

# Reverse flow in roots of *Sesbania rostrata* measured using the constant power heat balance method

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## ABSTRACT

This investigation was performed to examine qualitatively and quantitatively the reverse flow in partially dried roots of *Sesbania rostrata* using the constant power heat balance method. First, a semi-empirical technique for estimating sheath conductance of sap-flow sensors without assuming that sap flow is zero at night was proposed. Sap flow measured with the heat balance method was compared with water uptake as measured by a potometric method. Sap flow was overestimated by 56.1% for a 3.3-mm-diameter root, and by 40.0% for 6.1 mm and 33.3% for 8.8 mm roots. However, high correlation coefficients between the rates of water uptake and sap flow demonstrated that calibration would provide reliable values for root sap flow. To detect reverse flow, a split root experiment was conducted using a *S. rostrata* plant with its root system divided between dry and wet compartments. Daily sap flow of the drying compartment declined whereas that in 'wet' root increased, suggesting that the decrease in water uptake by 'dry' roots was offset by the 'wet' roots. Reverse flow was observed at night in the root on the dry side of the container when the soil water potential was less than  $-0.30$  MPa. The total amount of water released into the soil during the night period was estimated to be 22.5 g.

**Key-words:** hydraulic lift; root sap flow; sap flow; sap-flow sensor; split roots.

## INTRODUCTION

It is known that reverse flow, which refers to the movement of water from roots into soil (Baker, Wraith & Dalton 1992), can occur when part of a root zone is wet and part is dry. When water moves from deep wet soil layers into the drier upper horizons through plant root systems, the phenomenon is called hydraulic lift (Richards & Caldwell 1987). Reverse flow has been observed not only for trees (e.g. Emerman & Dawson 1996) and shrubs (e.g. Richards & Caldwell 1987) under natural conditions, but also for herbaceous plants (van Bavel & Baker 1985; Baker & van Bavel 1988; Blum & Johnson 1992; Xu & Bland 1993) in split root experiments. It has been suggested that increases in soil moisture in the dry layer resulting from reverse flow may provide benefits to the plant itself and/or to neigh-

bours (van Bavel & Baker 1985; Richards & Caldwell 1987; Dawson 1993). If an increase in soil moisture is significant, reverse flow may lead to the efficient use of water in intercropping or agroforestry systems in semi-arid areas during dry periods. However, this possible advantage is poorly documented (see also Ong *et al.* 1996).

Evidence of reverse flow has been detected by measurements of soil water content (van Bavel & Baker 1985; Baker & van Bavel 1988; Xu & Bland 1993), soil water potential (Richards & Caldwell 1987; Blum & Johnson 1992) or by using deuterated water as a trace (Caldwell & Richards 1989). Thermic methods such as Huber's heat pulse method and the stem heat balance method (Sakuratani 1981) are considered to be useful for the direct measurement of reverse sap flow in roots. Regarding the heat pulse method, heat pulse probes may need to be installed in an inverse configuration on roots when reverse flow is measured using conventional probes, because the two thermal sensors are asymmetrical with respect to the heater (e.g. Cohen *et al.* 1988; Green & Clothier 1988). In contrast, the thermocouples of a sap-flow sensor designed for the heat balance method (Sakuratani 1981), termed the constant power heat balance method (Dugas 1990), are usually located symmetrically with respect to the heater. Thus, it may be easily applicable to measurement of reverse flow. Lott *et al.* (1996) successfully used a constant temperature heat balance method (Khan & Ong 1995) to measure sap flow in lateral tree roots but did not report reverse flow. Few attempts to calibrate the constant power heat balance method for roots or measure reverse flow in roots using the method have been reported.

The first step in the present study was to examine the applicability of the constant power heat balance method to the measurement of root sap flow. Secondly, split root experiments were conducted to detect reverse flow. As a test plant, we used *Sesbania rostrata*, a green manure plant, because it tends to have roots suitable for the installation of the sensors.

## MATERIALS AND METHODS

### Estimation of sheath conductance

The theory of the constant power heat balance method and the sensor design is described elsewhere (Sakuratani 1981, 1984). The rate of flow,  $F$ , in a plant stem is determined from the following equation:

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$$F = \frac{Q - \lambda A \frac{\Delta T_u + \Delta T_d}{\Delta x} - kE}{c\Delta T} \quad (1)$$

where:  $Q$  is the heat supply to the stem segment;  $\lambda$  and  $A$  are the thermal conductivity and cross-sectional area of the heated segment;  $\Delta T_u$  and  $\Delta T_d$  are the vertical temperature difference upward and downward from the heater;  $\Delta x$  is the distance between the two thermocouples used to measure  $\Delta T_u$  and  $\Delta T_d$ ;  $E$  is the voltage across a radial thermopile encircling the heater;  $k$  is the constant of the heat flow sensing element, the so-called sheath conductance (Baker & van Bavel 1987);  $c$  is specific heat of water; and  $\Delta T$  is the temperature difference across the heater.

