
Sap flow variation in selected riparian woodland species in the Okavango Delta, Botswana

Aobakwe K. Lubinda^{1*}, Mike Murray-Hudson¹ and Steve Green²

¹University of Botswana Okavango Research Institute, Private Bag 285, Maun, Botswana and ²Plant & Food Research Palmerston North, Private Bag 11030, Manawatu Mail Centre, Palmerston North 4442, New Zealand

Abstract

In the tropical Okavango Delta, transpiration by trees is an important process partly responsible for maintaining the basin as a freshwater environment. Quantification of evapotranspiration from terrestrial landforms of the delta, fringed by riparian woodlands, is one of the main contributors to uncertainty in current hydrological modelling. We investigated sap flow of common trees in the distal, mid- and upper delta in July–August 2012, November–December 2012 and February–April 2013 using the compensation heat pulse velocity method. In the distal delta, four *Diospyros mespiliformis* individuals of different sizes were studied. Four trees of different species were studied in the mid- and upper delta. Sap flow density (SFD; flow per unit cross-sectional area) was used as a common unit to facilitate comparison. Sap flow varied with tree size, species, season and location. It was positively correlated with tree size ($r^2 = 0.67$). Sap flow variation between seasons and across locations in all the species studied indicated two distinct groups. Group 1 transpired the least during the hottest season, November–December, and Group 2 the most. In Group 1, the highest average SFD was $1.17 \text{ l cm}^{-2} \text{ day}^{-1}$ during July–August; in Group 2, it was $1.07 \text{ l cm}^{-2} \text{ day}^{-1}$ during November–December. Changes in the hydrology of the delta would negatively affect the riparian woodland.

Key words: compensation heat pulse velocity, evapotranspiration, water balance, water use

Résumé

Dans le delta de l'Okavango, tropical, la transpiration des arbres est un processus important partiellement

*Correspondence: E-mail: bkwlubinda08@gmail.com

responsable du fait que ce bassin reste un environnement d'eau douce. La quantification de l'évapotranspiration de la topographie terrestre du delta, bordée de forêts riveraines, est un des principaux contributeurs de l'incertitude dans la modélisation hydrologique actuelle. Nous avons étudié la coulée de sève d'arbres communs dans le delta distal, moyen et supérieur en juillet-août 2012, novembre-décembre 2012 et février-avril 2013 par la méthode de compensation heat pulse velocity. Dans le delta distal, nous avons étudié quatre individus de *Diospyros mespiliformis* de taille différente. Quatre arbres d'espèces différentes ont été étudiés dans les deltas moyens et supérieur. La densité du flux de sève (DFS), flux par unité de surface de section, a servi d'unité commune pour faciliter la comparaison. Le flux de sève variait avec la taille et l'espèce des arbres, la saison et l'emplacement. Il était positivement lié à la taille des arbres ($r^2 = 0,67$). La variation du flux de sève avec les saisons et l'emplacement indiquait deux groupes distincts parmi toutes les espèces étudiées. Le Groupe 1 transpirait le moins pendant la saison la plus chaude, novembre-décembre, et le Groupe 2 transpirait le plus. Dans le Groupe 1, la DSF moyenne la plus haute était de $1,17 \text{ L/cm}^2/\text{jour}$ en juillet-août; dans le Groupe 2, elle était de $1,07 \text{ L/cm}^2/\text{jour}$ en novembre-décembre. Des changements dans l'hydrologie du delta affecteraient négativement la forêt riveraine.

Introduction

Riparian areas are zones along the edges of streams, rivers and wetlands, which are influenced by their proximity to water. Riparian vegetation, which lies at the interface between terrestrial and aquatic ecosystems, is an essential component of river ecosystems (Cordes, Hughes & Getty, 1997; O'Grady *et al.*, 2002). Water filtration, nutrient cycling, erosion control, maintenance of bank stability and

reduction in turbidity in surface water are some of the key ecosystem services provided by riparian vegetation (Cordes, Hughes & Getty, 1997; O'Grady *et al.*, 2002). These services may be impossible or extremely costly to replace. In the flood-pulsed Okavango Delta, the riparian woodland has been shown to drive critical sequestration of dissolved solids and heavy metals (McCarthy, Bloem & Larkin, 1998; Bauer *et al.*, 2006) through evapotranspirative concentration. Despite the importance of riparian vegetation, very little work has been carried out to examine its water use due to high spatial and temporal heterogeneity within the riparian zone (O'Grady *et al.*, 2002, 2006). Evapotranspiration (ET) is a major component of the water balance for many semi-arid watersheds, and therefore, accurate estimates of ET are vital for sound water resource management (Scott *et al.*, 2008).

