



Contrasting water use patterns of two important agroforestry tree species in the Mt Elgon region of Uganda

J. Buyinza, C. W. Muthuri, A. Downey, J. Njoroge, M. D. Denton & I. K. Nuberg

To cite this article: J. Buyinza, C. W. Muthuri, A. Downey, J. Njoroge, M. D. Denton & I. K. Nuberg (2019) Contrasting water use patterns of two important agroforestry tree species in the Mt Elgon region of Uganda, *Australian Forestry*, 82:sup1, 57-65, DOI: [10.1080/00049158.2018.1547944](https://doi.org/10.1080/00049158.2018.1547944)

To link to this article: <https://doi.org/10.1080/00049158.2018.1547944>



© 2019 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group.



[View supplementary material](#)



Published online: 22 Jan 2019.



[Submit your article to this journal](#)



Article views: 633



[View related articles](#)






[View Crossmark data](#)



Citing articles: 1 [View citing articles](#)

Contrasting water use patterns of two important agroforestry tree species in the Mt Elgon region of Uganda

J. Buyinza ^{a,b}, C. W. Muthuri^c, A. Downey^d, J. Njoroge^c, M. D. Denton ^a and I. K. Nuberg ^a

^aSchool of Agriculture Food and Wine, The University of Adelaide, Waite Campus, Urrbrae, Australia; ^bAgroforestry Research Programme, National Forestry Resources Research Institute (NaFORRI), Kampala, Uganda; ^cSystems Science Theme, World Agroforestry Centre (ICRAF), Nairobi, Kenya; ^dPlant Science Applications and Research, ICT International, Armidale, Australia

ABSTRACT

Lack of information on water use of key agroforestry species is an obstacle to understanding their influence on crop productivity. *Cordia africana* and *Albizia coriaria* are the dominant tree species of smallholder farming systems in the Mt Elgon region of Uganda and have multiple uses in agroforestry systems. This study deployed six sap flow meters on stems of three selected trees each of *C. africana* and *A. coriaria* on-farm. The objective of the study was to assess the daily water use patterns of these agroforestry tree species at different times of the year. We measured the daily sap flow of these two species using the heat ratio method over a period of 18 months. There was a significant main effect of the interaction between tree species and season on daily water use. The two species show contrasting patterns of seasonal water use across leaf shedding stages characterised by episodes of reverse flow in *A. coriaria* at specific periods of the year. We propose that reverse flows in *A. coriaria* were triggered by leaf shading while the zero flows in *C. africana*, which occurred during rainfall events, could have resulted from a lag phase, an indication that the two species may have different water-use strategies. Although *C. africana* uses 12–15 l day⁻¹ and *A. coriaria* uses 20–32 l day⁻¹ based on the study trees, *C. africana* generally uses 12% more water than *A. coriaria* on a standardised daily basis. *Albizia coriaria* exhibited radial variation of sap velocities between the inner and outer thermocouples at different periods of measurement, a phenomenon worth investigating further. The leaf shedding patterns of the two trees provide an opportunity for maximising the temporal complementarities of agroforestry systems where these trees exist. This knowledge of *C. africana* and *A. coriaria* tree water use provides critical insight for developing successful long-term tree monitoring and management programs in agroforestry systems.

ARTICLE HISTORY

Received 7 May 2018
Accepted 8 September 2018

KEYWORDS

sap flow; agroforestry; leaf phenology; *Cordia africana*; *Albizia coriaria*

Introduction

Sustainable use of soil water resources has been associated with improved food security and livelihoods (Cai et al. 2011). Global food demands have been projected to increase as a result of scarcity, degradation and overuse of water resources (FAO 2011; Descheemaeker et al. 2013). Agroforestry is recognised as one of the most functional components of farming systems that can enhance sustainable use of water and nutrient resources and assist in the provision of global food demands (Pinho et al. 2012). It is an important component of climate-smart agriculture that supports food and nutritional security through provision of food, contributing to household income and fuel needs. While agroforestry offers effective means to restore degraded lands (Sales et al. 2016), most smallholder farmers with trees on-farm have failed to realise the co-benefits, due to poor management of the tree component. These farmers also lack knowledge of tree selection and arrangement of the agroforestry components. Success in agroforestry systems is primarily based on selecting the right tree-crop combinations that exploit spatial and temporal complementarities in resource use (Descheemaeker et al. 2013).

One of the fundamental steps towards enhancing the complementarity and stability of food production in

smallholder agroforestry systems is gaining an understanding of the water use of the tree component. Understanding tree water-use physiology has received increasing research attention in response to emerging environmental issues such as land-use change (Ellison et al. 2017), degradation of agricultural land (Muthuri et al. 2005) and climate change (Linares et al. 2012; Webber et al. 2014; Strobl et al. 2017), which all impact on household food security. However, most of the studies on water use in agroforestry trees have not monitored individual tree water use in the field, due to technological limitations. Field-based experiments provide useful scientific knowledge about plant hydraulic function that can be used to better understand and model field scenarios (Steppe et al. 2015). Field monitoring also allows subsequent observations to be made on other tree physiological events including leafing phenology and response to rainfall patterns. Understanding how farmers interact with the trees on a daily basis provides an opportunity for real time measurements that can be used for improved management. Knowledge of daily water use can not only inform water requirements of interacting components of farming systems but also on best bet management options for farmers.

The deciduous nature of the focal tree species (*Cordia africana* Lam. and *Albizia coriaria* Welw. ex Oliv.) provides an opportunity to improve crop productivity through temporal complementarity with crop plants. A key factor when choosing suitable agroforestry tree species is their leaf phenology, as the timing and extent of leaf shedding and replacement during the annual cycle affects the pattern and rate of soil water extraction and the effects on associated crops (Broadhead et al. 2003). Differences in leaf phenology can influence the extent of competition and complementarity in agroforestry systems (Muthuri et al. 2009). For example, Chinese red birch, *Betula albosinensis* Burk., can adopt different water use strategies to cope with changes in soil water (Yan et al. 2018) which can influence the yield of the associated crop. Therefore, understanding water use patterns of deciduous agroforestry species such as *C. africana* and *A. coriaria* is crucial to determining the extent of competition and complementarity.

As *C. africana* and *A. coriaria* are important components of agroforestry systems in eastern Africa, we assessed sap flow of these species in two farmers' fields using the heat ratio method (HRM), as established by Burgess et al. (2001). We hypothesised that the water use patterns would be seasonally influenced through leaf traits and rainfall, and that these would have important consequences to agricultural crops growing in these systems.

