Sap flow measurements of lateral tree roots in agroforestry systems

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Received October 25, 1995

Summary Successful extension of agroforestry to areas of the semi-arid tropics where deep reserves of water exist requires that the tree species be complementary to the associated crops in their use of water within the crop rooting zone. However, it is difficult to identify trees suitable for dryland agroforestry because most existing techniques for determining water uptake by roots cannot distinguish between absorption by tree and crop roots. We describe a method for measuring sap flow through lateral roots using constant temperature heat balance gauges, and the application of this method in a study of complementarity of water use in agroforestry systems containing Grevillea robusta A. Cunn. Sap flow gauges were attached to the trunks and roots of Grevillea with minimum disturbance to the soil. Thermal energy emanating from the soil adversely affected the accuracy of sap flow gauges attached to the roots, with the result that the uncorrected values were up to eightfold greater than the true water uptake determined gravimetrically. This overestimation was eliminated by using a calibration method in which nonconducting excised root segments, with sap flow gauges attached, were placed adjacent to the live roots. The power consumption and temperature differentials of the excised roots were used to correct for external sources and internal losses of heat within the paired live root. The fraction of the total sap flow through individual trees supplied by the lateral roots varied greatly between trees of similar canopy size. Excision of all lateral roots, except for one to which a heat balance gauge was attached, did not significantly increase sap flow through the intact root, suggesting that it was functioning at near maximum capacity.

Keywords: Grevillea robusta, heat balance sap flow gauge, water use.

Introduction

Agroforestry is a term used to describe land-use systems in which woody perennials (e.g., shrubs or trees) are grown in association with herbaceous species (e.g., crops or pastures) or livestock or both (Anderson and Sinclair 1993). The potential benefits of agroforestry for subsistence farmers include increased productivity and a wider product base. However, the success of an agroforestry system can be assured only if its adoption is based on a sound understanding of the ecological interactions involved, both above- and belowground.

Agroforestry research in dryland areas has demonstrated that when trees such as Leucaena leucocephala ((Lam.) de Wit) are combined with annual crops, competition, especially for water, may seriously reduce crop yield (Singh et al. 1989, Ong et al. 1991, Daniel et al. 1991, Corlett et al. 1992). The ideal system would reduce belowground competition either through spatial separation of tree and crop roots within the soil profile or by temporal separation of maximum activity by tree and crop roots. The degree of spatial or temporal complementarity achieved between trees and crops is critical in ensuring the long-term success of agroforestry in resource-limited environments.

Identification of tree species that complement crops in the extraction of belowground resources has largely focused on observations of root architecture. For example, Laycock and Wood (1963), Jonsson et al. (1988) and Mwihomeke (1993) all suggested that Grevillea robusta A. Cunn. has a high potential for spatial complementarity with annual or perennial crops because it produces few superficial lateral roots and most roots are orientated in a predominantly vertical plane. Crop yields may nevertheless be substantially reduced in systems containing Grevillea in areas of limited water availability, indicating that selection of tree species with a degree of complementarity appropriate to specific climatic and soil conditions requires knowledge of both root distribution and water uptake capacity.

Several approaches may be used to determine water uptake by roots, including studies of soil water depletion and root distribution (Daniel et al. 1991, Ong et al. 1991, Howard et al. 1995), and stable isotope analysis of xylem sap (Dawson and Ehleringer 1991). Although these approaches provide information on water uptake from specific horizons, they cannot distinguish between absorption by tree and crop roots. Sap flow techniques for measuring transpiration by both woody and herbaceous plants are now well established (see Ong et al. 1996 for review), but have rarely been adopted for use with woody roots (Ong and Khan 1993). We describe the application of constant temperature heat balance gauges to measure sap flux in lateral roots of Grevillea trees growing in an agroforestry system in Kenya, and assess the degree of belowground complementarity in water use with associated crops.
Materials and methods

The research was carried out at the Machakos Field Research Station, ICRAF, Kenya (1°33’ S, 37°14’ E, altitude 1660 m) during the rainy season (February–June) and the following dry season (July–September) of 1995. Measurements were made on three-year-old Grevillea robusta A. Cunn. trees (local Embu provenance) planted at a 3 × 4 m spacing on an area of about 0.3 ha in April 1992. The land had no known cropping history before being cleared of the natural scrubby vegetation. The soil was a well drained, sandy clay loam overlying petropelinithe (murrum) with numerous stony bands, and ranged in depth from 0 to 120 cm. The annual distribution of rainfall at Machakos is bimodal, with long rains extending from March to June and short rains from October to December, each providing a seasonal average of 300–350 mm. The 220 mm of rain received during the experimental period was therefore less than expected. Trees were inter-cropped with cowpea (Vigna unguiculata L.) or maize (Zea mays L.) during the three previous seasons.