To determine  $k$ , it is usually assumed that  $F$  is zero during the predawn period. However, it is known that small amounts of sap flow may continue to flow in stems at night and the conditions of  $F = 0$  may not therefore occur; this is an important consideration if reversal of sap flow at night is suspected because periods when  $F = 0$  are then likely to be transient. To estimate  $k$  without assuming  $F = 0$ , we used a new method. Rearranging Eqn 1 yields the following equation:

$$k = \frac{Q - \lambda A(\Delta T_u + \Delta T_d)/\Delta x}{E} - \frac{cF}{E}\Delta T$$

$$= k_a - s\Delta T \quad (2)$$

where  $k_a = [Q - \lambda A(\Delta T_u + \Delta T_d)/\Delta x]/E$ ,  $s = cF/E$  and  $k_a$  is defined as apparent sheath conductance. Equation 2 is rewritten as:

$$k_a = k + s\Delta T \quad (3)$$

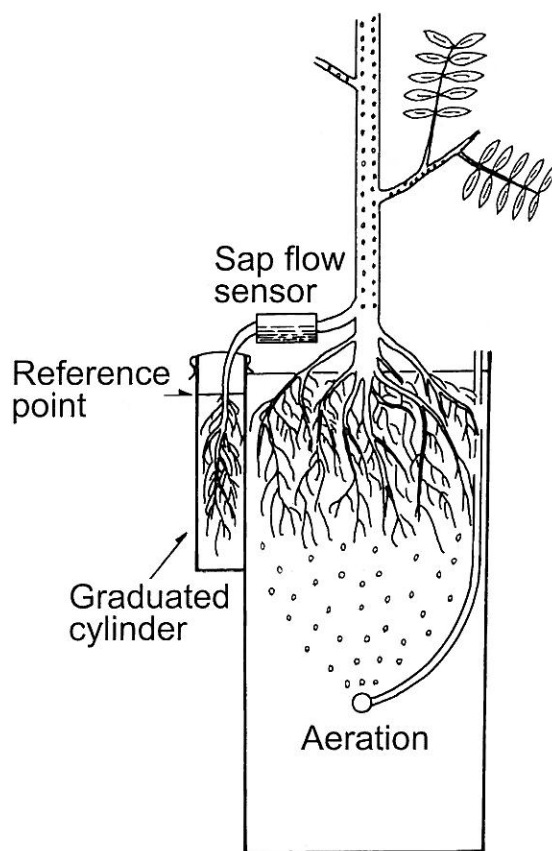
Equation 3 shows that a plot of  $k_a$  against  $\Delta T$  gives a straight line, if  $s$  is assumed to be a constant under conditions that  $F$  is very small. The intercept of the extrapolated line on the  $k_a$ -axis may give  $k$  even though  $\Delta T > 0$ .

### Test of sap-flow sensor

It has been reported that the heat balance sensors would measure sap flow in the stem of plants usually with an accuracy of  $\pm 10\%$  without calibration (e.g. Sakuratani 1981; Baker & van Bavel 1987). However, Ham & Heilman (1990) showed that a heat balance sap-flow sensor with a narrow heater overestimated sap flow when flow was high, and that a wider heater improved sensor performance. To avoid overestimation due to a narrow heater, sap-flow sensors with a heater width of 15 mm, 5 mm longer than the original sensor (Sakuratani 1984), were constructed for the present study. The internal thermocouples of the sensors were wired according to Steinberg, van Bavel & McFarland (1990). Prior to the investigation, the performance of this modified sensor was tested by comparing the sap flow rate of a *Sesbania rostrata* root, as measured by a sensor, with water uptake by the same root, as determined by a potometric method.

*Sesbania rostrata* seeds which had been germinated in wet sponge rubber were grown in 1.5 dm<sup>3</sup> plastic pots filled

with a nutrient solution which consisted of a half strength 'Enshi' solution (Yamasaki 1982) for macro elements and the Arnon solution (Arnon & Hoagland 1940) for micro elements. After reaching a height of about 0.3 m, three seedlings were transplanted in stainless steel containers (0.25 m long, 0.25 m wide and 0.5 m deep) filled with nutrient solution and then grown in a greenhouse. When the largest roots reached about 10 mm in diameter at the base of the stem, a plant with a root suitable for the installation of sensors was selected and a sap-flow sensor was installed on the upper part of the root (Fig. 1). Both the sensor and stem sections above and below the sensor was covered by insulation (cork) 0.05 m long and 0.015 m thick, and aluminum foil to minimize the influence of fluctuations in solar radiation and air temperature. Sensor signals were logged at 30 s intervals using a datalogger (model 21X; Campbell Scientific Inc., Logan, UT, USA) and averaged over 30 min periods. Sap flow in the root was measured continuously



**Figure 1.** Experimental set-up for testing the performance of the constant power heat balance method on roots. Sap flow in *Sesbania rostrata* grown in stainless steel containers filled with nutrient solution was compared with water uptake measured by a potometric method. The surface of the container was covered by insulation (foam polystyrene) to reduce evaporation. The top of the graduated cylinder was also covered by aluminium foil. The cylinder was wrapped with black friction tape to exclude light.