The Okavango Delta (hereafter, the Delta) is characterized by high rates of ET, especially from trees on the islands formed within the Delta region. Previous mass-balance studies (McCarthy *et al.*, 1986; McCarthy & Ellery, 1994, 1998; Ringrose, 2003; McCarthy, 2006) indicated that most of the water flowing into the Delta is lost to the atmosphere via evaporation and transpiration. On average, the Okavango River delivers about 10,000 million cubic metres (MCM) of water into the Delta per annum, augmented by about 5000 MCM from local rainfall. Approximately 14,500 MCM per annum is lost via evaporation and transpiration (Dincer, Child & Khupe, 1987). The remaining 200 and 300 MCM are lost to deep groundwater and surface outflow, respectively (Dincer, Child & Khupe, 1987). Potential evapotranspiration (PET) is about 1400 mm per annum, exceeding rainfall by a factor of four (Snowy Mountains Engineering Corporation, 1987). Evaporation leads to water loss from open water and from the soil surface through capillary rise in the barren island centres. In wetlands, floating leaves and emergent vegetation suppress water loss via evaporation from open water ensuring transpiration contributes more to the water loss (Kadlec, 1989). In the Okavango, neither of these components of the water budget has been quantified, but the area of open water is a small fraction (~3%) of the area of floodplains covered by aquatic macrophytes (Gumbricht, McCarthy & McCarthy, 2004; McCarthy, Gumbricht & McCarthy, 2005). Transpiration is a large contributor to water losses, and an important constituent of this transpiration occurs through island fringes, which are dominated by broad-leaved trees (McCarthy & Ellery, 1998).

Riparian ET is thus a major component of the Delta water budget and requires quantification to improve hydrological modelling. However, information on transpiration rates and processes is largely unavailable for the Delta (Ringrose, 2003). The aim of this study was to provide first estimates of water losses through trees in the riparian woodland in the Delta. The questions addressed are as follows:

- 1 How is sap flow related to tree size and species?
- 2 Does sap flow vary spatially in the Delta?
- 3 Does sap flow vary seasonally in different riparian species?

Materials and methods

Site description

The Delta has a semi-arid climate with an average rainfall of 490 mm that falls between October and March. The seasonal flood pulse originating from Angola causes seasonal expansion and contraction of the flooded area, resulting in a zonation of the Delta, with some areas being permanently inundated whilst some are flooded for a part of each year (seasonally) and others may only be occasionally inundated under years of high inflow. This variation is the primary driver of the floodplain vegetation ecology of the Delta (Murray-Hudson, Wolski & Ringrose, 2006). For this study, three sites were investigated along a north-west (NW) south-east (SE) transect from Seronga to Maun, characterized by a major hydrological gradient from wetter in the NW to drier in the SE. That is to say, one site was chosen from each of the three major ecoregions of the Delta. Seronga represented the upper Delta, Nxaraga mid-Delta and Maun lower Delta. Duration and variation of flooding are greatest in Seronga, intermediate in Nxaraga and lowest in Maun, such that Seronga is in a perennially flooded area, whilst Nxaraga and Maun are in areas subject to progressively shorter seasonal flooding (Fig. 1).

Sample trees

We identified the islands from recent imagery available on Google Earth. Work by Tsheboeng, Murray-Hudson & Kashe (2016) informed the choice of common species. Eight different species were studied in total. One individual of each species was studied per site except in Maun where four individuals of different sizes of the same species were