Materials and methods

Study area

The study was conducted in Manafwa district located in Eastern Uganda, with a land area of 452 km², bordering the Republic of Kenya in the east, Bududa district to the north, Mbale district to the west and Tororo to the south-west. About 98% of the human population in Manafwa is rural based, with an annual population growth rate of 3.4%. In terms of climate, the average annual rainfall is 1500 mm, with two peak rainy seasons that occur in the months of April–June and August–November. Manafwa registers a mean annual maximum and minimum temperature range between 32°C and 15°C.

Tree species under study

Albizia coriaria (locally called Mugavu in Luganda and Swahili, and Kumoluko in Lugisu) is a deciduous nitrogen-fixing tree in the family Fabaceae (Katende et al. 1995). It is a pioneer species that grows to a height of 36 m with a distribution from West Africa through eastern, southern and parts of central Africa (Orwa et al. 2009). The absence of *A. coriaria* in closed canopy rainforests is largely the result of its high light requirements (Janani et al. 2014). Although *A. coriaria* is reportedly a slow growing tree, it is widely regarded as a multipurpose tree, providing various products and services (Tabuti & Mugula 2007). There have also been claims that the tree bark provides a useful medicine for malaria and coughs (Namukobe et al. 2011) and has dye-yielding properties for plain woven cotton fabrics (Janani et al. 2014). *Albizia coriaria* is one of the most common multipurpose tree species used in indigenous agroforestry systems of Uganda (Bukomeko et al. 2017). It was chosen for this project because it is a popular

tree already widely grown by farmers in Mt Elgon region and for its ability to fix nitrogen.

Cordia africana (commonly known as large-leaved Cordia, locally called Mukebu in Luganda and Chichikiri in Lugisu) is a deciduous tree that belongs to the family *Boraginaceae* (Katende et al. 1995). The species is widely distributed from South Africa to Saudi Arabia and Yemen at altitudes between 550m and 2600 m above sea level, in warm and moist areas, often along riverbanks. The mature fruits of *C. africana* have a sweet edible pulp (Kebebew & Balemie 2006). *Cordia africana* was exceptionally well ranked by farmers as an important agroforestry tree species in coffee plantations in Eastern Uganda (Gram et al. 2018). Silvicultural studies of the species indicate that increased spacing of *C. africana* increases branch diameter (knot size) and crown diameter (Mehari & Habte 2006), making it a good agroforestry candidate tree species. This tree species was selected for this study because it has been widely integrated in coffee systems in Mt Elgon region.

Research design and instrumentation

Tree water use was assessed using six SFM1 Sap Flow Meters (ICT International, Armidale, Australia) installed on three *C. africana* and three *A. coriaria* trees existing in two farmers' fields. There were three trees of one species on one farm and three of the other species on the other farm, making six trees in all. The two farms are approximately 2 km from each other. The trees are spaced at a distance of 10–12 m and are integrated with coffee at a spacing of 3 × 3 m. Tree species selection was based on the fact that these two species are the most common in the farming systems in the area, predominant in coffee agroforestry systems. Sap flow instrumentation (SFM1 Sap Flow Meter) used in this study is based on the HRM as it is non-destructive and has the ability to detect low and reverse flow rates over extended periods (Burgess et al. 2001).

Site selection and installation of Sap Flow Meters

During selection of sites and trees for installing the Sap Flow Meters, care was taken to select healthy, straight trunk representative trees, within the same diameter class. The host farmers (land and tree owners) were fully engaged before starting the installation exercise, which ensured protection of the Sap Flow Meters and the solar panels on their farms.

Prior to installation the bark depth of each tree was measured using a bark depth gauge, and an increment borer was used to determine sap wood thickness. These parameters were then used to determine the correct radial placement of the measurement needles within the water conducting tissue of the tree at approximately 1.3 m height or diameter at breast height over bark (DBHOB) on the tree trunk. Two measurement needles were positioned 0.5 cm equidistant above and below the central heater. The three needles were lightly greased with an inert silicon vacuum grease, to improve thermal coupling between the needles and the stem. Each needle was then inserted into the pre-drilled holes in the water conducting xylem of the tree. A solar panel was directly connected to the non-polarised charging ports to trickle charge the internal battery of each Sap Flow Meter for continuous field operation. Sap flow was continuously monitored at 30-min temporal resolution over an 18-month period from November 2015 to April 2017.

Information on tree leafing phenology was also collected by noting the months of the year when the trees shed their leaves through the sap flow measurement period.

Data analysis

The downloaded data was analysed using the Sap Flow Tool (SFT) software and the Combined Instrument Software (CIS) to obtain daily flows (l day^{-1}) and sap velocity (cm h^{-1}). We performed a linear transformation on the heat pulse velocity to obtain corrected zero flow baselines for asymmetry of installation. The daily flows were analysed and compared with rainfall patterns using a line graph (for daily flows) and bar graphs (for rainfall data). Daily flow data was exported from the SFT software as a .csv file and used for further analysis. Pearson's correlation coefficients between rainfall and seasonal daily sap flow in *C. africana* and *A. coriaria* were obtained using Minitab 18 (Minitab Inc., Pennsylvania, USA).

An analysis of variance General Linear Model (Two-way ANOVA-GLM) was also performed in Minitab to assess the interaction between tree species and season on daily sap flow with 'tree species' and 'season' as the main effects at $P \leq 0.05$ significance level. The two-way ANOVA would establish whether either of the two independent variables (tree species and season) or their interaction are statistically significant.

A schematic representation of existing farming systems with the two tree species, coffee and common beans was constructed from the smallholder farmers' perspective. This was integrated with information on rainfall patterns, tree leaf phenology, coffee flowering and harvesting as well as planting and harvesting of common beans.

Results

Assessment of the daily sap flow of the study trees

Table 1 provides a summary of the average daily sap flow of the six trees that were monitored during the study. The maximum daily sap flow was 87.6 l day^{-1} for *A. coriaria* and 52.3 l day^{-1} for *C. africana*. *Albizia coriaria* trees generally used more water registering average daily flow of $20\text{--}32 \text{ l day}^{-1}$ against $12\text{--}15 \text{ l day}^{-1}$ used by *C. africana*. *Albizia coriaria* trees had larger diameter at breast height (DBH $41\text{--}53 \text{ cm}$) than *C. africana* (DBH $28\text{--}37 \text{ cm}$).

To obtain standard comparable daily sap flow in the two tree species, the daily flows were computed per cross-sectional area of the tree at 1.2 m height ($\text{l day}^{-1} \text{ cm}^{-2}$) as shown in Table 1. The overall average daily sap flow of *C. africana* ($0.018 \text{ l day}^{-1} \text{ cm}^{-2}$) was higher than that

A. coriaria ($0.015 \text{ l day}^{-1} \text{ cm}^{-2}$), an indication that *C. africana* used 12% more water than *A. coriaria*. Unlike *C. africana*, negative daily sap flow was registered in *A. coriaria*. It is, however, likely that other factors including soil properties and competitive relationships of the trees with the associated crops (not covered under this study) may also influence the differences in tree water use. The study therefore focused on assessing trends in daily and seasonal tree water use of the two tree species that occur within an agroforestry setting.

