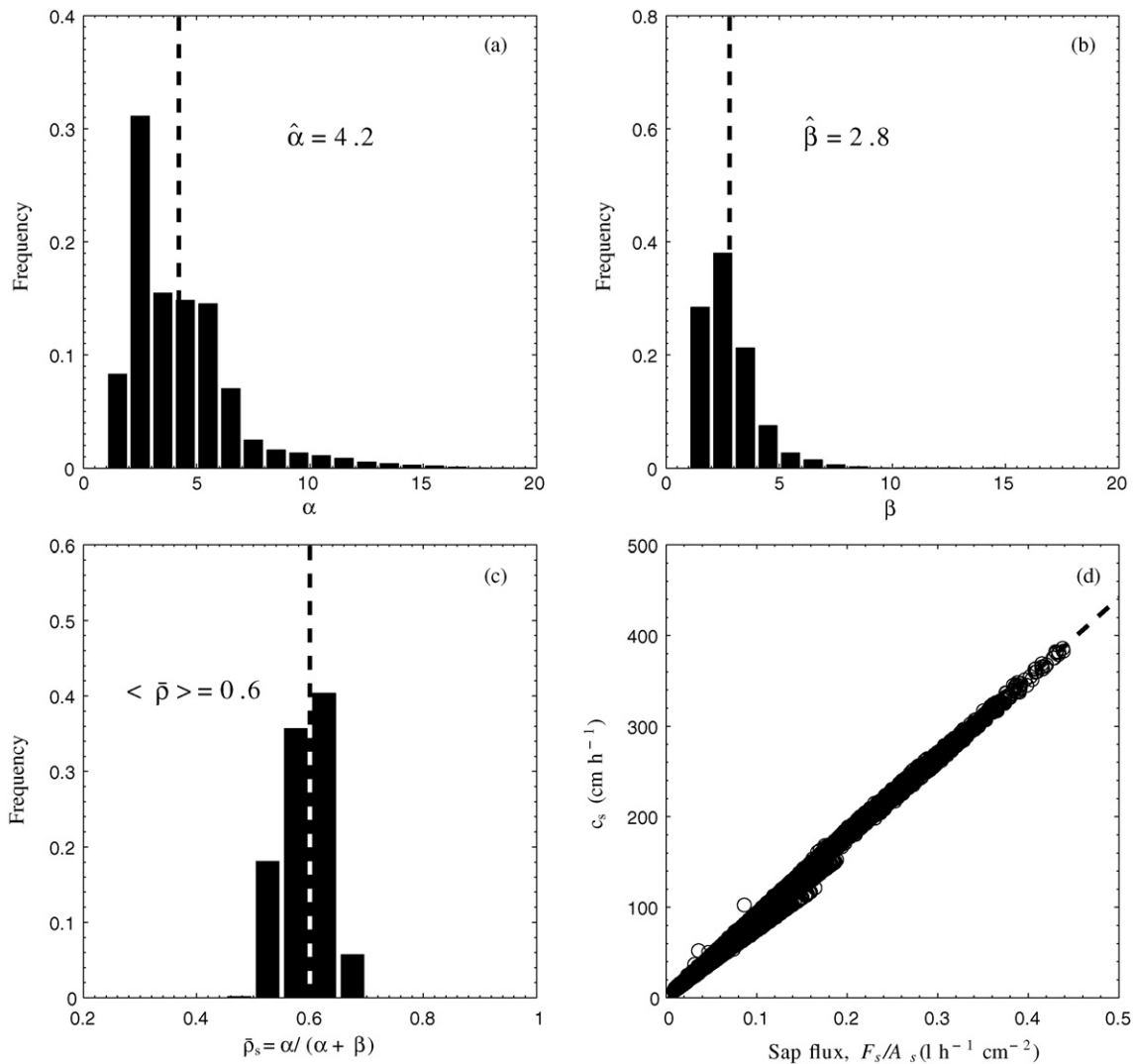


**Fig. 2** – Distribution of  $\alpha$  (panel a),  $\beta$  (panel b), and  $\rho_s$  (panel c) values observed in *Acer saccharum* during the course of a 3-week field observation period ( $N = 19,926$ ). The dimensionless parameters  $\alpha$  and  $\beta$  describe the radial profile of sap velocity, and the ratio  $\alpha/(\alpha + \beta)$  (panel c) describes the distribution of the radial location containing the average flow velocity ( $\rho_s$ ). Panel d provides the relationship between estimated sap flux,  $F_s/A_s$  and  $c_s$ , which are strongly linearly correlated as expected from Eq. (10).

