

A model describing sap velocity in poplars

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Abstract

Populus species are frequently used in hill country soil conservation programmes in New Zealand, because of their rapid transpiration rate and widely distributed root system. Recently, transpirational water loss from trees has been estimated as the water flux through the xylem, measured by the heat pulse technique. Potential transpiration during bright days has been reported, based on daylight values of sap flux. However, sap flux has been described only as a sinusoidal profile, without establishing parameters for statistical inference. This paper explores the modelling of sap velocity using a Beta function to describe temporal sap velocities and sap flow. Parameters for night basal velocity, day length, maximum daylight velocity or maximum daylight sap velocity (amplitude) for each probe depth were fitted using the program Sigmaplot. The implications of the model for the description and prediction of sap velocities and estimation of potential sap velocity are discussed.

Additional key words: *sapflow, water balance, poplar, trees, silvopastoral, model*

Introduction

Populus species are frequently used in hill country soil conservation programmes in New Zealand, because of their rapid transpiration rate and widely distributed root system (Edwards, 1987; Hicks, 1995; Zwart, 1996). Few measurements of transpiration have been made on individual mature poplar trees, because of the limitations of the techniques, and the size of the trees involved (Edwards and Booker, 1984).

Recently, transpirational water loss from branches, roots or complete tree canopies (Hinckley *et al.*, 1994), has been estimated as the water flux through the xylem, measured by the heat pulse technique (HPT) (Swanson, 1994). The HPT provides an efficient method of measuring sap flow in single trees at remote locations (Edwards, 1987), and has been widely used for estimating sap velocity at one position within the xylem of individual woody plants (Hatton *et al.*, 1990).

The simplifying assumption that sap velocity is constant across the sapwood conducting area does not hold for most of the species examined. Sampling at several depths into the sapwood is usually necessary to characterise the sap velocity profile in large trees (Edwards and Booker, 1984). If the radial profile of sap velocity is known, sap flow can be calculated by integrating radial increments of sapwood area with the corresponding sap velocities (Edwards and Booker, 1984).

Because of the changing nature of tree transpiration, the HPT is usually set to sample the sap velocity at short time intervals (15-30 minutes). Even a time series of sap flow of a single day results in a rather complex model, and these have not been analysed routinely. Instead the daily total sap flow of the tree (Cérmak *et al.*, 1992; Caspari *et al.*, 1993), or the stand (Becker 1996), in near ideal meteorological conditions have been used for statistical comparisons. However, using the daily average overlooks important information on the transpirational activity of the trees, and a model that describes this is needed.

A model that parameterises temporal variations of sap velocity and sap flow under near ideal meteorological conditions may assist statistical inference of tree transpiration relations and potential transpiration. Transpiration patterns between tree species, or among trees of different canopy dominance status, size or age, can be easily compared using parameters that characterise the main features of the tree sap flow.

Simulation of values by such a model may be helpful in the estimation of missing values, based on data sets of the same tree or other trees used in the investigation. Estimation of missing values is often required as the local fauna (possums or keas) can damage equipment, when unattended at remote locations.

This paper explores the modelling of sap velocity using a Beta function to describe temporal sap velocities. The flexibility of this family of functions and its different

parameters can be incorporated into a model representing the asymmetrical distribution of sap flux during the day, flow initiation and cessation, and overnight activity. Since sap velocity is usually measured at several depths into the sapwood, parameters for each depth may be useful when describing radial variation in the axial conductivity.

The objective of this work is to present a model that represents sap velocities for poplars under near ideal conditions, considering that such a model has not been found in the literature.

Materials and Methods

The research (Guevara-Escobar *et al.*, 1997) was conducted at a commercial farm in the Pohangina Valley, 44 km north east of Palmerston North, New Zealand (latitude 42° S, longitude 172° E, 200-250 m elevation) from 1 November to 12 December 1996.