Tree water use in *Albizia coriaria* and *Cordia africana*

The study made a comparison between the daily sap flow in *C. africana* and *A. coriaria* with rainfall data. The data presented in Figure 1 is mean daily sap flow for *C. africana* and *A. coriaria* covering 10 months of sap flow measurement. *Cordia africana* exhibited higher daily sap flow than *A. coriaria* from the start of the experiment until early March 2016 (Fig. 1). This was followed by a gradual decline below *A. coriaria* thereafter through the rainfall season. However, daily sap flow in both trees generally increased during the dry season and declined during high rainfall days. Unlike *A. coriaria*, total daily sap flow in *C. africana* drastically decreased during the main rainfall season between April and June.

The minimum daily sap flow for each tree was registered at different periods of the year (Fig. 1). In *C. africana*, the minimum daily flows occurred between April and May (peak rainfall months), and between February and March (dry season) in *A. coriaria* (also characterised by reverse flows). The consistent occurrence of reverse flows in *A. coriaria* between January and February were also observed following analysis of additional data covering 506 days (Fig. 2).

Relationship between rainfall and daily sap flow

Pearson's correlation indicated that rainfall was highly correlated ($P < 0.05$) with daily sap flow in both *C. africana* and *A. coriaria* trees, predominantly in the dry season (Table 2). However, the positive correlation coefficients observed in *A. coriaria* in the dry season is an indication that there could be factors other than rainfall, that are influencing the daily sap flow in the tree during the dry season. The positive correlation implies that the daily sap flow increased with rainfall. The higher the rainfall the less the evaporative demand, and the more water in the soil both of which enhance transpiration. The negative correlation in *C. africana*, where water use seems to be decoupled from rainfall, may be attributed to a strong lag between the start of the wet season and recovery in tree water use following the dry season.

Interaction between tree species and season on daily sap flow

In Table 3 below, the two-way ANOVA performed shows that there was a significant interaction between tree species and season (tree species* season) on the mean daily sap flow ($F(1,548) = 56.48, P < 0.001$). While there were statistically significant differences in mean daily sap flow between *C. africana* and *A. coriaria* ($F(1,548) = 275.3, P < 0.001$), there was no statistically significant difference in mean daily sap flow between the dry and wet seasons ($F(1,548) = 1.44, P = 0.231$).

Table 1. Summary of maximum, minimum and average daily sap flow per tree and sap flow standardised to tree area for *Albizia coriaria* and *Cordia africana* over a 10-month period of the experiment

Tree species	Tree ID	DBH (cm)	Daily sap flow (l day^{-1})			Daily sap flow ($\text{l day}^{-1} \text{ cm}^{-2}$)	
			Min	Max	Average	Tree	Overall
<i>Albizia coriaria</i>	Tree 1	40.9	-0.8	87.6	24.8	0.019	0.018
<i>A. coriaria</i>	Tree 2	52.5	-5.8	34.7	20.6	0.010	
<i>A. coriaria</i>	Tree 3	51.4	-8.2	75.4	31.5	0.015	
<i>Cordia africana</i>	Tree 1	36.6	1.3	48.7	15.3	0.015	
<i>C. africana</i>	Tree 2	31.6	1.2	41.5	12.8	0.016	
<i>C. africana</i>	Tree 3	28.3	0.5	52.3	15.2	0.024	

DBH, diameter at breast height.

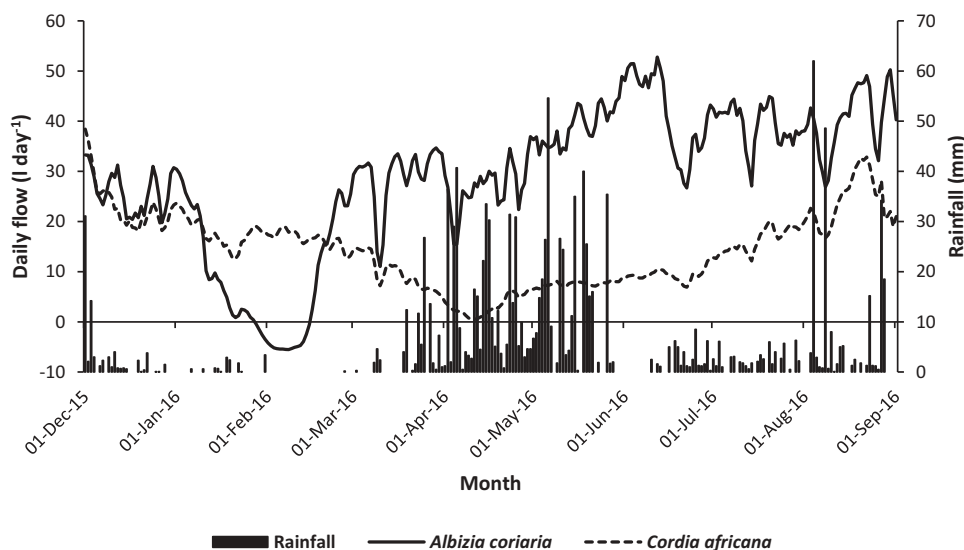


Figure 1. Daily average sap flow in *Albizia coriaria* and *Cordia africana* over a 10-month period. Rainfall events indicate the early wet season (April–June) and the start of the late wet season (August–November)