Sap flow

Sap flow was measured by means of constant temperature heat balance gauges similar to those described by Ishida et al. (1991) and modified by Khan and Ong (1995). The heater coil comprised a length of constantan wire with a resistance of 15 ohms, wound tightly around a smooth and uniform section of root to ensure good contact. Copper-constantan thermocouples were secured to the root surface 2 cm above (T₀) and below (Tₐ) the heater coil with insulating tape; the thermocouple lead wires were wrapped once around the root, both for support and to minimize conduction down the wires. Thermocouples were also attached to the heater coil (Tₜₙ) and to the root 4 cm upstream of the heater (T₀); the latter served as a reference for controlling the heater input. The installation was insulated with a close-fitting styrofoam block to minimize radial heat exchange and interference from fluctuations in ambient temperature. Similar installations were used to measure sap flow through the trunks.

The thermocouples were linked as two pairs, T₈₉ to T₀ and Tₐ to Tₜₙ, to permit differential temperature measurements. Thermocouple T₈₉ was maintained 8 °C above thermocouple T₀ using a relay and power provided from a car battery. The battery voltage, the count time of the relay (loop count) and the temperature differences, T₈₉ - T₀ and Tₐ - Tₜₙ were recorded with Campbell Scientific 21X dataloggers (Logan, UT). Radial and conductive heat losses were initially assumed to be negligible relative to convective transfer during the daylight hours (Khan and Ong 1995), and sap flux was estimated as:

\[ J_m = V^2/Rc_w(T_d - T_o) \]

where \( J_m \) represents the sap flux (g h⁻¹), \( V \) and \( R \), respectively, denote the voltage (V) and resistance (ohms) of the heater wire, and \( c_w \) is the specific heat capacity of water (4.18 J g⁻¹ °C⁻¹). Dataloggers were used to control three heat balance systems and record their outputs as 15-min mean sap fluxes for each root.

Measurements of sap flux through the trunks were corrected for errors resulting from differences in diameter as follows:

\[ J_s = \frac{J_m}{0.0001 d^2 - 0.0031 d + 1.0552}, \]

where \( J_s \) denotes the corrected sap flux (g h⁻¹) and \( d \) is the diameter of the trunk (mm).

Calibration of the heat balance system for roots

Lateral roots were carefully excavated, leaving a section still enclosed within an intact block of soil. The exposed root was severed just beyond the soil block, leaving the rest of the root connected to the tree. The soil blocks were placed in 10-liter plastic basins and kept well watered and fertilized to encourage root development and water uptake. The soil surface was covered with styrofoam and aluminium foil to minimize evaporative water loss and heating by solar radiation. After four weeks, a section of root closer to the trunk was exposed and a sap flow gauge attached; the installation and any part of the root still exposed were covered with expanded polystyrene and aluminium foil. The entire installation was covered with a tent made from a double layer of opaque polyethylene with a 2-cm wide air gap between the layers to minimize thermal errors introduced by differential heating of the soil resulting from irregular tree shading. Water loss from the soil block within the basin as a result of absorption by the roots was determined gravimetrically at 1-min intervals with a top-loading balance, and sap flow was measured at 3-s intervals and recorded as 15-min means. Because there were no branch roots between the basin and the heat balance installation, the gravimetric measurements permitted the heat balance system to be calibrated against absolute measurements of sap flow.

Correction for thermally induced errors

Previous experience has shown that, to measure sap flow through stems, heat balance gauges should be located as far as possible from the soil surface to minimize errors induced by conductive or convective transfer of heat to the thermocouples. As this precaution is not possible with roots, the effects of ambient temperature changes must be quantified and corrected for, particularly those effects arising from differential heating of the soil caused by diurnal variation in shading by the tree canopy. To achieve this, a freshly excised and therefore non-conducting length of root of similar diameter was placed alongside each live root under examination and heat balance systems were installed at the same relative positions on the living and excised roots, in a modification of a technique previously recommended for stems (Baker and van Bavel 1987). The measured sap flow values (\( J_m \)) for live roots were corrected as follows:

\[ J_s = J_m D_l / (D_t - D_c), \]

where \( J_s \) represents the measured sap flow (g h⁻¹) corrected for errors introduced by external heat sources, and \( D_l \) and \( D_c \) are
the temperature differentials \((T_u - T_d)\) for the live and excised roots, respectively.