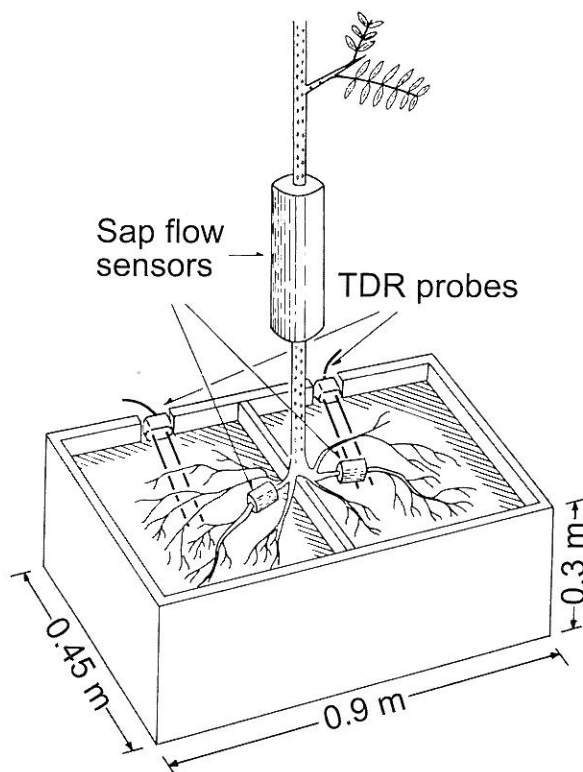
through the day and night. the value of  $k$  was determined from measurements at night using Eqn 3.

The lower half of the measured root, having many lateral roots, was placed in a graduated cylinder (0.2 dm<sup>3</sup> capacity) filled with the nutrient solution described above. Water uptake by the root was obtained by measuring the volume of water supplied to a reference point on the cylinder every 30 min. A comparison was made for three roots with different diameters between approximately 1000 and 1700 h Japan standard time (JST) so that different levels of sap flow were obtained. This test was conducted for several 1–2 d periods in October 1994.

### Split root experiment

*Sesbania rostrata* plants which had been germinated in a vermiculite seed bed were grown in 2.0 dm<sup>3</sup> plastic pots for 100 d. On 4 June 1996 two selected plants were transplanted into two wooden root boxes as shown in Fig. 2. The root system of the plant was split with approximately half of the roots on either side of a vertical barrier. The growing medium was a sandy loam soil. Water was applied daily to both compartments to maintain wet soil conditions.

The split root experiment started 30 d later using one of the boxes. Prior to the experiment, roots near the base of



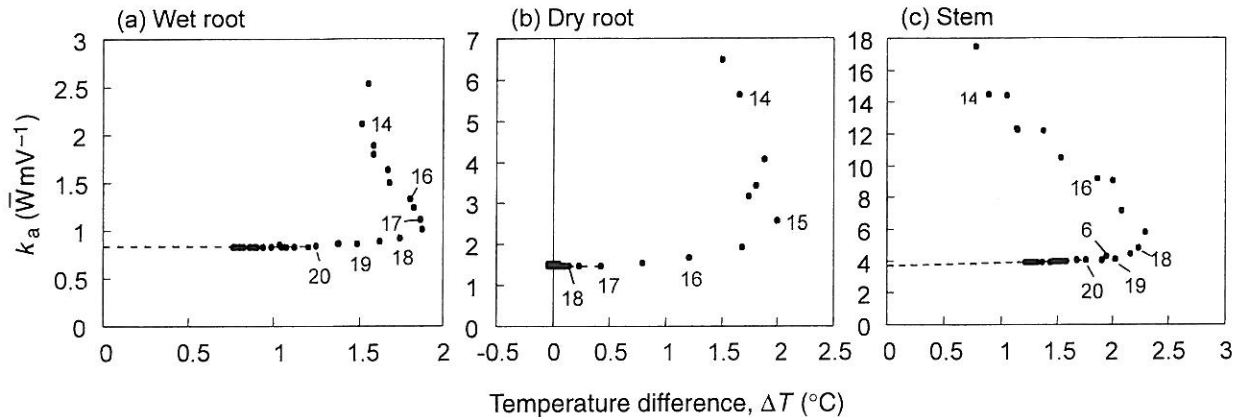
**Figure 2.** Two-compartment wooden box in which a *S. rostrata* plant was grown. The arrangement of the TDR probes and the heat balance sap-flow sensors on the stem and two large roots of the plant is shown. The box was nailed to prevent leakage of water between the compartments.