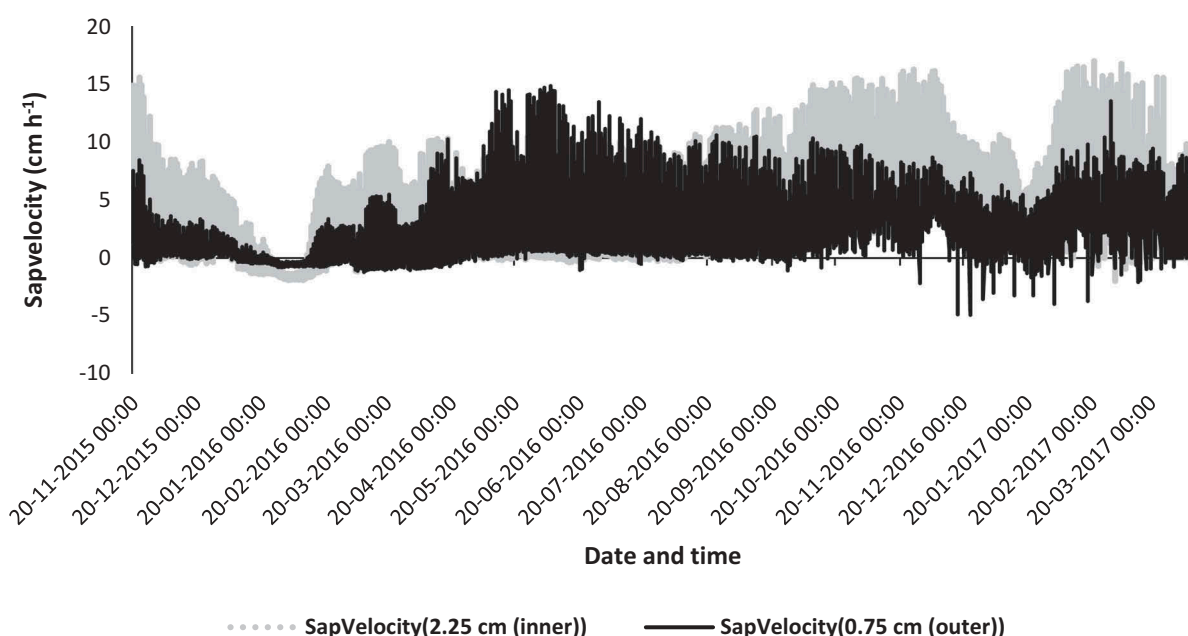


Figure 2. Radial changing of sap velocity in *Albizia coriaria* registered by the inner and outer thermocouples (data presented are average values from the three trees)

Table 2. Pearson's correlation coefficients between rainfall and seasonal daily sap flow in *Cordia africana* and *Albizia coriaria*

Tree species	Pearson's correlation coefficients		
	Dry season	Wet season	All
<i>Albizia coriaria</i>	0.326*	-0.107 ^{ns}	0.136*
<i>Cordia africana</i>	-0.199*	-0.149 ^{ns}	-0.228*

Correlations significant, at the level of $P < 0.05$, are indicated by *; those that are non-significant are labelled as ns.

Radial changing of sap velocities between outer to inner thermocouples in *Albizia coriaria*

An analysis of the sap velocity of *A. coriaria* over an extended period (November 2015–April 2017) showed radial changing of sap velocities between the inner and outer thermocouples (Fig. 2).

The inner thermocouple generally registered higher sap velocities than the outer thermocouple at various stages of water stress especially between November and March in 2016

and 2017 (Fig. 2). However, between the months of April and early June 2016, the outer thermocouple recorded higher sap velocities than the inner thermocouple. This scenario extended through the rainfall season until October 2016.

Existing agroforestry systems in Mt Elgon region

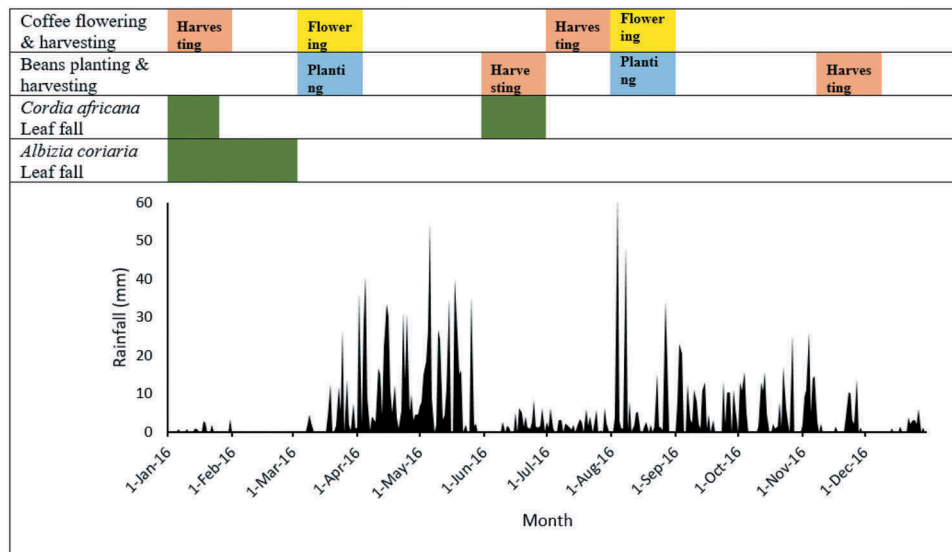
Most farmers in Mt Elgon region are small landholders with 1–2 acres of land, which forces them to till the land intensively throughout the year in order to grow multiple crops. The agroforestry systems are mainly characterised by coffee (*Coffea arabica* L.) and beans (*Phaseolus vulgaris* L.) with scattered trees, predominantly *Cordia africana* and *A. coriaria* (Fig. 3). Coffee normally flowers twice every year at the onset of the rain seasons, coinciding with the planting of beans.

Both tree species are deciduous, with *C. africana* shedding its leaves at the onset of the dry seasons (Fig. 3).

Table 3. A two-way ANOVA to assess the interaction between tree species and season on daily sap flow

Tests of between-subjects' effects					
Dependent variable: Daily sapflow					
Source	Type III sum of squares	Df	Mean square	F	Sig.
Corrected model	36 480.043 ^a	3	12 160.014	103.258	0.000
Intercept	255 990.935	1	255 990.935	2173.781	0.000
Tree species	32 422.605	1	32 422.605	275.321	0.000
Season	169.577	1	169.577	1.440	0.231
Interaction between tree species and season	6651.270	1	6651.270	56.480	0.000
Error	64 534.101	548	117.763		
Total	358 618.298	552			
Corrected total	101 014.144	551			

^aR² = 0.361 (adjusted R² = 0.358).


Figure 3. Key agroforestry systems and phenological events in Mt Elgon region of Uganda, indicated in terms of 2016 rainfall for the region

However, *A. coriaria* is observed to have one major annual leaf fall which occurs in January, sometimes extending into February.

Discussion

Differences in tree water use

Water-use studies of agroforestry tree species are essential for understanding their interactions with other agroforestry components. A number of individual tree water-use studies have focused on the species *Eucalyptus grandis* W.Hill (Dye 1996), *Acacia tortilis* (Forssk. Hayne) (Do et al. 2008), *Eucalyptus camaldulensis* Dehnh. (O'Grady et al. 2009), *Grevillea robusta* A.Cunn. ex R.Br. (Lott et al. 1996), *Vitellaria paradoxa* C.F.Gaertn. (Bazié et al. 2017) and *Senna spectabilis* (DC.) H.S.Irwin & Barneby (Namirembe et al. 2008) (Table 4). However, *C. africana* and *Albizia coriaria* are important agroforestry tree species whose water use is not well documented. Prior to standardisation of the daily sap flow this study revealed that *A. coriaria* generally uses more water than *C. africana* (Fig. 1), an indication that *A. coriaria* exhibits a higher transpiration rate than *C. africana*. We propose a number of reasons for this contrast in tree species water use including differences in tree sizes, rooting depth, and sap wood area and density among other factors.