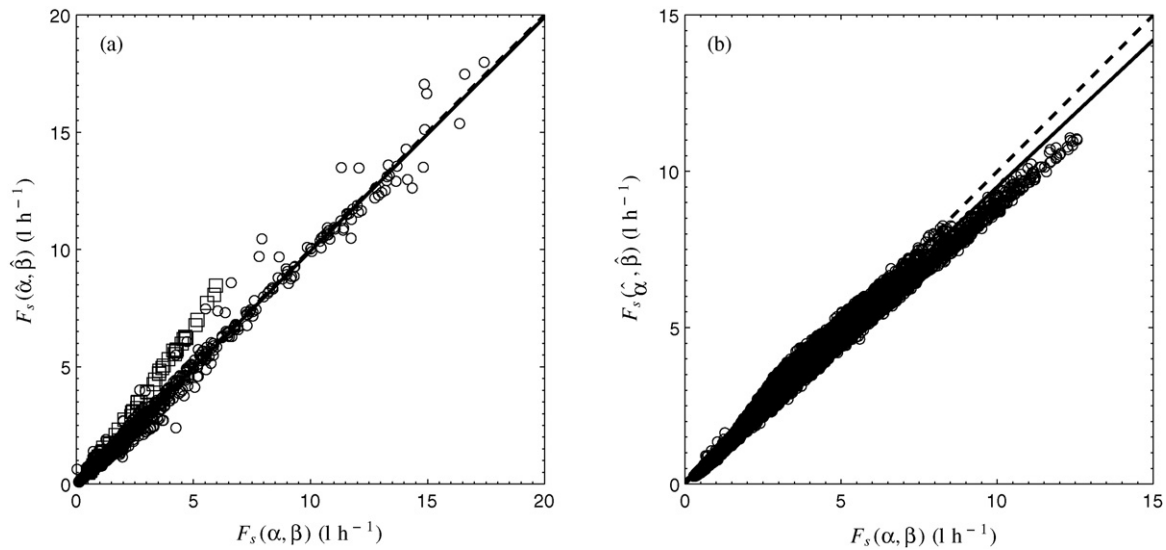
Atmospheric VPD in the mixed forest stand at the Morgan Monroe State Forest facility where we measured the sugar maples was never greater than 2.5 kPa during the observation period. However, soil water availability showed a marked decline beginning at the end of August, which is a common occurrence in this area at the end of the summer. Average daily volumetric water content ranged between 20% and 40% with a constant decline until the end of August, followed by a sharp increase after a large rainfall event. The overall temporal dynamics of soil moisture are further complicated at the MMSF site by spatial heterogeneity in water availability driven by topography and lateral soil moisture redistribution. Nearby-tree measurements taken along the topographic gradient showed that the spatial variability in volumetric water content was as large as temporal variability: in fact, concurrent volumetric soil moisture observations ranged from 10% at the top of the hillslope to 30% at the bottom. Periods of low soil moisture conditions caused partial water stress in the

sampled sugar maples at the top of the hillslope, and they generated substantial heterogeneity in the spatial patterns of transpiration driven by patterns of water demand and availability. Environmental controls on tree water use are addressed in detail within the second part of this manuscript (Dragoni et al., 2009).

For both the sugar maples and apple trees, radial profiles in sap velocities were obtained over a wide range of environmental conditions and tree size (cf. Table 1, Dragoni et al., 2009 and Dragoni et al., 2005 for details). Nevertheless, the distributions of parameters  $\alpha$  and  $\beta$  are strongly unimodal and very peaked in both species (Figs. 2 and 3, panels a and b). The average values of  $\alpha$  and  $\beta$  across all profiles are  $\hat{\alpha} = 5.3$  and  $\hat{\beta} = 2.0$  for sugar maples and  $\hat{\alpha} = 4.2$  and  $\hat{\beta} = 2.8$  for apple trees. For both apples and maples, the distribution of  $\bar{\rho}_s$  is strongly unimodal and very peaked (Figs. 2c and 3c). We find that the time-varying component of sap flow – the distribution of stem conductance,  $c_s$  – is more variable than either of the two



**Fig. 3** – Distribution of  $\alpha$  (panel a),  $\beta$  (panel b), and  $\rho_s$  (panel c) values observed in genetically identical orchard-grown dwarf apple trees *Malus domestica* (var. ‘Royal Empire’) during a 4-month field observation period ( $N = 18,392$ ) during 2002. The dimensionless parameters  $\alpha$  and  $\beta$  describe the radial profile of sap velocity, and the ratio  $\alpha/(\alpha + \beta)$  (panel c) describes the distribution of the radial location containing the average flow velocity ( $\rho_s$ ). Panel d provides the relationship between estimated sap flux,  $F_s/A_s$  and  $c_s$ , which are strongly linearly correlated as expected from Eq. (10).