The 3.5 ha area was under silvopastoral land use and had a north-west facing aspect and a 20.5° ±0.54 (mean ±standard error of the mean) slope. As an overstorey the hill had spaced *Populus deltoides* (16.4 m ±0.4), with a mean diameter at breast height (DBH) of 0.7 m ±0.02, and 14.9 m ±0.75 crown diameter. Four trees were selected randomly from trees within one standard deviation from the mean DBH of the stand, and located in unbroken terrain. Sap flow was measured using the HPT on four trees (Edwards and Warwick, 1984). Records of the heat pulse times were kept every 20 minutes from four sets of heat probes and thermistors inserted at 5, 10, 20 and 40 mm depth into the sapwood at 1m height, around the tree. Sap velocities were calculated using HP8000 software (CSIRO, Australia - HortResearch, New Zealand). A core sample from the stem was taken near to where the probes were implanted to determine, by colour and texture, the approximate inner and outer boundaries of the sapwood (Zimmermann, 1983), and its volume fractions of wood and water (Swanson, 1994). Sap flow recorded at each probe depth was considered representative of a ring of sapwood with limits defined by the midpoint between successive probe depths, or by the interface with the cambium or the heartwood (Edwards and Booker, 1984). Total sap flow was calculated as the sum of these partial areas multiplied by their associated sap velocities. The calculated sap flow was assumed to be a direct estimator of the transpirational water loss of the tree. Records for two fine days were used to model 24-hour sap velocities from two trees (#9 and #73).

The Beta function (Mood *et al.*, 1974) is a three parameter function in various forms, used to model

phenomena defined over a finite interval $a < x < b$. It has a wide variety of shapes and can be expressed as:

$$y = \alpha(a-x)^\beta(x-b)^{\beta-\gamma} \quad (1)$$

often a and b are scaled to 0 and 1, respectively. α is an amplitude (scale) parameter. β and γ are shape parameters. Lower values (less than 5) of β indicate flatness while higher values indicate a sharp peak. γ is a skewness (or symmetry) parameter, zero indicating symmetry.

Common parameters for β and γ were used to describe the shape of all profiles. However, the activity at the four depths was denoted by the subscript i , allowing for the specification of simultaneous fits of particular parameters at each depth along with common parameters.

Three different areas of activity were identified for modelling: before dawn, daylight and night. A parameter k_i represents the overall night basal velocity, and the beta function characterises the daylight activity in addition to k_i .

The parameter a was represented as s_i+l_i , where s_i is the commencement of daytime sapflow and l_i the duration of daytime sapflow. The parameter α was used to describe the different amplitudes. All the parameters were incorporated as follows:

$$\text{Sapflow} = k_i \quad \text{for } 0 \leq t \leq s_i \quad (2)$$

$$= k_i + \alpha(s_i+l_i-t)^\beta(t-s_i)^{\beta-\gamma} \quad \text{for } s_i \leq t \leq s_i+l_i \quad (3)$$

$$= k_i \quad \text{for } s_i+l_i \leq t \leq 1 \quad (4)$$

for each probe depth $I = 1 \dots 4$, regarding 24 hour period as time $t = 0 \dots 1$, and for each tree.

Model fits were obtained using the program Sigmaplot (SPSS Inc., 1997). Parameters were compared with analysis of variance (Mood *et al.*, 1974) using the Minitab subroutines (Minitab Inc., 1995).

Results and Discussion

Time courses of the observed sap velocities for trees #9 and #73 on 3 and 24 November (days 3 and 24, respectively) are shown in Figure 1. Two main components of the sap velocity course can be identified:

- i A basal component, showing activity distinct from zero and decreasing overnight, especially in the more superficial sampling areas into the sapwood. Although the source of this sap flow could not be identified, it was consistently present on different days and trees.