In terms of tree size, a study in the Republic of Panama on trees of difference trunk diameters reported a similar trend

where tree size played a dominant role in determining the water use and water storage characteristics of four individual tree species (Meinzer et al. 2004). In that study, mean daily water use increased with tree size from 42 kg day⁻¹ in a 34 cm diameter *Cordia alliodora* (Ruiz & Pav.) Oken tree to 785 kg day⁻¹ in a 98 cm diameter *Anacardium excelsum* L. (Table 4). Daily reliance on stored water was also reported to increase with tree size in two temperate coniferous and one temperate angiosperm species (Phillips et al. 2003), thus partially explaining the difference in water use between larger diameter *Albizia coriaria* and smaller diameter *C. africana* in the current study.

However, when daily sap flow was assessed in terms of daily sap flow per cross-sectional area of the tree at 1.2 m height, the results showed that *C. africana* used 12% more water than *A. coriaria* (Table 1). This may be due to differences in the wood biophysical properties. Sapwood properties, including wood density, have been reported to influence the water economy of trees, showing a negative correlation between species-specific water use and sapwood density (Oliva Carrasco et al. 2015). *Cordia africana* has been reported to have wood density of 0.40 g cm⁻³ (Buyinza et al. 2014), which is lower than *A. coriaria* at 0.59 g cm⁻³ (Ojelel et al. 2015). Trees with high wood densities have smaller xylem vessel diameters than those with low wood densities. A related study of species-specific water use in *Ceiba speciosa* (A.St.-Hil., A.Juss. & Cambess.) Ravenna, deciduous tree native to the tropical and subtropical forests of South America,

Table 4. Tree water use and tree parameters including method used for different tree species

Tree species	Method ^a	DBH (cm)	Water use	Source
<i>Acacia aneura</i>	CHPM	12	14 kg day ⁻¹	(O'Grady et al. 2009)
<i>A. tortilis</i>	TTD	17	48 l day ⁻¹	(Do et al. 2008)
<i>Eucalyptus camaldulensis</i>	CHPM	18	87 kg day ⁻¹	(O'Grady et al. 2009)
<i>E. grandis</i>	CHPM	30	141 kg day ⁻¹	(Dye 1996)
<i>E. pilularis</i>	CHPM	11–14	18 l day ⁻¹	(Adrienne et al. 2013)
<i>Grevillea robusta</i>	CHPM	n/a	12 kg day ⁻¹	(Lott et al. 1996)
<i>Cordia alliodora</i>	CHPM	34	42 kg day ⁻¹	(Meinzer et al. 2004)
<i>Anacardium excelsum</i>	CHPM	98	785 kg day ⁻¹	(Meinzer et al. 2004)
<i>Vitellaria paradoxa</i>	HRM	55.5	151 l day ⁻¹	(Bazié et al. 2017)
<i>Senna spectabilis</i>	CHPM	7.9	4.8 kg day ⁻¹	(Namirembe et al. 2008)

^aMethods used is indicated by compensation heat pulse method (CHPM), heat ratio method (HRM), transient thermal dissipation (TTD). DBH, diameter at breast height.

showed that sap flow increased exponentially with increasing sapwood density (Oliva Carrasco et al. 2015). The large quantities of discharge water into the transpirational stream were consistent with the very low wood density of *C. speciose*. This could partly explain the lower tree water use in *A. coriaria* on a standardised daily basis in this study. However, despite using more water on a daily basis, *Cordia africana* is more efficient in its water use (since water use expressed on an area basis relates to water use efficiency). This is because higher water use efficiency generally means less water used per carbon gained, a quality that would clearly benefit small-holder farmers in the Mt Elgon region.

The differences in daily water use of *C. africana* and *A. coriaria* during different times of the year (dry and wet season) were further investigated by performing a two-way ANOVA with 'tree species' and 'season' as the main effects. The results show that interaction between tree species and season (tree species^x season) had a significant effect on the mean daily water use (Table 3). However, there was a non-significant effect of season on daily water use, an indication that the dry and wet seasons may not be sufficient in explaining the differences in daily water use of *C. africana* and *A. coriaria*. However, in *C. africana*, likelihood of a lag in the recovery of tree water use following the dry and wet season traits linked to deep rooting depth and high stem capacitance may facilitate the species to maintain high rates of water use, early in the dry season.

Reverse flows in *Albizia coriaria*

Reverse flows have been reported in trees such as *G. robusta* (Burgess et al. 1998; Smith et al. 1999), *E. camaldulensis* (Burgess et al. 1998), *Fraxinus velutina* Torr. and *Juglans major* Torr. A. Heller (Hultine et al. 2003) predominantly occurring when surface soils are dry. The HRM used in this study has the capacity to detect reverse flows (Burgess et al. 2001). While this study did not measure water potential, other studies have indicated that reverse flows in trees result from low soil water potential (Smith et al. 1999). When the atmosphere is wetter than the soil, the soil will have a higher water potential than the atmosphere, so water flows to the soil. Water in a tree will always flow towards areas where the water potential is least. This can be through or across the stem, a process also referred to as hydraulic redistribution (Matimati et al. 2014; Hafner et al. 2017). A study conducted on the neotropical savanna trees of Brazil reported occurrence of reverse sap flow in deciduous and brevi-deciduous species during the dry season that was consistent with hydraulic lift (Scholz et al. 2008). In this study, reverse flows in *A. coriaria* coincided with the consistent annual tree leaf

fall events between late January and February. The occurrence of reverse flows and leaf shedding during the dry season is a water saving strategy for *A. coriaria*.

Albizia coriaria increased its water use about one month prior to the start of the wet season, between mid-February and early March (Fig. 1). This may be because *A. coriaria* trees start flushing with new leaves at that time of the year in preparation of a presumably very predictable start to the wet season.

Influence of tree leaf phenology on water use

The two tree species in this study also show varying patterns in water use across seasons and leaf phenology stages characterised by small reverse flows in *A. coriaria* (Fig. 1). We observe that the reverse flows in *A. coriaria* could have been triggered by leaf shedding, while the reduction in sap flow in *C. africana* occurred during rainfall events. However, there might be a lag in the recovery of *C. africana* tree water use following the dry season, hence following the wet season, traits linked to deep rooting depth and high stem capacitance may facilitate *C. africana* to maintain high rates of water use into the early part of the dry season. This is an indication that the two species may have different water-use strategies.