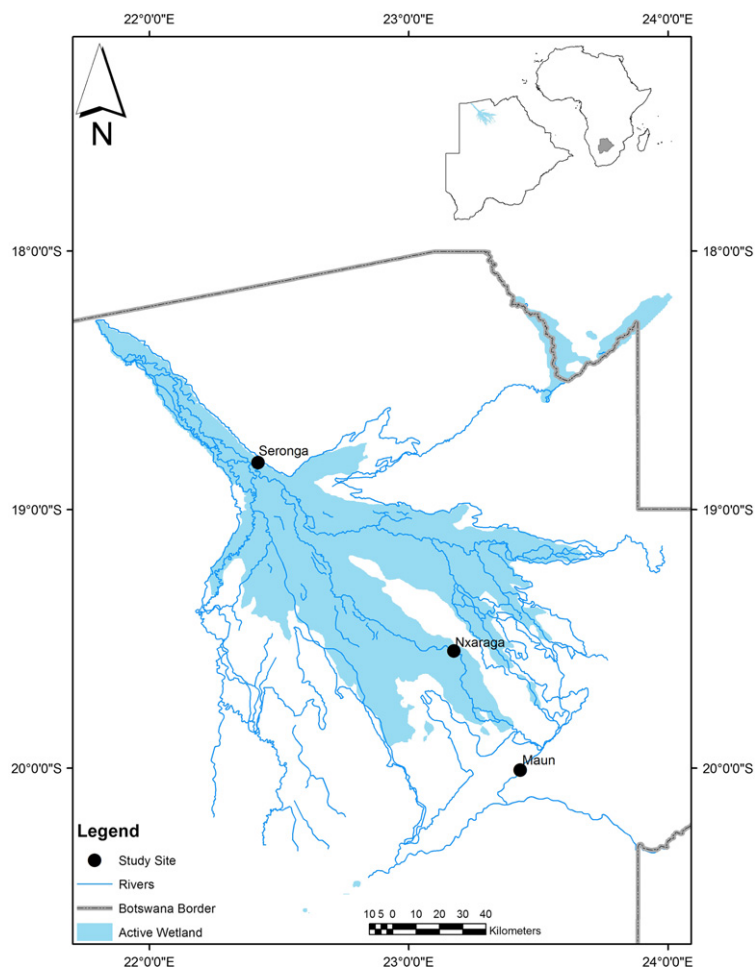


Fig 1 Map of Okavango Delta showing the three study sites: Maun, Nkaraga and Seronga [Colour figure can be viewed at wileyonlinelibrary.com]

investigated. The species were distributed across the sites as indicated in Table 1.

Tree water use

Water use was investigated in July–August 2012, November–December 2012 and February–April 2013 in each study site. Water from the catchment in Angola is discharged into the Delta at the apex, starting to rise around November. The water then moves downwards until it reaches the distal regions 4 months after onset of the pulse at the apex. Hence, water levels vary along the Delta as the flood wave moves downstream. We chose time periods that depict varying water levels in each study site: that is, in each study site, we measured transpiration during low, medium and high water levels. July–August 2012 depicted high water levels, November–December

Table 1 Sample trees and their locations

Distal delta	Mid-delta	Upper delta
<i>Diospyros mespiliformis</i> (4 individuals)	<i>Diospyros mespiliformis</i> <i>Kigelia africana</i> <i>Croton megalobotrys</i> <i>Hyphaene petersiana</i>	<i>Garcinia livingstonei</i> <i>Ekebergia capensis</i> <i>Philenoptera violacea</i> <i>Phoenix reclinata</i>

2012 depicted low water levels and February–April 2013 medium water levels in Maun and Nkaraga. In Seronga, however, July–August 2012 coincided with medium water levels, November–December 2012 low water levels and February–April 2013 high water levels. The compensation heat pulse velocity method (Marshall, 1958; Green, Clothier & Jardine, 2003) was used to estimate sap velocity, which was converted to volumetric sap flow, *Q*. Two pairs of probes (700 SF-100; Tranzflo, Palmerston

North, New Zealand) were inserted per tree. Twenty millimeters-long probes, with sensors at 5 and 15 mm, were inserted into trees with diameters <12 cm. For trees with diameters larger than 12 cm, 50-mm-long probes were used, which had sensors at 5, 15, 25 and 40 mm. Volumetric sap flow was estimated by integrating point measurements over the conductive tissue. Probes were generally inserted at breast height (1.3 m), but for trees that branched lower than this, the probes were inserted below the divergence of the stems.

A line heater was inserted radially into the stem with a thermocouple probe below and above the heater. The upstream probe was located 5 mm away from the heater and the downstream probe 10 mm away. A heat pulse was fired every 30 min and crossover times, t_z , recorded. T_z values were analysed as described by Green, Clothier & Jardine (2003) to give sap velocity, which was converted to flow, Q , by integration. Wound corrections were made using constants as outlined by Swanson & Whitfield (1981). Sap flow was recorded for five consecutive days initially, and after establishing that there were no major variations in sap flow between days, this was reduced to 3 days. A CR1000 Campbell data logger was used to record data. No attempt was made to correct records for short-term variations caused by cloud cover as observed by Poblote-Echeverría *et al.* (2012). Therefore, our data must be interpreted with caution as lack of data on cloud cover may make our estimates too low.

Statistical analyses

The data were tested for normality using the Shapiro–Wilk test. They were found to be normally distributed, $P = 0.092$. Mauchly's test was used to test the data for the assumption of sphericity. The assumption was violated, with $X^2(35) = 5132.914$, and $P < 0.001$. The Greenhouse–Geisser correction (Field, 2009) was therefore applied to the data. There were no significant outliers in the data, and no transformations were made. To determine whether there were significant differences in sap flow between the tree species, seasons and between sites, one-way ANOVA with repeated measures was used. A simple regression model of the relationship between tree size and sap flow was developed.

Results

Sap flow in the studied trees began to increase from minima between 0500 and 0700 h and generally reached a maximum around 1600 h.