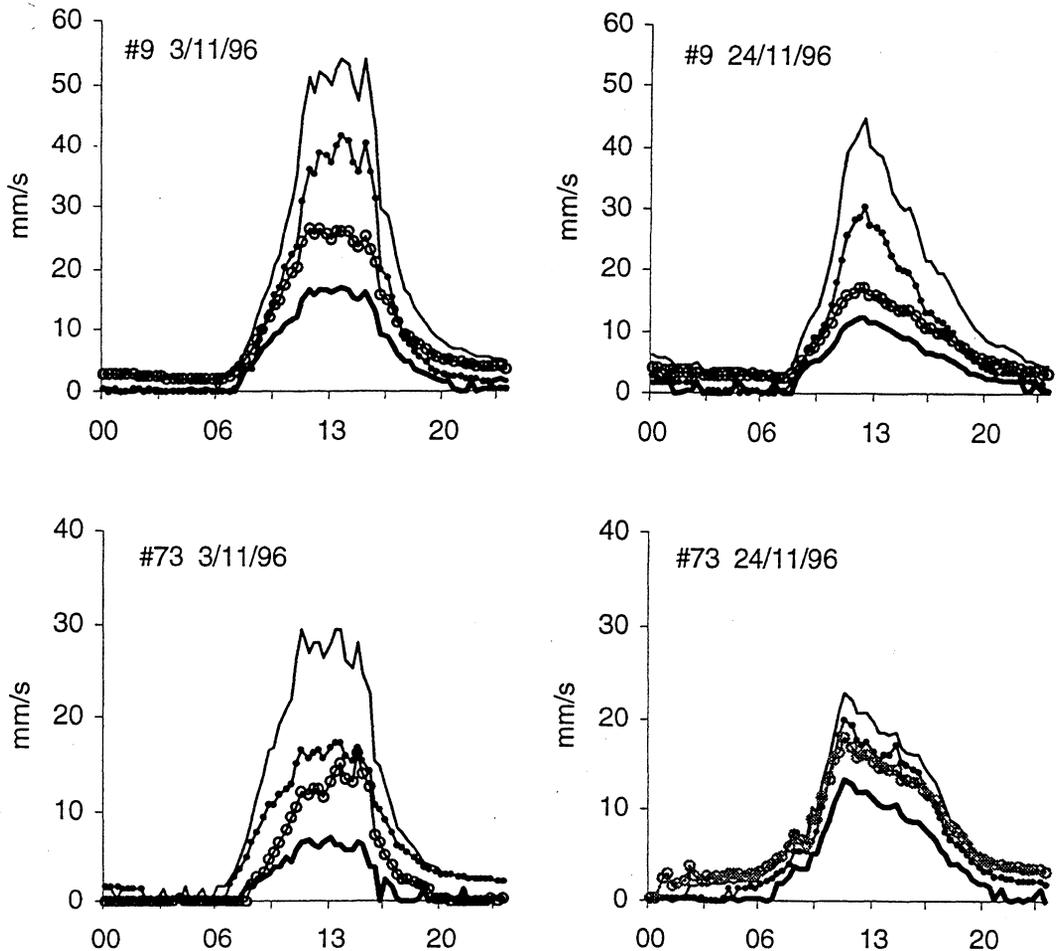


Figure 1. Time courses (NZST) of sap velocity measured at four depths (\rightarrow 5mm, \dashrightarrow 10mm, $\cdot\cdot$ 20mm, — 40mm) in the sapwood of two *Populus deltoides* trees during two fine days at Pohangina Valley, New Zealand on 3 and 24 November 1996.

ii A peak sap velocity during daylight. The slope of the curve in the morning and afternoon showed a clearly asymmetrical pattern. The onset of the activity was followed by a sharp rise until noon and then a slow decrease during the afternoon and early night periods. This pattern is highly correlated with the course of photon flux density and has been demonstrated for many species (Cérmak *et al.*, 1995; Arneth *et al.*, 1996; Granier, 1996b).

Differences between days and trees were noticeable. Day 3 had a greater sap velocity over a longer time than day 24. Tree #9 had greater activity than tree #73, for a similar duration.

Figure 2 shows a plot of the four model fits to trees #9 and #73. Focus was primarily on differences between probe depths into the sapwood.