The leafing phenological pattern of *A. coriaria* has a greater influence on tree water use than in *C. africana*, suggesting that the consistent and predictable leaf shedding pattern in *A. coriaria* may be beneficial for planning farming activities among smallholders. The magnitude and duration of whole tree water use may be caused by reduction in photosynthetic leaf area (Adrienne et al. 2013), normally triggered by environmental variability (rain and dry seasons). The dry season is an important trigger for leaf abscission and leaf and branch emergence in seasonal tropical forest and savanna (Dalmolin et al. 2015). Deciduous species avoid drought by dropping their entire canopy to minimise the rate of transpiration in the dry season (Eamus 1999). Consequently, this also reduces competition for soil water and nutrient resources. The leaf shedding pattern of *A. coriaria* provides an opportunity for maximising the temporal complementarities of agroforestry systems.

Trees can reduce competition through their species-dependent differences in leafing phenology and rooting patterns and activity. While this study did not focus on tree rooting patterns and activity, leafing phenology has been associated with seasonal time courses for partitioning soil moisture, where species showing the smallest seasonal variation in leaf area are able to tap deep sources of soil water during dry seasons (Meinzer et al. 1999). This study suggests

that leafing phenology has an important role in determining the patterns and rates of soil water extraction, yet tree phenology is a neglected aspect of agroforestry research. Furthermore, the importance of studying the response of trees with differing leafing phenology to drought as such information would help provide an improved understanding of water management in agroforestry systems (Eamus 1999).

Variability in radial sap velocities in *Albizia coriaria*

The changing radial pattern in sap velocities between the outer to inner thermocouples in *A. coriaria* point to a number of factors including the microclimate, sap wood area and meteorological conditions. While it is widely reported that sap flow is essentially driven by the microclimate, especially the evaporative demand and radiation (Ford et al. 2004; Fiora & Cescatti 2006), the possible influence of climatic conditions on radial variability is yet to be thoroughly investigated. A related study showed that sap flow in *Avicennia marina* (Forssk.) Vierh. varied significantly throughout the sapwood and that radial patterns in sap flux density were dependent on meteorological conditions (Van de Wal et al. 2015). A field experiment that assessed sap flow in mature mangrove of *Avicennia germinans* L. trees of different sizes also observed that the shape of the radial patterns differed between the wet and dry season of their experiment (Muller et al. 2009). Essentially, the surface roots are connected to the outer region of the sapwood area while the deeper tap roots are physiologically connected to the inner region of the sapwood area. It is anticipated that when it rained and soil moisture increased, the outer thermocouple was able to access the excess moisture from the soil due to its close proximity to the moisture in the surrounding soil surfaces. The ability of the tap roots to draw water from deeper soil regions during water stress periods could suggest another water saving strategy by *Albizia coriaria*.

However, observing radial variations in sap velocities in the outer and inner thermocouples may also introduce errors in estimating total tree water use, especially in trees with large sapwood area. A number of studies have acknowledged that woody species with deep functional sapwood present a challenge in scaling point measurements of sap velocity to whole-stem sap flow and the need to account for radial variability of sap velocity in the stem (Wullschleger & King 2000; Nadezhdina et al. 2002; Ford et al. 2004; Fiora & Cescatti 2006). The sapwood can remain active up to a depth of 8 cm (Muller et al. 2009) which renders such a stem more susceptible to radial variations. Radial variation can account for discrepancies of up to 25% (Van de Wal et al. 2015). Therefore, it is recommended that radial variability is determined prior to sap flow measurement by first using sensors with multiple measuring points along a stem radius followed by single-point measurement with sensors at a predetermined depth.

Tree water use influence from associated crops

Tree water use of the study tree species could also be influenced by the associated crops, including coffee and common beans that are commonly integrated in the agroforestry farming systems in the study sites (Fig. 3). Trees and agricultural crops growing together on the same piece of land may compete for available soil water, especially where soils are shallow. Studies have reported greater

depletion of water at depth in the tree-crop treatments than sole tree plots (Jackson et al. 2000; Lott et al. 2003) in the upper soil layers. However, some trees have dimorphic rooting morphology which allows them to shift from predominantly shallow to deeper sources of water when water availability in the upper soil layers is low (Priyadarshini et al. 2016), an adaptive strategy employed to overcome seasonal water limitation. This was reported for *V. paradoxa* where soil moisture in the upper soil layers was significantly lower during the dry season and as a result *V. paradoxa* shifted to deeper water sources, obtaining approximately 30% of its water requirement from groundwater (Tobella et al. 2017). Knowledge about the sources and patterns of tree water use provides crucial information to better understand how trees influence the local water balance in agroforestry systems. However, in this current study, the differences between the soil and competing relationships between the two farms could have limited species comparisons and need to be considered in the subsequent studies.

Conclusion

Cordia africana generally uses more water than *A. coriaria* on a standardised daily basis, based on stem cross-sectional area. While both tree species exhibited low daily sap flow during certain stages of the experiment, they occurred at different periods. The reverse flows in *A. coriaria* could have been triggered by leaf shedding which occurs in January–February. However, the period of low flows in *C. africana* coincided with the rainfall events, an indication that the two species may have different water-use strategies. There was a significant main effect of the interaction between tree species and season on daily water use. The leaf shedding pattern of *A. coriaria* has a greater influence on tree water use than in *C. africana*, suggesting that the consistent and predictable leaf fall in *A. coriaria* may be beneficial for planning farming activities among smallholders. The study recommends further studies to monitor sap flow in the associated crop (coffee) to better understand the interactions among the different agroforestry components. Such studies should also seek to understand the underlying causes of radial changing of sap velocities between outer to inner thermocouples, a characteristic observed in *A. coriaria* under the current study.

Agroforestry has attracted considerable attention in recent years because of its potential to reduce poverty, improve food security, reduce land degradation and mitigate climate change. However, progress in promoting agroforestry is held back because decision-makers lack reliable tools to accurately predict yields from tree-crop mixtures. We recommend further studies to establish convergence of tree traits related to plant water use such as sap wood density, photosynthetic active radiation, leaf area, xylem water potential, sap flow, sapwood area, tree diameter (stem increment) and height. Identifying convergence in water use of these important agroforestry tree species can potentially provide powerful tools for scaling physiological processes in natural ecosystems (O'Grady et al. 2009). Such information would be useful in modelling trade-offs between carbon accumulation and water loss in agroforestry systems. Understanding these factors will also facilitate development of appropriate tree management regimes for optimal utilisation of soil water, thus enhancing productivity of agroforestry systems among smallholder farmers.