Differences in sap flow between tree sizes

Stem cross-sectional area was used as a proxy for size. For comparisons to be made across different-sized trees, sap flow was calculated per unit cross-sectional area, that is sap flux density (SFD). Sap flux density varied with tree size. There was a negative correlation between the two variables, SFD and cross-sectional area ($r = -0.66$, $n = 22$, $P < 0.001$, Fig. 2). The relationship between SFD and cross-sectional area is best described by the function $y = -0.086 \ln(x) + 0.846$ (Fig. 2), where y is SFD in $l\ cm^{-2}\ day^{-1}$ and x is cross-sectional area in cm^2 , and 0.086 and 0.846 are regression constants. For approximately each 3 cm^2 reduction in cross-sectional area, we found 0.001 $l\ day^{-1}$ increase in the SFD; that is, as trees get larger, proportionally less water is moved through them.

Differences in sap flow between species

The repeated-measures ANOVA showed statistically significant differences between SFD and species [$F(2.192, 484.483) = 142.838$, $P < 0.001$]. Although the different species behaved differently in all the seasons, there was an observable contrasting pattern in their SFDs giving rise to two groupings according to the trends they exhibited. Species whose sap flow was lowest during the hottest season, compared to other seasons (November–December 2012), fell into one group, Group 1 (Fig. 3), and those whose sap flow was highest during that period fell into another, Group 2 (Fig. 4). After grouping the species, there were still some statistical differences in sap flow: Group 1 [$F(2.013, 444.854) = 130.445$, $P < 0.001$] and Group 2 [$F(1.812, 605.345) = 28.315$, $P < 0.001$].

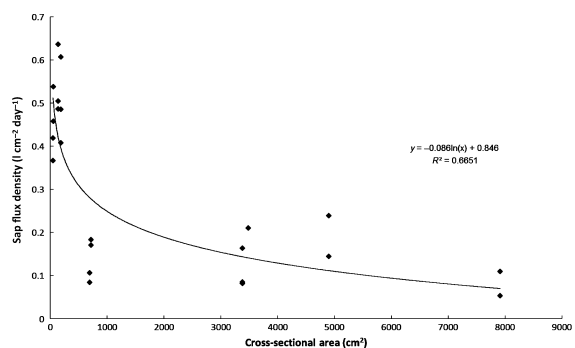


Fig 2 Relationship between cross-sectional area and sap flux density (SFD). sap flux density decreased with increasing cross-sectional area

Differences in sap flow between seasons

Sap flow was highest during high floods in the distal and mid-Delta sites and lowest during low floods. However, in the upper Delta, high and medium floods led to lower sap flow than low floods. Statistically, these differences between sap flow and season were significant as determined by ANOVA [$F(1.809, 1530.517) = 19.293$, $P < 0.001$]. ANOVA also revealed that mean SFD differed statistically significantly between sites [$F(1.736, 1929.137) = 41.404$, $P < 0.001$].

Discussion

Sap flow varied with species, tree size, season and site. These findings are similar to those found by O'Grady *et al.* (2002), who examined spatial and temporal patterns of

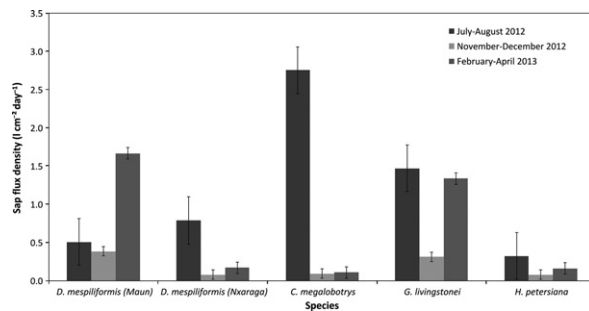


Fig 3 Sap flux densities in Group 1 species. Comparison in sap flow between species that transpired the least in November–December 2012 compared to the other two seasons

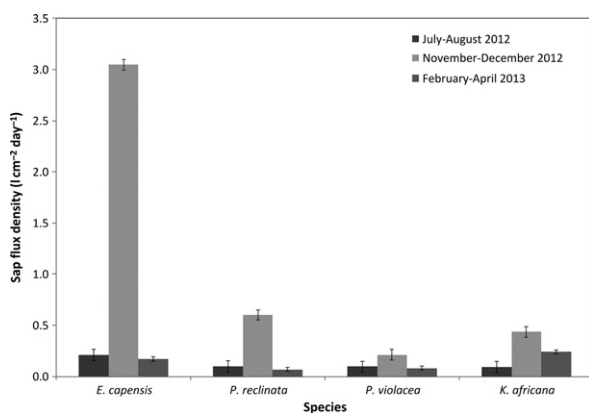


Fig 4 Sap flux densities in Group 2 species. Comparison in sap flow between species that transpired the most during low water stage (Group 2 species)

water use in two riparian trees species, occupying different niches, along the Daly River in northern Australia. They found that water use varied as a function of species, size of tree and time of day.