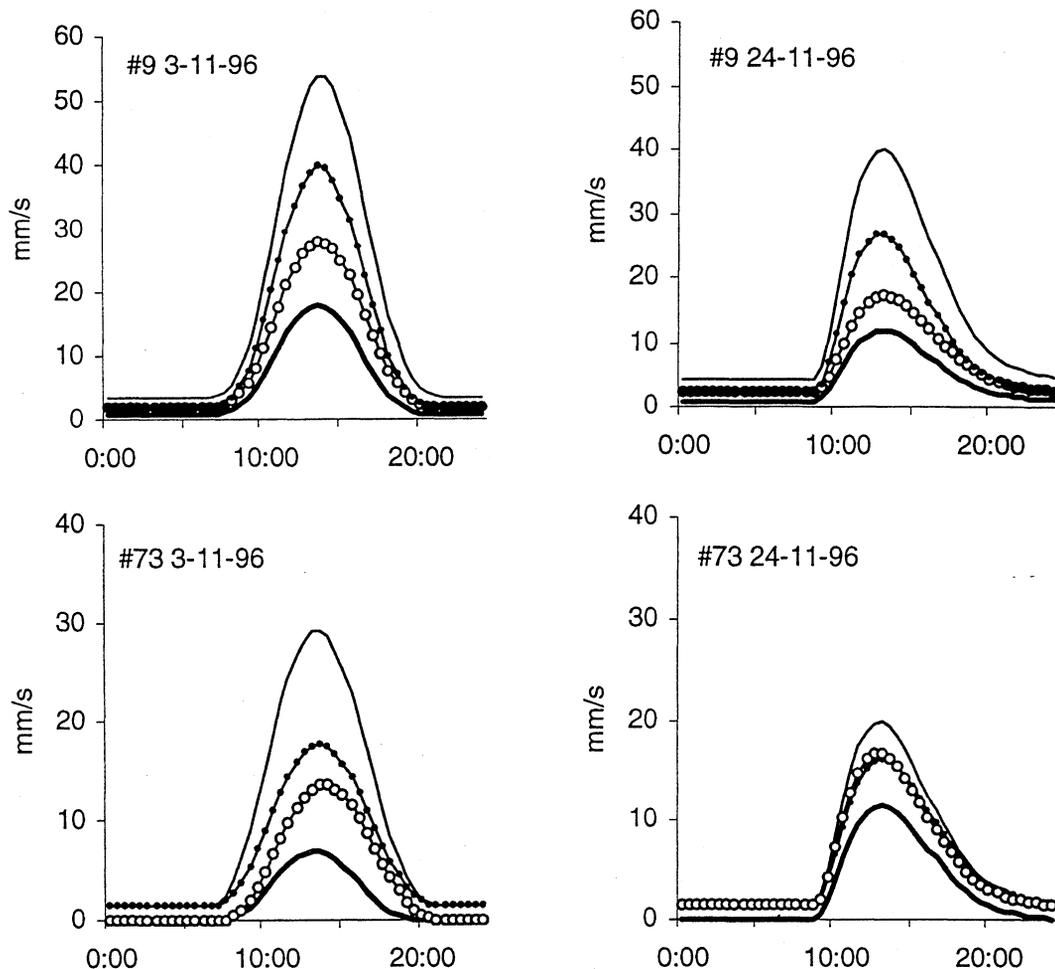


Figure 2. Modelled fits for time courses (NZST) of sap velocity in *Populus deltoides* (tree #9 and #73) at different depths (— 5mm, -•- 10mm, -○- 20mm, — 40mm) in the sapwood.

Night basal velocities, k_i

Sap velocity at the innermost probe was clearly the lowest, rising to the highest flows at the outermost ($P < 0.05$). Differences between trees were significant ($P < 0.01$), but differences between days were not ($P > 0.05$). Thus, it seems relevant to retain the k_i in the model subject to the constraint $0 \leq k_1 \leq k_2 \leq k_3 \leq k_4$.

Onset of daylight flows s_i

The start times were almost the same at each probe depth, showing no significant differences ($P > 0.05$). It,

therefore, should suffice to use a single parameter, s , to signify the simultaneous onset of daytime flow at all probe depths. Differences between days and between trees were significant ($P < 0.01$ and $P < 0.05$, respectively).