Acknowledgements

This work is part of a postgraduate research study at the University of Adelaide funded by the Australian Centre for International Agricultural Research (ACIAR). The data is part of the Trees for Food Security Project 1 and 2 in Uganda. Joel Buyinza is a recipient of the ACIAR John Allwright Fellowship. The authors are grateful for the support rendered by the World Agroforestry Centre, the National Agricultural Research Organization through the National Forestry Resources Research Institute of Uganda and ICT International.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Australian Centre for International Agricultural Research [FST/2015/039]; Australian Centre for International Agricultural Research [John Allwright Fellowship]; Australian Centre for International Agricultural Research (ACIAR) [FST/2015/039].

ORCID

J. Buyinza  <http://orcid.org/0000-0003-3844-4347>

M. D. Denton  <http://orcid.org/0000-0002-2804-0384>

I. K. Nuberg  <http://orcid.org/0000-0003-1942-1190>

References

- Adrienne BN, Smith RGB, Ryde J, Dane ST, David IF, Philip JA, Jürgen B. 2013. Changes in whole-tree water use following live-crown pruning in young plantation-grown *Eucalyptus pilularis* and *Eucalyptus cloeziana*. *Forests*. 4:106–121.
- Bazié HR, Sanou J, Bayala J, Bargaues-Tobella A, Zombré G, Ilstedt U. 2017. Temporal variations in transpiration of *Vitellaria paradoxa* in West African agroforestry parklands. *Agroforestry Systems*. 92:1673–1686.
- Broadhead JS, Black CR, Ong CK. 2003. Tree leafing phenology and crop productivity in semi-arid agroforestry systems in Kenya. *Agroforestry Systems*. 58:137–148.
- Bukomeko H, Jassogne L, Tumwebaze SB, Eilu G, Vaast P. 2017. Integrating local knowledge with tree diversity analyses to optimize on-farm tree species composition for ecosystem service delivery in coffee agroforestry systems of Uganda. *Agroforestry Systems*. p. 1–16. doi: 10.1007/s10457-017-0172-8
- Burgess SSO, Adams MA, Turner NC, Beverly CR, Ong CK, Khan AAH, Bleby TM. 2001. An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. *Tree Physiology*. 21:589–598.
- Burgess SSO, Adams MA, Turner NC, Ong CK. 1998. The redistribution of soil water by tree root systems. *Oecologia*. 115:306–311.
- Buyinza J, Tumwebaze SB, Namaalwa J, Byakagaba P. 2014. Above-ground biomass and carbon stocks of different land cover types in Mt. Elgon, Eastern Uganda. *International Journal of Research on Land-Use Sustainability*. 1:51–61.
- Cai X, Molden D, Mainuddin M, Sharma B, Ahmad M-U-D, Karimi P. 2011. Producing more food with less water in a changing world: assessment of water productivity in 10 major river basins. *Water International*. 36:42–62.
- Dalmolin Á, Almeida Lobo F, Vourlitis G, Silva P, Dalmagro H, Antunes M, Ortiz C. 2015. Is the dry season an important driver of phenology and growth for two Brazilian savanna tree species with contrasting leaf habits? *Plant Ecology*. 216:407–417.
- Descheemaeker K, Bunting SW, Bindraban P, Muthuri C, Molden D, Beveridge M, Van Brakel M, Herrero M, Clement F, Boelee E, et al. 2013. Increasing water productivity in agriculture. In: Boelee E, editor. *Managing water and agroecosystems for food security*. Wallingford (UK): CABI Publishing; p. 104–123.
- Do FC, Rocheteau A, Diagne AL, Goudiaby V, Granier A, Lhomme J-P. 2008. Stable annual pattern of water use by *Acacia tortilis* in Sahelian Africa. *Tree Physiology*. 28:95–104.
- Dye PJ. 1996. Response of *Eucalyptus grandis* trees to soil water deficits. *Tree Physiology*. 16:233.
- Eamus D. 1999. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends in Ecology & Evolution*. 14:11–16.
- Ellison D, Morris CE, Locatelli B, Sheil D, Cohen J, Murdiyarso D, Gutierrez V, Noordwijk MV, Creed IF, Pokorny J, et al. 2017. Trees, forests and water: cool insights for a hot world. *Global Environmental Change*. 43:51–61.
- FAO (Food and Agricultural Organization). 2011. *The state of the world's land and water resources for food and agriculture: managing systems at risk*. 1st ed. Milton Park: Earthscan.
- Fiora A, Cescatti A. 2006. Diurnal and seasonal variability in radial distribution of sap flux density: implications for estimating stand transpiration. *Tree Physiology*. 26:1217–1225.
- Ford CR, Goranson CE, Mitchell RJ, Will RE, Teskey RO. 2004. Diurnal and seasonal variability in the radial distribution of sap flow: predicting total stem flow in *Pinus taeda* trees. *Tree Physiology*. 24:951–960.
- Gram G, Vaast P, van der Wolf J, Jassogne L. 2018. Local tree knowledge can fast-track agroforestry recommendations for coffee smallholders along a climate gradient in Mount Elgon, Uganda. *Agroforestry Systems*. 92(6): 1625–1638. doi: 10.1007/s10457-017-0111-8
- Hafner BD, Tomasella M, Häberle K-H, Goebel M, Matyssek R, Grams TEE, Mencuccini M. 2017. Hydraulic redistribution under moderate drought among English oak, European beech and Norway spruce determined by deuterium isotope labeling in a split-root experiment. *Tree Physiology*. 37:950–960.
- Hultine KR, Williams DG, Burgess SSO, Keefer TO. 2003. Contrasting patterns of hydraulic redistribution in three desert phreatophytes. *Oecologia*. 135:167–175.
- Jackson NA, Wallace JS, Ong CK. 2000. Tree pruning as a means of controlling water use in an agroforestry system in Kenya. *Forest Ecology and Management*. 126:133–148.
- Janani L, Hillary L, Phillips K. 2014. Mordanting methods for dyeing cotton fabrics with dye from *Albizia coriaria* plant species. *International Journal of Scientific and Research Publications*. 4:1–6.
- Katende AB, Birnie A, Tengna SB. 1995. *Useful trees and shrubs for Uganda: identification, propagation and management for agricultural and pastoral communities*. Nairobi (Kenya): Regional Soil Conservation Unit. Technical Handbook No. 10.
- Kebebew F, Balemie K. 2006. Ethnobotanical study of wild edible plants in Derashe and Kucha Districts, South Ethiopia. *Journal of Ethnobiology and Ethnomedicine*. 2:53.
- Linares JC, Covelo F, Carreira JA, Merino JA. 2012. Phenological and water-use patterns underlying maximum growing season length at the highest elevations: implications under climate change. *Tree Physiology*. 32:161–170.
- Lott JE, Khan AAH, Black CR, Ong CK. 2003. Water use in a *Grevillea robusta*-maize overstorey agroforestry system in semi-arid Kenya. *Forest Ecology and Management*. 180:45–59.
- Lott JE, Khan AAH, Ong CK, Black CR. 1996. Sap flow measurements of lateral tree roots in agroforestry systems. *Tree Physiology*. 16:995–1001.
- Matimati I, Verboom GA, Cramer MD. 2014. Do hydraulic redistribution and nocturnal transpiration facilitate nutrient acquisition in *Aspalathus linearis*? *Oecologia*. 175:1129.
- Mehari A, Habte B. 2006. Influence of initial spacing on growth and branching characteristics of *Cordia africana* trees established on Eritrean Highland. *New Forests*. 31:185–193.
- Meinzer FC, Andrade JL, Goldstein G, Holbrook NM, Cavellier J, Wright SJ. 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia*. 121:293–301.
- Meinzer FC, James SA, Goldstein G. 2004. Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees. *Tree Physiology*. 24:901–909.
- Muller E, Lambs L, Fromard F. 2009. Variations in water use by a mature mangrove of *Avicennia germinans*, French Guiana. *Annals of Forest Science*. 66:Article no. 803.
- Muthuri CW, Ong CK, Black CR, Ngumi VW, Mati BM. 2005. Tree and crop productivity in *Grevillea*, *Alnus* and *Paulownia*-based agroforestry systems in semi-arid Kenya. *Forest Ecology and Management*. 212:23–39.