the stem were partially exposed on each side of the barrier by careful excavation. On each side, sap-flow sensors of the type described above were carefully installed on the largest root at a distance of about 0.05 m from the stem. These sensors were covered by insulation described above. A sap-flow sensor with a heater width of 20 mm was also attached to the stem at a distance of about 0.20 m above ground level. The heater width was chosen on the basis of previous findings that the heater should be wider than the diameter of stem to ensure thermal equilibrium between the xylem fluid and sensor. Insulation that was 0.1 m long and 0.02 m thick was fitted over the sensor described above. The diameters of the roots on the wet and dry sides and of the stem used for the sap flow measurements were, respectively, 4.8, 4.6 and 11.0 mm at the start of the experiment. Since the sensors were held in place by elastic rubber bands, growth of the roots and stem was possible during the measurement period. Sensor signals were logged and averaged as described above. The value of  $k$  was determined graphically for every night on the basis of Eqn 3 and was used to calculate  $F$  for a period from 1200 h to 1200 h on the following day. The reason that  $k$ -value was permuted at noon was that  $F$  is insensitive to  $k$  when sap flow is high. When  $\Delta T = 0$ , Eqn 1 is undefined and when  $|\Delta T|$  is close to 0, large errors occur in  $F$ . However, when  $\Delta T = 0$ , theoretically  $F = 0$ ; thus, in this experiment,  $F$  was assumed to be zero when  $|\Delta T| \leq 0.2$  °C.

Time domain reflectometry (TDR) (model CS615; Campbell Scientific Inc.) was used to monitor changes in soil water content. A TDR waveguide of 0.3 m in length was installed into the soil in each compartment with an angle of 30° from one side of the compartment towards the central part of the soil parallel to the barrier, 0.2 m away from the barrier. Thus, the tip of the probe was 0.15 m from the soil surface. Solar radiation was also measured. The experiment was carried out in a greenhouse between 4 and 16 July 1996. One compartment was allowed to dry between 4 and 14 July, and rewatered at 1145 h on 15 July. The other compartment was watered daily to maintain wet soil conditions throughout the experimental period. It was visually confirmed that there was no water leakage from the wet to the dry compartment.

At the end of the experiment, the dry weight of the dry roots in both compartments was determined. The ratio of dry weight of the root on which the sensor was installed to the total dry weight was used to estimate total sap flow for all roots in each compartment assuming that sap flow in the roots is proportional to their dry weight. Diameter,  $D$ , in the root segments on which the sensors were installed was also measured at the end of the experiment. The value of  $D$  for every day was estimated by assuming that the thickness of the roots increased at constant rate during the experiment.

To obtain a relation between volumetric water content ( $\theta$ , m<sup>3</sup> m<sup>-3</sup>) and water potential ( $\Psi_s$ , MPa) for this soil, an experiment was started on 20 August 1996 using another box. A ceramic-tipped tensiometer was installed near the TDR probe in the dry compartment. Values of  $\Psi_s$  that were



**Figure 3.** Relation between temperature difference across the heater of a sap-flow sensor,  $\Delta T$ , and apparent sheath conductance,  $k_a$ , for a period from 1300 to 0700 h. Numbers in the figure shows times for a period when decreases in  $\Delta T$  or  $k_a$  was distinguished.

greater than  $-0.063$  MPa was determined by the tensiometer and  $\Psi_s$  values less than  $-0.064$  MPa by a thermocouple psychrometer (model Tru Psi; Decagon, Pullman, WA, USA). The psychrometer measurements were conducted by sampling small amounts of the soil near the TDR probe. The relation between  $\theta$  and  $\Psi_s$  was:

$$\Psi_s = -\exp(6.93 - 178.52\theta + 870.38\theta^2 - 1381.6\theta^3) R^2 = 0.974 \quad (4)$$

## RESULTS AND DISCUSSION

### Relation between $\Delta T$ and $k_a$

Figure 3 shows typical examples of relation between  $\Delta T$  and  $k_a$  obtained for 'wet' and 'dry' roots and the stem in the split root experiment between 1300 h on day of year (DOY) 191 and 0700 h on DOY 192. The patterns for the three are not greatly different. As expected,  $k_a$  decreases slowly toward evening. The relation between  $k_a$  and  $\Delta T$  can be approximated by a straight line for night-time hours (on this day, 2100–0700 h for the wet root and stem measurements 1700–0700 h for those for dry roots). The value of  $k$  is estimated by extrapolating the line to the  $k_a$  axes. In the case that reverse flow occurs for the 'dry' root as described below,  $k_a$  tends to reach a minimum at  $\Delta T = 0$ . Similar relations between  $k_a$  and  $\Delta T$  were obtained in all measurements in this experiment. These results verified the assumption that  $k$  can be estimated on the basis of Eqn 3.