Daytime duration of elevated sapflow, l_i

As with onset times, no differences were evident between probe depths ($P > 0.05$). A single daytime duration for sap velocity, l , can, therefore, be used to signify the simultaneous reversion to basal velocity. When different s_i and l_i were used in the model, the

duration and amplitude parameters, α_i , at each depth were affected, not being independently determinable. fixing s and l solved this problem. The daytime duration differed significantly among days and between trees ($P < 0.01$ in both cases).

Shape parameter, β (kurtosis)

The values on day 3 (48 for tree #9 and 3.3 for tree #73) were significantly ($P < 0.05$) lower than those on day 24 (13.8 and 11.7 respectively). This indicated the more sharply peaked nature of the sap velocity on day 24, common to all probe depths (Fig. 2).

Shape parameter, γ (skewness)

Again, these values were lower on day 3 (0.47 for tree #9 and 0.4 for tree #73) than on day 24 (11.5 and 9.6 respectively), although the difference was not significant ($P > 0.05$). Comparing the data in Figures 1 and 2, day 24 sap velocity had a more pronounced asymmetry (positive skew), common to all probe depths. With the high skewness evident on day 24, the end of the daytime flow was estimated to be in the beginning of the next day. In extreme cases it may be that reversion to baseline may not have occurred before the onset of the next daytime sap flow.

Note that keeping β and γ common to all probe depths retained the same shape to all flow profiles. Supporting the intuitive appeal of this was our observation in preliminary model fitting that only minor and insignificant differences were obtained between different probe depths. Flow profiles, therefore, differ only in amplitude (scale) between probe depths.

Amplitudes, α_i

These values were not well estimated in the above model, and the standard errors were high. This was a consequence (at least in part) of allowing the s_i and l_i to differ. Therefore, analysis of α_i was not informative, although it was clear from the data and from a sensible biological perspective that the α_i should be allowed to vary subject to the constraint $\alpha_1 \leq \alpha_2 \leq \alpha_3 \leq \alpha_4$.

Goodness of fit, R^2

All values were high, ranging between 0.97 to 0.98. A model incorporating covariate(s) may explain the obvious day to day differences, most noticeably in the shape of the sap velocity profiles. Day 24 was a calm day, whereas day 3 was fine and had high wind runs. When the aerodynamic conductance greatly exceeds canopy conductance, the stomatal control of canopy-level transpiration is generally insignificant (Köstner *et al.*, 1992).

The differences obtained between trees are a consequence of the unadjusted sap velocities used. Transformation of the xylem sap flow by dividing it by the projected tree crown area (a surrogate of occupied ground area) has been shown to reduce the variability between trees (Köstner *et al.*, 1992; Hatton *et al.*, 1995; Arneith *et al.*, 1996; Granier *et al.*, 1996a). Table 1 shows some allometrics of the studied trees. These adjustments can be made after the model is fitted.

Table 1. Characteristics of the trees sampled for sap flow measurements.

Tree	DBH ^a (m)	Projected Crown area (m ²)	Height (m)	Sapwood area (m ²)
9	0.729	134	35	0.1975
73	0.700	131	32	0.1699

^a diameter at breast height (1.30m) on the uphill side of the tree.

Further modelling of the crown volume as a geometric solid (Wilkinson, 1995), and then adjusting the sap flow accordingly may reduce the individual variation. However, because trees have complex fractal shapes, this raises the question to what extent can the tree crown shape be simplified while still providing realistic results.

Conclusion

The Beta function can provide a good model fit of xylem sap velocities. Description of the sap velocity and hence, sap flow, can be mathematically expressed in a rather simple form. For further modelling parsimony, only k_i and α_i should be allowed to vary, with the other parameters kept common. However, day to day and tree to tree differences must be allowed for.

The statistical differences encountered when evaluating the parameters of the model accounted for the individual and temporal variations between the sap velocity courses, and were in accordance with qualitative descriptions of the original data. The fitted model showed differences that were difficult to ascertain in the plotted time courses of the original sap velocities.

Trees #9 and #73 were neighbouring trees in the stand and had similar allometry. However, they had different transpirational activity as the model demonstrated. Further adjustments to the individual data sets can be advised with this statistical base.

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