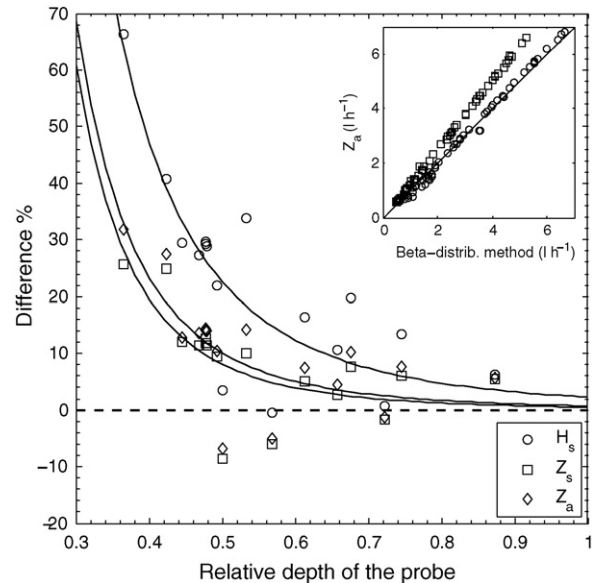


**Fig. 4 – Comparison of sap flux estimates using time-varying estimates of  $\alpha$  and  $\beta$  ( $F_s(\alpha, \beta)$ ) and estimates obtained using the average values of parameters,  $F_s(\hat{\alpha}, \hat{\beta})$ , where  $\hat{\alpha}$  and  $\hat{\beta}$  are taken from Fig. 2a and b (*Acer saccharum*, panel a) and Fig. 3 a and b (*Malus domestica*, panel b). In both panels, the dashed line represents the 1:1 line between  $F_s(\alpha, \beta)$  and  $F_s(\hat{\alpha}, \hat{\beta})$ . For *A. saccharum* (panel a), a linear fit for all data points (solid line) is  $F_s(\hat{\alpha}, \hat{\beta}) = 1.0 \times F_s(\alpha, \beta) - 0.04$  ( $r^2 = 0.99$ ), and squares highlight values associated with a single tree with 40% error. For *M. domestica*, a linear fit for all data points (solid line) is  $F_s(\hat{\alpha}, \hat{\beta}) = 0.94 \times F_s(\alpha, \beta) + 0.10$  ( $r^2 = 0.98$ ).**

parameter describing the radial profile of sap velocity,  $\alpha$  or  $\beta$  (data not shown). However, the relative consistency in  $\bar{\rho}_s$  leads to a strong linear correlation between the value of  $c_s$  and the instantaneous sap flux, which is the sap flow,  $F_s$ , expressed per sapwood area,  $A_s$  (Fig. 3d). This observation of a uniform linear correlation between stem conductance and sap flow is anticipated from Eq. (10).

To determine the feasibility of neglecting variation (within or between trees) in the values of  $\alpha$  and  $\beta$ , we recalculate hourly averages of sap flow in apple trees and sugar maples using the fixed values of  $\hat{\alpha}$  and  $\hat{\beta}$  and fitting our sap velocity profiles using only  $c_s$ . A comparison between sap flow based on maximum likelihood estimates of all three parameters ( $\alpha$ ,  $\beta$ , and  $c_s$ ) and sap flow estimates based only on varying  $c_s$  shows that the difference is minimal (Fig. 4), with the majority of the trees showing differences less than 10%. The one exception is a single sugar maple tree that resulted in about 40% greater flow using  $\hat{\alpha}$  and  $\hat{\beta}$ . Overall, a regression between total sap flow values obtained by fitting each profile to all three parameters, and flow values determined using  $\hat{\alpha}$ ,  $\hat{\beta}$ , and  $c_s$  results in a slope of 0.99 with a regression coefficient of 1.0 for sugar maples and a slope of 0.94 with a regression coefficient of 0.98 for apple trees (Fig. 4).