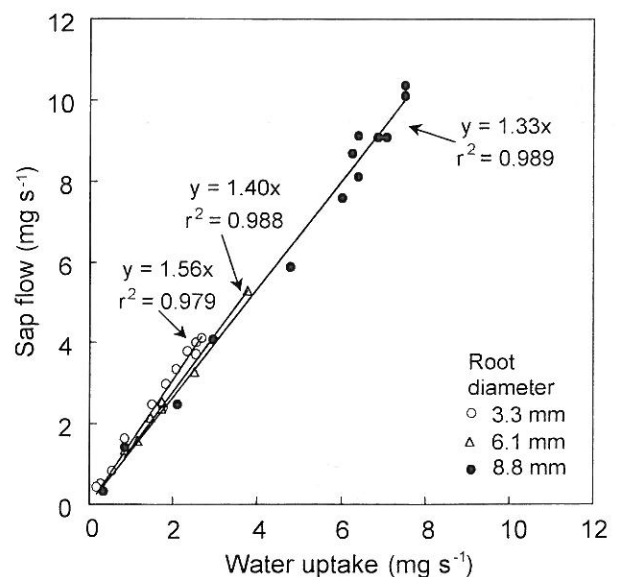
### Performance of the sap-flow sensor

Figure 4 compares the sap flow rates determined by the sap-flow sensor and water uptake by the root obtained by the potometric method. Although the heater length had been increased, sap flow was still overestimated by 56.1, 40.0 and 33.3%, respectively, for 3.3, 6.1 and 8.8 mm-diameter roots. The relation between the root diameters,  $D$ , and the reciprocal of the slopes in Fig. 4, which is defined as the calibration factor,  $\kappa$ , was presented as:

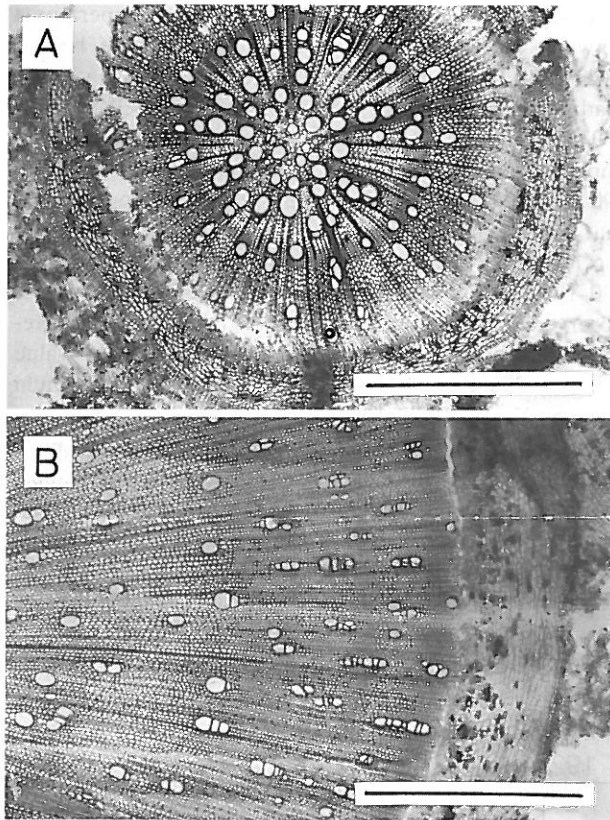
$$\kappa = 1.88D^{-0.163} \quad r^2 = 0.988 \quad (5)$$

$\kappa$  was used in Eqn 1 to correct for  $F$  in roots.

To explore the cause of the overestimation, the cross-sectional distribution of xylem vessels was observed microscopically for other segments sampled from lateral roots at a distance of 0.05–0.1 m from the basal part of the stem. As can be seen in Fig. 5, the largest xylem vessels tended to be distributed towards the centre of the root rather than towards the surface. Those in the smaller root, which presumably was younger than the larger one, were concentrated more towards the centre than the larger roots. From these observations and the dynamics of heat-balance sap-flow sensors during high flow conditions (Ham & Heilman



**Figure 4.** Comparison of water uptake measured using a potometric method and sap flow measured on three roots with different diameters.