Differences in sap flow between tree sizes

We found that the larger the cross-sectional area, the lower the SFD, $r^2 = 0.67$ (Fig. 2; $P < 0.001$), consistent with the results of Cermak & Nadezhkina (1998) and Delzon *et al.* (2004), who found that sap flow decreased with increasing depth into the sapwood with the declines greater in large trees than in small ones. This was explained by the fact that active sap-conducting tissue made up most of the cross-sectional area in small trees whilst large trees had heart wood which does not conduct sap. Dye, Olbrich & Poulter (1991), however, hypothesized that the old xylem (which is towards the stem interior) that transported sap to the first branches when the tree was young no longer participates in sap transport once those branches are shaded or dead. It should be noted, however, that the decline in SFD with increasing tree size does not imply a decline in whole-tree water use. The increase in sap wood area with increasing tree size is more than sufficient to compensate for the decrease in SFD, provided SFD does not decline steeply (Meinzer, Goldstein & Andrade, 2001).

It may be postulated, then, that if the Delta riparian woodland was comprised of only large trees (greater than $\sim 700 \text{ cm}^2$), assuming equal tree density, transpiration rates would be significantly reduced leading to low groundwater recharge. On the other hand, if only trees with cross-sectional areas ranging from 50 to 700 cm^2 (these were the size class ranges that exhibited the highest sap flow density)

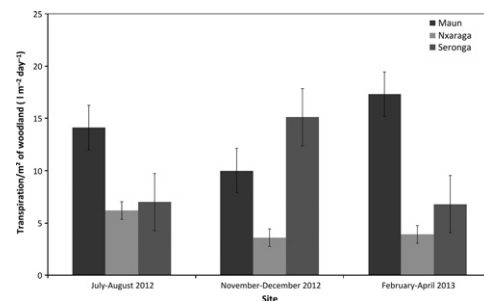


Fig 5 Upscaled transpiration in the three sites. Comparison of transpiration per m^2 of woodland in the three study sites throughout the seasons

made up the riparian woodland, transpiration rates would be higher, creating a greater hydraulic head between floodplains and islands. As a result, water would move at a faster rate from the surrounding swamps towards islands, thereby accelerating the sequestration of solutes under islands. Small trees, however, demonstrate greater sensitivity to environmental factors that influence sap flow such as soil water deficits and increased evaporative demand than large trees (Dawson, 1996). This means that during unfavourable conditions, for example during the hot summer months, water use of the small trees might be greatly reduced due to the sensitivity of the stomata.

Climate change, hydrology, deforestation resulting from growing populations of people living in and around the Delta and a large and rapidly growing population of African elephant, *Loxodontus africanus* (Natural Resources and People, 2007), pose a threat to the health, composition and distribution of the riparian woodland. Tsheboeng, Murray-Hudson & Kashe (2016, unpublished) studied the ecological drivers of population structure, composition and distribution of the Okavango Delta riparian woodland. In their study, although not quantified, they observed more damage by elephants through herbivory, felling of the trees and debarking, thereby eliminating certain tree sizes. In Moremi Game Reserve, elephants are mainly responsible for transforming the woodland structure from trees to shrubs (Ben-Shahar, 1996). Communities living in the Delta rely on the riparian woodland for food, building material and construction of canoes. Overexploitation of these trees to meet the people's needs would upset the composition of the riparian woodland and consequently transpiration. Hydrology is the main factor driving vegetation ecology in the Delta (Ellery, Ellery & McCarthy, 1993). Tsheboeng & Murray-Hudson (2013) indicate that hydrology is one of the factors resulting in varying recruitment patterns of riparian species in the Delta. They found that during high water levels, some species establish but fail to reach maturity after the passage of the floods; that is, low water levels or drying prevents the establishment of the species into larger size classes. However, some species have mechanisms in place to escape this; their developmental stages coincide with favourable conditions. Therefore, it is important to maintain the Delta's hydrology as is.