Comparison between sugar maple sap flows estimated using our approach and the  $H_s$ ,  $Z_s$ , and  $Z_a$  methods confirms that the fraction of radial depth covered by the probes is critical for accurate measurements (Fig. 5). Indeed, we find that the error between the true sap flow and the estimate derived from any of these techniques can be as high as 40% when only a small fraction (i.e. about 30%) of active xylem is sampled (e.g. an 5 cm probe inserted into a 50 cm dbh tree with 15 cm of active xylem). The pattern of increasing error with decreased probe depth is generally similar across the



**Fig. 5 – Comparison between different integration methods of radial patterns of sap velocity as a function of the relative depth a single sap flow probe observation. Lower values in the x-axis indicate probe insertion that covers a smaller portion of the total sapwood. Although the inset demonstrates the correlation between prior methods (y-axis) and our method (x-axis), the larger panel shows that there were strong biases between the methods (i.e. slopes unequal to 1 in the inset). A power function was fit on the entire dataset (solid line), assuming also that the error is 0 when the relative depth of the probe is 1.**



three methods, although the Hatton method clearly performs worst, with errors in excess of 50% when the probe does not extend more than half-way into the active xylem (Fig. 5). Differences between the zero-step ( $Z_s$ ) and zero-average ( $Z_a$ ) methods are minimal across all the depths. For all three methods, relative error approaches (and exceeds) 100% very quickly once the relative depth of the probe is reduced below 0.3.

While the  $H_s$ ,  $Z_s$ , and  $Z_a$  methods each attempt to extrapolate observations across the active xylem using basic algebraic rules, the approach we describe here is most similar to the Gaussian method of describing sap velocity profiles developed by Ford et al. (2004). This method sought to describe the entire profile of sap velocities using a shifted Gaussian distribution to fit the observed values over the range of measurements. The result is a 3-parameter fit that stretches, shifts, and normalizes a symmetric Gaussian distribution to fit the observed data over the range of active xylem transport. When we use the Ford et al. (2004) approach to describe the radial profiles we observed in our sugar maple data, we obtain coefficient of determination values greater than 0.9 for only 65% of sap velocity profiles, which is much lower than the 85% obtained with the Beta distribution function. The frequency of poor correlations is also much higher using the Gaussian method, with 23% of cases having coefficients of determination below 0.8, where as only 5.4% of the Beta distribution function fits yielded coefficient of determination values below 0.8. Overall the use of the Ford et al. (2004) method with our observations provided an average coefficient of determination of 0.84, while our Beta distribution function approach had an average coefficient of determination of 0.95.

## 5. Discussion

Our results demonstrate that the relative sap velocity profiles within our sampled trees (described by the parameters  $\alpha$  and  $\beta$ ) appear to be consistent both among and within trees of the same species, so that a single species-specific parameter set –  $\hat{\alpha}$  and  $\hat{\beta}$  – can be used to describe the radial profile of sap velocities in all of our sample trees. As expected, radial integrated sap velocity obtained using the  $H_a$ ,  $Z_s$  and  $Z_a$  methods are linearly correlated with each other, with regression coefficients higher than 0.9 and intercept not significantly different from zero (Fig. 5, inset). However, the slopes of these regression lines are significantly different than 1, which indicates a bias between the various methods. In particular, we find that the  $H_a$ ,  $Z_s$  and  $Z_a$  methods for inferring radial profiles of sap velocity all result in larger total sap flows, especially when the extent of the measured radial profile is considerably smaller than the xylem depth (Fig. 5). Generally, when the relative depth of the probe is less than 0.6 (i.e. the probe extends less than 60% of the way into the total xylem depth), the  $H_s$ ,  $Z_s$ , and  $Z_a$  methods lead to sap flow estimates 30–40% higher than those estimated using our analytical Beta distribution function approach.

The analytical approach we present here extends the potentially active portion of the xylem to the center of the tree, which introduces a slight overestimate of the actual sap velocity near the sapwood/heartwood interface. Therefore,

our observation that prior approaches still tend to predict higher total sap flows is especially surprising, while the fact that this bias increases as the area sampled decreases is not. Because prior methods do not consider the relative sap velocity profile across a normalized (i.e. dimensionless) gradient of xylem tissue, they are particularly vulnerable to error when the sampled portion of the xylem is small relative to the entire width of the xylem tissue. This implies that prior methods would greatly under-estimate large tree transpiration, while more accurately approximating small tree sap flow. In contrast, our method is un-biased with respect to tree size. Obviously, we cannot determine which one of these methods provides the most accurate absolute estimates, as it was not possible to perform any independent verification of our observations. However, the analytical Beta distribution function approach demonstrates very high correlation coefficients when the probe extends for most of the xylem depth in both small and large diameter trees. This consistency allows us to be confident in the framework we present even when the probe only covers a smaller portion of the total xylem depth.

When applied to our sugar maple data, the Gaussian approach implemented by Ford et al. (2004) results in fits that yield lower correlation coefficients than the Beta distribution function approach we present here. Ford et al. (2004) do not provide data on their correlation coefficients and so we are unable to confirm if their method provided better representation of radial sap velocity profiles in their pine species than it does for the sugar maples we measure here. It is indeed quite possible that different species may present different ‘shapes’ for the radial profile of sap velocity and thus that a Gaussian function may provide a reasonable approximation of the sap velocity curve in some species more than others. However, there are few characteristics of both distributions that may make the Beta distribution function a more suitable and useful approach for describing sap velocity profiles.