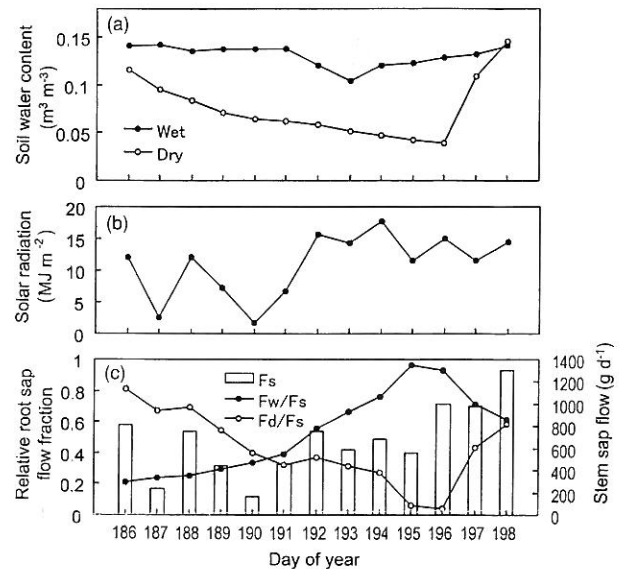
**Figure 5.** Cross-sections of the roots of *S. rostrata* grown in nutrient solution. Root diameter: a, 3.1 mm; b, 10.5 mm. The sampled roots were cross-sectioned, without fixation, by a microslicer to provide 25  $\mu\text{m}$  in sections for optical microscopic observation. Scale bar = 1 mm.

1990), it is suggested that the overestimation provided by the root sap-flow sensor resulted from a lack of thermal equilibrium between the xylem fluid and the sensor on the stem surface. The high correlation coefficients between the water uptake and sap flow, however, indicate that appropriate calibration may provide reliable values for root sap flow in species with roots similar in structure to *S. rostrata*.

## Split root experiment

### Soil water content

The soil water contents at 1300 h on DOY 185, the day preceding the start of the experiment, were somewhat different for the two compartments, namely, 0.153 and 0.127  $\text{m}^3 \text{m}^{-3}$ , respectively, for wet and dry compartments. However, the difference was acceptable because both compartments were well-watered in the morning. While mean water content in the wet compartment remained between 0.104 and 0.142  $\text{m}^3 \text{m}^{-3}$  during the experiment, that in the dry compartment gradually decreased, reaching 0.039  $\text{m}^3 \text{m}^{-3}$  on DOY 196 (Fig. 6a). After applying water on DOY 197, the soil water content of the dry compartment increased to 0.146  $\text{m}^3 \text{m}^{-3}$  on DOY 198.



**Figure 6.** (a) Daily mean volumetric soil water content in the wet and dry compartments, measured with TDR; (b) solar radiation and (c) sap flow in the stem,  $F_s$ , the ratio of sap flow in 'wet' root,  $F_w$ , to  $F_s$  and the ratio of sap flow in 'dry' root,  $F_d$  to  $F_s$ . Irrigation to the dry compartment was stopped on the afternoon of day of year (DOY) 185. The 'dry' roots were rewatered at 1145 h on DOY 197.

### Daily sap flow

Figure 6(c) indicates the time course in stem sap flow,  $F_s$ , the ratio  $F_w/F_s$ , where  $F_w$  is sap flow estimated for all roots in the wet compartment, and  $F_d/F_s$ , where  $F_d$  is sap flow estimated for all roots in the dry compartment. The sum of  $F_w/F_s$  and  $F_d/F_s$  ranged from 0.717 to 1.205, implying that  $F_w$  and  $F_d$  were within an acceptable error.  $F_w/F_s$  was 0.207 at the start of the experiment (DOY 186) while  $F_d/F_s$  was 0.812, although the difference in diameter between these roots was small. A possible explanation is that the root used to measure sap flow on the wet side had poor lateral roots at the beginning of the period of observation.

As the soil dried,  $F_d/F_s$  declined, whereas  $F_w/F_s$  increased. Sap flow in the 'wet' roots was 926.2  $\text{g d}^{-1}$  on DOY 196, namely 5.52 times greater than on DOY 186, although solar radiation was greater only by 24.1% (Fig. 6b). This suggests that new roots grew rapidly in the wet compartment while the soil was drying in the dry compartment to compensate for the decrease in water uptake by the 'dry' roots. Green & Clothier (1995) found in Kiwifruit vines that previously 'dry' roots responded quickly to irrigation, becoming more active in their uptake of water. In *S. rostrata*, the 'wet' roots became more active, possibly due to their ability to grow rapidly in submerged soils as was shown by Patcharapreecha, Taja & Wada (1993).