Differences in sap flow between species

As mentioned earlier, species were grouped according to the contrasting patterns in their SFDs during November–

December 2012, which coincides with summer. Looking at individual species, some transpired the most during that period, which would be expected given high temperatures during summer, whilst others transpired the least. These groupings indicate that some species are least affected by unfavourable conditions, hence the high SFD, whilst others are sensitive. In Group 1, comparisons in SFD were made between *Croton megalobotrys*, *Diospyros mespiliformis*, *Hyphaene petersiana* and *Garcinia livingstonei*. *Croton megalobotrys* showed the highest SFD during July–August 2012, losing $2.75 \text{ l cm}^{-2} \text{ day}^{-1}$ (Fig. 3). The SFD dropped from $2.75 \text{ l cm}^{-2} \text{ day}^{-1}$ to 0.08 and $0.11 \text{ l cm}^{-2} \text{ day}^{-1}$ during low and medium water levels, respectively. *Croton megalobotrys* may be opportunistic in its water uptake. Opportunistic water uptake patterns allow species to maximize their photosynthesis and growth rates, hence increased transpiration rates during windows of opportunity, which in this case would be high water levels.

Ekebergia capensis, which was in Group 2 (high hot season SFD), exhibited the highest SFD of all species measured, $3.05 \text{ l cm}^{-2} \text{ day}^{-1}$ (Fig. 4), during November–December 2012. In the other seasons, the mean SFD recorded for *E. capensis* was 0.21 and $0.17 \text{ l cm}^{-2} \text{ day}^{-1}$ in July–August 2012 and February–April 2013, respectively. This species thrives where water is in abundance and has a dense, flattish crown (Orwa *et al.*, 2009). It produces succulent fruits in December, the time when measurements for November–December 2012 were taken. Thus, the larger sap flows may have been in support of fruit development as some trees require more water for the production of fruits (Woods *et al.*, 2005). The leaves, which were green during the hot November–December period, were showing yellowing due to senescence during July–August.

Changes in sap flow with season

Transpiration varies within and between days, largely due to changing weather conditions, primarily humidity and temperature (Shuttleworth, 1988). Increases in temperature lead to increases in transpiration. A lowering of air temperature results in a rise in relative humidity (RH). Unlike temperature, high RH inhibits transpiration, whilst low RH results in high transpiration. Light is yet another driver of transpiration as it triggers the opening of the stomata. Longer day lengths would mean stomata are open for longer producing higher net transpiration.

Therefore, normally, sap flow might be expected to be higher in summer (when air and soil temperatures are high and days longer) than in winter when temperatures are cool. However, we found that sap flow rates were generally higher during winter (July–August 2012) than summer (November–December 2012) in the mid- and distal Delta. Trees have mechanisms, structural and physiological, in place to minimize water loss during unfavourable conditions; thus, low sap flow rates were recorded in the hot summer. Physiological control occurs when changes in stomatal conductance (measure of the rate of passage of carbon dioxide or water vapour through the stomata of a leaf) result in changes in water vapour flux from the surface of vegetation (Smith & Jarvis, 1998). The stomata open and close in response to a variety of environmental factors; they close with temperatures warmer and colder than some optimal value. Low sap flow rates shown by our results during low water level (summer) indicate that the trees' stomatal conductance decreased. Structural mechanisms that help regulate water losses in trees include thick, hard leaves, often with few stomata. All of our studied trees had leathery, glossy leaves except *C. megalobotrys*. *Croton megalobotrys* is a deciduous tree that sheds its leaves in the dry season to minimize water loss and the rest of the trees are semi-deciduous or evergreen trees that do not lose their leaves hence the glossy hard leaves designed to minimize water loss.

David *et al.* (2004) studied seasonal sap flow patterns of an evergreen oak tree in Southern Portugal, and found transpiration rates were high in summer and declined in winter, contrary to what we found. This may simply be attributable to the Mediterranean climate in Southern Portugal with wet winters and dry summers, whereas in Botswana, the climate is subtropical with rainfall occurring in the hot summers and cool dry winters. This suggests that rainfall might have been a significant factor influencing declines in sap flow in both studies. In the Delta, rainfall might have contributed to the lower sap flows observed in summer, by depressing transpiration due to high RH. Cloud cover has also been observed to depress sap flow rates (Wullschleger, Wilson & Hanson, 2000). Unfortunately, we were unable to collect information on insolation, and so could not separate these two effects in this study. Poblete-Echeverría *et al.* (2012) have found strong variations in SFD which they attributed to cloud cover. They had measured solar radiation, which informed their conclusion that cloud cover influenced the variations they observed, using a silicon pyranometer. Having a full

meteorological station on site would help examine the effect of cloud cover on SFD. With climate change predictions of warmer, drier summers, and the fact that climate change might affect the pattern and temporal distribution of precipitation (Naumburg *et al.*, 2005), it may be expected that transpiration in the Delta will increase due to the warmer temperatures and the dry atmosphere until water is limiting.