Conduction of heat from the heater in the axial and radial directions and storage of heat within the root may also cause overestimation of sap flow (Fichtner and Schultze 1990). To correct for this, power absorption by the nonconducting excised root was determined from the loop count and battery voltage, and the following correction applied:

\[
J_x = J_s - 0.01913 \left(1.4C_c - 10\right)V_c^2 \left(D_1 - D_c\right),
\]

where \(J_x\) is the measured sap flow (g h\(^{-1}\)) corrected for both sources and losses of heat, and \(C_c\) and \(V_c\) are, respectively, the loop count and the heater voltage for the excised root (cf. Khan and Ong 1995).

**Contribution of lateral roots to total water uptake**

Sap flow gauges attached to the trunk and to all lateral roots of individual trees were used to determine the fraction of total absorption that was extracted from the surface soil horizons by the lateral roots. The selected trees had a similar canopy size and hence similar potential transpiration, but were growing in areas of differing soil depth (Table 1). Canopy size was calculated as an allometric product derived from extensive destructive measurements of neighboring trees. The allometric relationship established was capable of estimating the total leaf area of the tree canopy to within 5%. Heat balance gauges were also used to determine sap flow through lateral roots at various distances from the trunk.

**Compensation in water uptake**

Heat balance gauges were attached to the trunk and one lateral root (Figure 1a) of three trees of differing canopy size and to the trunks of paired control trees. After four days, all lateral roots, except for those with the sap flow gauges attached, were severed on the experimental trees (Figure 1b), and five days later, the root with the sap flow gauge attached was also cut (Figure 1c). The effect of root pruning on flow rates through the trunks of the experimental trees was assessed by comparison with the corresponding sap flow values for the paired unpruned control trees.

**Results and discussion**

Numerous studies have established close agreement between estimates of sap flow through the stem and transpiration measured gravimetrically for a range of species grown in containers (e.g., Sakuratani 1981, Valancogne and Nasr 1989, Ishida et al. 1991). However, because roots and stems differ morphologically and physiologically, it was necessary to validate the accuracy of the heat balance method with roots. Figure 2 demonstrates that, for roots, uncorrected measurements determined by the heat balance method may be seriously inaccurate because of thermally induced errors. An apparent sap flow was detected in excised roots placed beside living roots, and the values for living roots were not much greater than those of

![Figure 1. Sequence of lateral root pruning: (a) five lateral roots identified and heat balance gauge attached to one; (b) four lateral roots severed adjacent to the trunk; and (c) remaining lateral root with sap flow gauge severed.](image)

<table>
<thead>
<tr>
<th>Tree</th>
<th>Number of lateral roots</th>
<th>Total cross-sectional area of lateral roots (cm(^2))</th>
<th>Soil depth (cm)</th>
<th>Mean daily total transpiration (kg)</th>
<th>Daily absorption by all lateral roots (kg)</th>
<th>Fraction of transpiration supplied by lateral roots</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3</td>
<td>18.7</td>
<td>38</td>
<td>12.0</td>
<td>1.7</td>
<td>14%</td>
</tr>
<tr>
<td>2</td>
<td>5</td>
<td>23.4</td>
<td>72</td>
<td>3.8</td>
<td>2.5</td>
<td>66%</td>
</tr>
</tbody>
</table>
excised roots for much of the day. Because the excised roots were nonconducting, the apparent sap flow must have been an artifact.

Applying Equation 3, the temperature differentials recorded for the excised roots were used to correct for errors caused by external sources of heat in the sap flow values for living roots. Figure 3 shows that the uncorrected sap flow values for living roots obtained using heat balance gauges (diamonds) were substantially greater than the corresponding paired gravimetric values. Correction for errors resulting from external heat sources reduced the difference between the heat balance and gravimetric estimates of sap flow, but there remained a substantial discrepancy (Figure 3, triangles). Additional correction for conductive heat losses and storage of heat within the root using Equation 4 produced a further improvement in fit between the heat balance and gravimetric values (Figure 3, circles) (cf. Ishida et al. 1991, Khan and Ong 1995). A close fit to the 1/1 line was obtained at flow rates above 15 g h$^{-1}$ ($r^2 = 0.86$), but at lower flow rates the heat balance values underestimated the true sap flow, even after correction for thermal errors. Similar errors were recorded by Baker and van Bavel (1987), Sakuratani (1990), Groot and King (1992) and Senock and Ham (1993).