- Muthuri CW, Ong CK, Craigon J, Mati BM, Ngumi VW, Black CR. 2009. Gas exchange and water use efficiency of trees and maize in agroforestry systems in semi-arid Kenya. *Agriculture, Ecosystems & Environment*. 129:497–507.
- Nadezhdina N, Čermák J, Ceulemans R. 2002. Radial patterns of sap flow in woody stems of dominant and understory species: scaling errors associated with positioning of sensors. *Tree Physiology*. 22:907–918.
- Namirembe S, Brook RM, Ong CK. 2008. Manipulating phenology and water relations in *Senna spectabilis* in a water limited environment in Kenya. *Agroforestry Systems*. 75:197.
- Namukobe J, Kasenene JM, Kiremire BT, Byamukama R, Kamatenesi-Mugisha M, Krief S, Dumontet V, Kabasa JD. 2011. Traditional plants used for medicinal purposes by local communities around the Northern sector of Kibale National Park, Uganda. *Journal of Ethnopharmacology*. 136:236–245.
- O'Grady AP, Cook PG, Eamus D, Duguid A, Wischusen JDH, Fass T, Worldege D. 2009. Convergence of tree water use within an arid-zone woodland. *Oecologia*. 160:643–655.
- Ojelel S, Otiti T, Mugisha S. 2015. Fuel value indices of selected woodfuel species used in Masindi and Nebbi districts of Uganda. *Energy, Sustainability and Society*. 5:14.
- Oliva Carrasco L, Bucci SJ, Di Francescantonio D, Lezcano OA, Campanello PI, Scholz FG, Rodríguez S, Madanes N, Cristiano PM, Hao G-Y, et al. 2015. Water storage dynamics in the main stem of subtropical tree species differing in wood density, growth rate and life history traits. *Tree Physiology*. 35:354–365.
- Orwa C, Mutua A, Kindt R, Jamnadass R, Anthony S. 2009. *Agroforestry database: a tree reference and selection guide version 4.0*. Nairobi: World Agroforestry Centre.
- Phillips NG, Ryan MG, Bond BJ, McDowell NG, Hinckley TM, Čermák J. 2003. Reliance on stored water increases with tree size in three species in the Pacific Northwest. *Tree Physiology*. 23:237–245.
- Pinho RC, Miller RP, Alfaia SS. 2012. Agroforestry and the improvement of soil fertility: a view from Amazonia. *Applied and Environmental Soil Science*. 12:Article no. 616383.
- Priyadarshini KVR, Prins HHT, Bie S, Heitkönig IMA, Woodborne S, Gort G, Kirkman K, Ludwig F, Dawson TE, Kroon H. 2016. Seasonality of hydraulic redistribution by trees to grasses and changes in their water-source use that change tree–grass interactions. *Ecohydrology*. 9:218–228.
- Sales E, Rodas O, Valenzuela O, Hillbrand A, Sabogal C. 2016. On the way to restore Guatemala's degraded lands: creating governance conditions. *World Development Perspectives*. 4:16–18.
- Scholz FG, Bucci SJ, Goldstein G, Moreira MZ, Meinzer FC, Domec JC, Villalobos-Vega R, Franco AC, Miralles-Wilhelm F. 2008. Biophysical and life-history determinants of hydraulic lift in Neotropical savanna trees. *Functional Ecology*. 22:773–786.
- Smith DM, Jackson NA, Roberts JM, Ong CK. 1999. Reverse flow of sap in tree roots and downward siphoning of water by *Grevillea robusta*. *Functional Ecology*. 13:256–264.
- Steppe K, Vandegehuchte MW, Tognetti R, Mencuccini M, Oren R. 2015. Sap flow as a key trait in the understanding of plant hydraulic functioning. *Tree Physiology*. 35:341–345.
- Strobl S, Cueva E, Silva B, Knuesting J, Schorsch M, Scheibe R, Bendix J, Beck E. 2017. Water relations and photosynthetic water use efficiency as indicators of slow climate change effects on trees in a tropical mountain forest in South Ecuador. *Ecological Indicators*. 83:550–558.
- Tabuti JRS, Mugula BB. 2007. The ethnobotany and ecological status of *Albizia coriaria* Welw. ex Oliv. in Budondo Sub-county, eastern Uganda. *African Journal of Ecology*. 45:126–129.
- Tobella AB, Hasselquist NJ, Bazié HR, Nyberg G, Laudon H, Bayala J, Ilstedt U. 2017. Strategies trees use to overcome seasonal water limitation in an agroforestry system in semiarid West Africa. *Ecohydrology*. 10:e1808.
- Van de Wal B, Guyot A, Lovelock C, Lockington D, Steppe K. 2015. Influence of temporospatial variation in sap flux density on estimates of whole-tree water use in *Avicennia marina*. *Structure and Function*. 29:215–222.
- Webber H, Gaiser T, Ewert F. 2014. What role can crop models play in supporting climate change adaptation decisions to enhance food security in Sub-Saharan Africa? *Agricultural Systems*. 127:161–177.
- Wullschlegel SD, King AW. 2000. Radial variation in sap velocity as a function of stem diameter and sapwood thickness in yellow-poplar trees. *Tree Physiology*. 20:511–518.
- Yan C, Wang B, Zhang Y, Zhang X, Takeuchi S, Qiu GY. 2018. Responses of sap flow of deciduous and conifer trees to soil drying in a subalpine forest. *Forests*. 9:1–15.