In the Delta, the seasonal flood pulse from Angola provides water for transpiration. Sap flow was found to be high during high water levels despite suggestions by Ringrose (2003) that relatively little water is lost during that time. Ringrose (2003) found low reflectance values from trees in the distal Delta, indicating low available plant moisture, and interpreted this to imply low water use. This suggests that they considered sap flow to be independent of flood level and that rainfall might have contributed to lowering sap flow rates, not necessarily by increasing the amount of water available to drive sap flow, raising the water table, but by creating a humid, cool environment. On the other hand, Ringrose (2003) studied trees in the distal Delta (in September 2000) and the flood may have not reached their study area. This would mean that the water tables were depressed. During winter, there is relatively little available energy to drive ET. Coupling that with depressed water tables might result in low sap flow rates. On the other hand, summer coincides with low water levels. Although temperatures are higher and day length longer in summer than winter, trees have to draw water from greater depths as groundwater levels are low.

In the upper Delta, the results indicate that the higher the water level, the lower the sap flow. During the periods November–December 2012 and February–April 2013, water was abundant but sap flow recorded in both seasons was lower than in November–December 2012 when it was dry. With abundant water available, it would be expected that there be no physical limit to sap flow. During the high and medium flood stages, water was not only confined to the channel, but also spilled onto the islands. The local RH may therefore have been influenced by the abundance of surface water and the fault-bounded trough that gives the Panhandle its form resulting in the establishment of a localized microclimate with higher RH when the flood stage is high. High RH would lead to lowered evaporative demand hence low sap flow.

The seasonal flood which characterizes the Delta into the varying seasons (low, medium and high water levels) recharges the groundwater, and therefore, flood frequency

is taken as being indicative of groundwater recharge. The absence of flooding infers groundwater table lowering. Lowered groundwater levels may lead to a decline in pioneer species (Stromberg, Tiller & Richter, 1996), as riparian vegetation is sensitive to changes in the hydrological regime (Horton, Kolb & Hart, 2001), which means that species studied in this study may be lost if and when changes in the hydrology of the Delta occur. Cottonwoods, pioneer species in western North America, have been found to show a significant decline in their population due to river damming and water diversion along many rivers (Rood & Mahoney, 1990). Changes in the timing of floods may be enough to cause significant environmental change (Nilsson & Berggren, 2000). As climate change might affect the temporal distribution of precipitation, the flooding regime in the Delta might change. Changes in the flooding regime would lead to changes in the vegetation ecology of the Delta and consequently transpiration which will in turn affect the sequestration of toxic salts performed by the riparian woodland.

Conclusions

We have provided the first quantification of water fluxes through the common riparian woody species of the Okavango Delta from which the bulk of water is lost to the atmosphere via ET, especially from riparian woodlands. Hence, we have provided critical information needed for reducing uncertainty in hydrological modelling of the Delta and given insights for evapotranspirative losses in other subtropical wetlands.

Sap flow varied spatially and as a function of tree size. Size-related differences in water use from individual trees influence whole-stand transpiration and ultimately the whole ecosystem. Assuming equal density, riparian woodland comprised of only large trees in the Delta would lead to decreased transpiration rates, which might lead to salinization of water which people, flora and fauna are dependent on. Conversely, if Delta woodland was comprised of only young trees, transpiration rates would increase leading to decreased rates of salinization of water in the Delta and accelerated sequestration of salts in deep groundwater. However, small trees are more sensitive to unfavourable environmental conditions than large ones. Clearly, a population of riparian trees with active recruitment and larger numbers of small size classes but retaining large individuals is a desirable state for Delta ET processes.

Sap flow varied with season. Low sap flow rates were recorded in summer. The low sap flow in the summer might have been due to physiological responses of the trees to the high temperatures and limited access to groundwater as summer coincides with low water levels. Transpiration is an inevitable consequence of photosynthesis. Plants need to take in carbon dioxide from the atmosphere in order to photosynthesize through open stomata, through which water leaves the plant (Hemsley & Poole, 2004). Therefore, plants need to employ mechanisms to maintain their water balance throughout the seasons especially in arid regions where ET exceeds rainfall, so as not to compromise their requirements for metabolism and growth (Dawson, 1993). Low sap flow rates shown by our results during low water level (summer) indicate that the trees' stomatal conductance decreased, and the trees actually closed their stomata as possibly demand exceeded supply to prevent desiccation. With water tables low during that time, the trees had to draw water at a depth, and at the same time, temperatures were high therefore the need for the plant to cool off high. This means that transpiration during this time was limited by either water availability or physiological restrictions such as reduced stomatal conductance as a consequence of high temperatures. However, as mentioned before, these data must be treated with caution as lack of data on cloud cover may have resulted in less variability in SFD and low net transpiration rates. Climate change predictions of warmer, drier summers (Nisbet & Britain, 2005) imply that, provided water is not limiting, transpiration rates will increase due to high temperatures and lower RH. Climate change might also affect the pattern and temporal distribution of precipitation in the catchment and the Delta itself and thus groundwater recharge (Naumburg *et al.*, 2005) although this is less certain than the increase in temperatures. Reduced precipitation will cause a decrease in flooding frequency, which will result in declines in groundwater levels. Continued lowering of the water table may be detrimental to the Delta as lowered groundwater levels can reduce riparian plant growth or even lead to death of the riparian vegetation (Scott, Shafroth & Auble, 1999).