Typical diurnal time courses and daily totals for water use by two trees of equivalent canopy size, but growing on soils differing in depth, are shown in Figure 4 and Table 1. In both trees, sap flow through the trunk and the combined sap flow for all lateral roots exhibited distinct diurnal trends that closely followed the diurnal pattern of solar radiation, as has been previously reported for Grevillea by Howard et al. (1996). The mean volumetric soil water content for the horizons occupied by the lateral roots (upper 40–60 cm) at this time was only 5%
for both trees. Total water use was over three times greater in Tree 1 than in Tree 2, despite the shallower soil (Table 1). Nevertheless, Tree 1 received only 14% of its water supply from lateral roots, compared with 66% for Tree 2 (Table 1), suggesting that substantial quantities of water were being absorbed by deeper roots penetrating into fissures in the underlying friable bedrock, a conclusion supported by root excavation studies. The combined cross-sectional area of lateral roots was 25% greater in Tree 2 than in Tree 1, reflecting the greater quantity of water supplied by the laterals in this tree. These results demonstrate the existence of considerable functional variability among the root systems of trees of similar canopy size. This has important consequences for modeling water use by trees in forestry and agroforestry systems as it indicates that the common assumption that transpiration may be scaled from individual trees to the system level on the basis of canopy size is not universally applicable.

Figure 5a shows diurnal time courses of sap flow for three days during a 12-day experimental period when the lateral roots were successively severed. To account for differences in absolute water use between control and treatment trees before the experimental period, sap flow through the trunk is expressed relative to the maximum recorded value over the measurement period (1000 h on February 5, 1995). Sap flow through the instrumented lateral root (Figure 1) is expressed as a fraction of the total sap flow for the same tree. At the time of these measurements during the dry season, mean soil water content was 7% in the horizons occupied by lateral roots and 15–17% in deeper layers.

Marked diurnal variation in water use was apparent (Figure 5a), although the control and treatment trees exhibited similar daily sap flow patterns before the first root pruning (Figure 5b). Excision of all lateral roots, except for the one with the heat balance gauge attached (Figure 1b), reduced total water use by about 20% over a 4-day period relative to control trees (Figures 5a and 5b). Sap flow through the remaining lateral root was only slightly increased (Figure 5b), suggesting that this root was already operating near its maximum absorptive capacity for the prevailing soil conditions. The increase was insufficient to offset the reduced contribution by the other

Figure 4. Typical diurnal time courses for sap flow through the trunks and lateral roots of Tree 1 and Tree 2, growing on soil of 38 and 72 cm depth, respectively. Tree 1: trunk (■); and total for all lateral roots (□). Tree 2: trunk (○); and total for all lateral roots (○).
lateral roots and to prevent a reduction in total water use (Figure 5a). When the remaining lateral root was severed (Figure 1c), total water use showed a further slight decrease (Figures 5a and 5b). Total water use was nevertheless about 80% of that in undisturbed control trees, supporting previous evidence from root excavation experiments that Grevillea may extract up to 80% of its water requirements from below the crop rooting zone (Howard et al. 1996).

Sap flow through the lateral roots decreased sharply with increasing distance from the trees (Figure 6). These well-established, three-year-old trees nevertheless extracted substantial quantities of water from the crop rooting zone at distances of up to 190 cm from the trunk, at a time when the average volumetric soil water content was 11% in the upper 60 cm of the profile. This would cause large cumulative losses of water during the cropping season, because water extraction from the crop rooting zone by tree roots is likely to be much greater during the rainy season when the soil frequently approaches field capacity (19%). The importance of these competitive interactions between tree and crop roots is reflected by marked reductions in the growth and productivity of maize plants growing within 2 m of the trees in seasons of average or below average rainfall. Intercrop maize yields only approached the sole crop control values when seasonal rainfall was substantially above average (550 versus 300 mm).

Conclusions

The calibration procedures described here are capable of correcting for the substantial thermally induced errors that may occur when constant-temperature, heat balance sap flow gauges are used to measure water uptake by tree roots. When such corrections are made, the heat balance approach may be applied satisfactorily to study both the diurnal variation in sap flow within individual roots and the spatial variation in water uptake at various distances from the trunk. The results show that Grevillea is capable of extracting up to 80% of its water requirements from deep reserves during the dry season. However, the technique described is complicated and is susceptible to electrical short circuits caused by condensation or penetration of moisture during heavy rain. In view of these difficulties, we suggest that the heat pulse approach may be more appropriate for sap flow measurements in roots because the instrumentation is much less affected by penetration of moisture and by thermally induced errors, thus eliminating the need to use excised roots for calibration. The root containment method described here could be used to validate the heat pulse technique against gravimetric measurements of sap flow. We have demonstrated the potential of a technique capable of real-time measurements of water uptake by roots and the need to develop simple robust techniques that will assist in the selection of suitable tree species for dryland agroforestry systems.

Acknowledgments

This work was funded by the U.K. Overseas Development Administration (ODA) under contract R5810, administered by the Forestry Research Programme at Oxford University. Additional technical and material support was provided by ICRAF and Nottingham University. Information on soil water status was provided by Dr. N. Jackson and Dr. J. Wallace of the U.K. Institute of Hydrology.

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