Although the Gaussian distribution requires only one parameter, the need to re-scale and shift the distribution necessitates three parameters to achieve a fit to the radial sap velocity profile (Ford et al., 2004). We find that the use of only two parameters in the Beta distribution function allows for a more accurate characterization of the specific profile shape. This increased fidelity between the fitting curve and the observed radial profile of sap velocities is extremely advantageous when the profile shape is similar between individuals of the same species. The assumption of a Gaussian distribution implies symmetric profile shapes (i.e. the mean is equal to the mode). While the Beta distribution can also describe symmetric sap velocity profiles (e.g. when  $\alpha = \beta = 2$ ), Eq. (6) can also describe much more asymmetric curves, a condition that better describes the observed radial profiles of sap velocity. It is important to note that the Beta distribution is a bounded distribution, meaning that the distribution of relative sap velocity is constrained to occur between an inner and outer limit, which is the physical reality of sap transport across the tree xylem. In particular, for the typical unimodal shapes that characterize most sap velocity profiles (c.f. Fig. 1), the Beta distribution has the additional advantage that sap velocities always go to zero at the xylem/cambium interface, which is a physically reasonable expectation. In contrast, a Gaussian distribution is unbounded and its use ensures sap velocities

greater than zero at the sapwood/cambium interface. Given these limitations, the advantage of using a Gaussian function is confined to the accompanying increase in correlation between the functional form and the observed data. However, in our case, for the two species we present here, we find that the Gaussian function performs worse than the Beta distribution function approach we have adopted.

Of course, our overall method is not dependent on the use of a Beta distribution and any other bounded probability distribution would suffice. We chose the Beta distribution function not because it necessarily fits best, but because it is a distribution that has much in common with the physical system we are attempting to describe: a unimodal distribution of values (in this case relative sap velocities) distributed over a bounded region (in this case the active xylem of a transpiring tree). The fact that the Beta distribution we use here provides improved fits when compared to the Gaussian function approach proposed by Ford et al. (2004) is most likely due to the fact that the Beta distribution function does a better job of describing the true underlying distribution of sap velocities. The extremely high degree of consistency in the shape of the distributions we observe across two different species, a wide range of tree sizes, and a diverse suite of environmental conditions suggests the true empirical form of radial sap velocity distributions and our choice of an analytical function to represent it are in agreement.

In this work we presented evidence that it is possible to decouple radial sap flow variability in two components, and that one of them ( $\rho_s(x; \alpha, \beta)$ ) presents high degrees of consistency among trees of different size and at temporal scale. We also claimed that the other component ( $c_s$ ) includes most of the temporal variability induced by the dynamic in environmental factors (mainly water demand and supply). Partial evidence of this were provided by the very high linear correlations with sap flow rates. However, we present a more detailed analysis and evidence in a companion paper (Dragoni et al., 2009).

## 6. Conclusions

We have presented a novel theoretical framework for the study of individual tree sap flow that incorporates both spatial and temporal variability in sap velocities. Our method attempts to decouple variability in sap velocity into two separate components. The first, static component, describes the characteristic radial profile of sap velocities, which is likely linked to the species-specific anatomical and structural properties of the conducting xylem. The second, dynamic component, captures the time-varying rate of sap flow that is intimately linked to the dynamics of atmospheric water demand experienced within the vegetation canopy and individual tree water supply characterized by the root zone soil moisture. A fundamental aspect our approach is the description of a characteristic sap velocity distribution that is consistent between individuals within a single species, which we describe here using a Beta distribution.

The separation of radial and temporal variation in sap velocity observations provides: (1) a direct mechanism for investigating how stem conductance is governed by variation

in environmental conditions, particularly water supply/demand; (2) a means for comparing characteristic rates of plant water use among individual trees of varying size and between different species; (3) a consistent and physically meaningful method for extrapolating point observations of sap velocity across the entire depth of conducting xylem.

Experimental evidence confirms the utility of our approach in the case of a population of sugar maples in a mixed deciduous forest and apple trees in a homogenous orchard, despite the fact that observations were drawn from a wide range of tree sizes, under varying soil moisture levels and atmospheric conditions that determine water demand. While these results require further confirmation in order to be generalized, they nevertheless offer the basis to improve both the specific sampling strategies used to estimate whole-tree transpiration using sap velocity probes as well as methods employed to upscale water use of individual trees to larger scales for evaluation of landscape water balance.

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