Following the re-initiation of irrigation in the dry compartment (DOY 197), sap flow in the 'dry' root recovered rapidly. On the following day (DOY 198)  $F_d/F_s$  reached 0.587 which was approximately equivalent to  $F_w/F_s$ ,

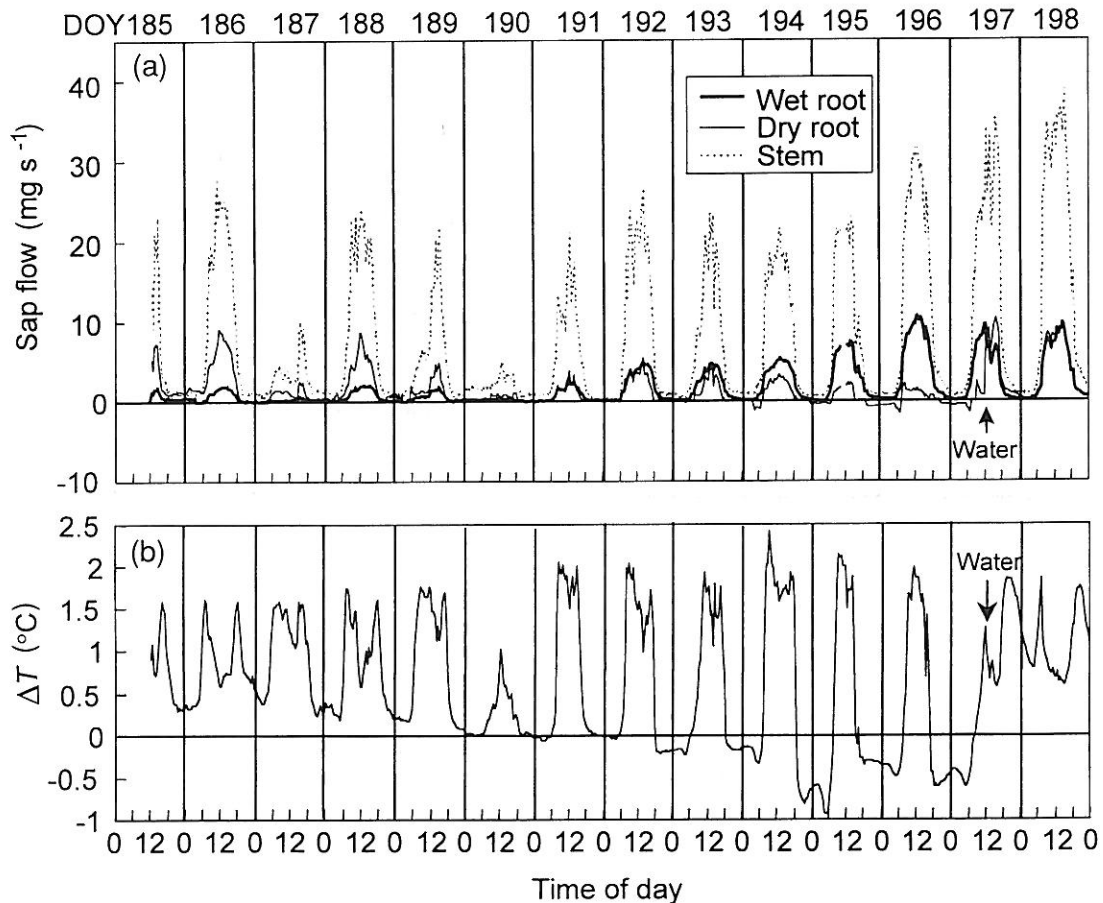
although the dry mass of the 'dry' roots (3.85 g) was smaller than that of 'wet' roots (4.85 g). This indicates that the dry period had not caused damage to the roots in the dry compartment.  $F_w/F_s$  decreased to 0.619 on DOY 198, implying that activity of the 'wet' roots decreased. This is in accord with the finding that the decrease in water uptake by dry roots during the drying cycle was offset by the increase in the activity of the 'wet' roots. Such an increase in activity of 'wet' roots of partially irrigated trees has been observed by others (Moreshet, Cohen & Fuchs 1983; Clothier, Smettem & Rahardjo 1990).

#### Reverse flow

Figure 7(a) shows the diurnal changes in sap flow recorded for the 'dry' and 'wet' roots and the stem. Reverse flow was observed in the early morning on DOY 194, and during the night on DOYs 195 and 196. Yet, reverse flow might have occurred earlier than on DOY 194, as  $F$  was assumed to be zero when  $\Delta T$  was between 0.2 and  $-0.2$  °C. To detect when

reverse flow began, the difference in root temperatures between the down- and upstream points of the heated segment,  $\Delta T$  was used (Fig. 7b). The value of  $\Delta T$  at night gradually decreased over the period between DOY 186 and 189, and reached zero early in the morning of DOY 190, implying that sap flow ceased. Subsequently, between DOY 190 and 196, negative values of  $\Delta T$  in the 'dry' root suggest that reverse flow occurred, although at rates that were too low to be detected by the sap-flow sensor on DOYs 190–193. The soil water content when reverse flow was first observed at 2330 h on DOY 190 was  $0.063 \text{ m}^3 \text{ m}^{-3}$ , corresponding to a soil water potential of  $-0.30 \text{ MPa}$ . This value is higher than the value ( $-0.55 \text{ MPa}$ ) obtained for sorghum roots by Xu & Bland (1993).

Sap flow in the stem and the 'wet' root was always positive at night (Fig. 7a). This suggests that, when reverse flow occurred, the water supplied to the 'dry' roots and the stem came from roots in the wet side. The total amount of sap flow in the 'wet' and 'dry' roots for the period when reverse flow was occurring was estimated (Table 1). A reliable value



**Figure 7.** (a) Sap flow recorded for the stem, and for the dry and wet roots on which the sap-flow sensor was installed. (b) Difference in temperature between the down- and upstream points of the heated segment,  $\Delta T$  in the dry root. Positive values in root sap flow and  $\Delta T$  indicate flow of sap towards the stem. On a dry matter basis, the dry and wet roots to which sap-flow sensors were attached represented, respectively, 41.8 and 38.1% of the total root system in each compartment at the end of experiment (DOY 199).

Time period (h) and day of year	Sap flow (g)			
	Wet roots <sup>a</sup>	Dry roots <sup>a</sup>	Stem <sup>a</sup>	Stem <sup>b</sup>
2000 (194)–0700 (195)	54.5	–22.5	32.3	32.0
1900 (195)–0700 (196)	53.5	–74.4	32.7	–20.9
2100 (196)–0700 (197)	59.5	–63.8	39.5	–4.3

<sup>a</sup> Represents sap flow measured with the constant power heat balance method.

<sup>b</sup> Represents sap flow obtained as the sum of sap flow in wet and dry roots.

was obtained for the period from 2000 h on DOY 194 to 0700 h on DOY 195, because the sum of the sap flow in the 'wet' and 'dry' roots was approximately equivalent to the measured sap flow in the stem. However, sap flow in the 'dry' roots was largely overestimated for the other two periods. This was attributable to the relatively small  $|\Delta T|$  on these days.

Water that is transferred to 'dry' roots will either increase their water content or be released into the soil. We could not distinguish between these two components, because soil moisture content was not measured near the roots. If it is assumed that all the amount of reverse flow was released into the soil, it would be 22.5 g (Table 1), corresponding to 2.05 g h<sup>-1</sup>. The estimated exudation of water was 3 to 10% of that observed in bermuda-grass (Baker & van Bavel 1986) and 5 to 15% of that in cotton (Baker & van Bavel 1988) using split-root boxes with dimensions similar to ours. Ozawa (1998) observed that 10 g h<sup>-1</sup> of water was transferred to the dry soil at night in his split root experiment using a tomato plant with root dry weight 1.81 times larger than ours. The rate of reverse flow may be represented by a function of root water conductance, gradient of water potential and root density. Thus the differences in the quantity of water exuded among the experiments referred to above are probably attributable to differences in the species used, root and shoot growth, and the water status in the plant and the soil.

Maintenance of fine root viability and improvements of plant nutrient and water status have been suggested as eco-physiological implications of reverse flow (Burgess *et al.* 1998). These benefits may largely depend on the quantity of water transferred by reverse flow. Our results showed that the constant power heat balance method provides a means of quantifying reverse flow. Very recently, Burgess *et al.* (1998) used a modified heat pulse method in which temperature probes were placed at equal distance down- and upstream from a heater, and detected the 'reverse' of hydraulic lift in tree roots. Further application of both thermic methods to research in root flow can be expected to provide new insight into reverse flow.

## CONCLUSIONS

Limited data showed that a semi-empirical method for estimating sheath conductance of the sensor,  $k$ , could provide reliable values for sap flows in 'wet' and 'dry' roots and stem

**Table 1.** Total sap flow in the roots and stem for the time period when reverse flow occurred. Negative represents reverse flow

of *S. rostrata* at night. When part of the root zone was allowed to dry in a split root experiment, a decrease in daytime water uptake by the 'dry' roots was compensated for by the 'wet' roots. Reverse flow in roots was observed for *S. rostrata* using heat balance sensors; this occurred at night when the soil water content was less than 0.063 m<sup>3</sup> m<sup>-3</sup>, corresponding to a water potential of –0.30 MPa. The stem heat balance method should be a useful tool for examining the dynamics of water uptake by plant roots, including reverse flow phenomena.

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