Water table lowering may also be due to anthropogenic reasons. Should there be major developments upstream of the Delta such as damming and large-scale irrigation schemes, riparian areas downstream will be negatively affected. As a consequence of damming and large irrigation schemes, the volume of water coming into the Delta

would be reduced leading to declining water tables. Declining water tables will cause stress in trees as they have to invest more energy in accessing a permanent water source (Naumburg *et al.*, 2005). This might result in a shift from tree species that rely primarily on groundwater (obligate phreatophytes) to a community of shallow-rooted species or those that use both water from the saturated and unsaturated zones (facultative phreatophytes). Obligate phreatophytes may be lost if the water table declines beyond a threshold giving way to a new community.

References

- BAUER, P., SUPPER, R., ZIMMERMANN, S. & KINZELBACH, W. (2006) Geoelectrical imaging of groundwater salinization in the Okavango Delta, Botswana. *J. Appl. Geophys.* **60**, 126–141.
- BEN-SHAHAR, R. (1996) Woodland dynamics under the influence of elephants and fire in northern Botswana. *Vegetation* **123**, 153–163.
- CERMAK, J. & NADEZHINA, N. (1998) Sapwood as the scaling parameter-defining according to xylem water content or radial pattern of sap flow?. *Ann. Sci. For.* **55**, 509–521.
- CORDES, L., HUGHES, F. & GETTY, M. (1997) Factors affecting the regeneration and distribution of riparian woodlands along a northern prairie river: the Red Deer River, Alberta, Canada. *J. Biogeogr.* **24**, 675–695.
- DAVID, T., FERREIRA, M., COHEN, S., PEREIRA, J. & DAVID, J. (2004) Constraints on transpiration from an evergreen oak tree in southern Portugal. *Agric. For. Meteorol.* **122**, 193–205.
- DAWSON, T.E. (1993) Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia* **95**, 565–574.
- DAWSON, T.E. (1996) Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiol.* **16**, 263–272.
- DELZON, S., SARTORE, M., GRANIER, A. & LOUSTAU, D. (2004) Radial profiles of sap flow with increasing tree size in maritime pine. *Tree Physiol.* **24**, 1285–1293.
- DINCER, T., CHILD, S. & KHUPE, B. (1987) A simple mathematical model of a complex hydrologic system - Okavango Swamp, Botswana. *J. Hydrol.* **93**, 41–65.
- DYE, P., OLBRICH, B. & POULTER, A. (1991) The influence of growth rings in *Pinus patula* on heat pulse velocity and sap flow measurement. *J. Exp. Bot.* **42**, 867–870.
- ELLERY, W.N., ELLERY, K. & MCCARTHY, T.S. (1993) Plant distribution in islands of the Okavango Delta, Botswana: determinants and feedback interactions. *Afr. J. Ecol.* **31**, 118–134.
- FIELD, A.P. (2009) *Discovering Statistics using SPSS*. SAGE publications, Los Angeles.
- GREEN, S., CLOTHIER, B. & JARDINE, B. (2003) Theory and practical application of heat pulse to measure sap flow. *Agron. J.* **95**, 1371–1379.
- GUMBRICHT, T., MCCARTHY, J. & MCCARTHY, T.S. (2004) Channels, wetlands and islands in the Okavango Delta, Botswana, and their relation to hydrological and sedimentological processes. *Earth Surf. Proc. Land.* **29**, 15–29.
- HEMSLEY, A.R. & POOLE, I.E. (Eds.) (2004) *The Evolution of Plant Physiology*. Academic Press, Cambridge, MA.
- HORTON, J., KOLB, T. & HART, S. (2001) Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. *Plant, Cell Environ.* **24**, 293–304.
- KADLEC, R.H. (1989) Hydrologic factors in wetland water treatment. In: (Ed. HAMMER D. A.). *Constructed Wetlands for Wastewater Treatment: Municipal, Industrial and Agricultural*, 21–40. CRC Press, Boca Raton, FL.
- MARSHALL, D.C. (1958) Measurement of sap flow in conifers by heat transport. *Plant Physiol.* **33**, 385–396.
- MCCARTHY, T. (2006) Groundwater in the wetlands of the Okavango Delta, Botswana, and its contribution to the structure and function of the ecosystem. *J. Hydrol.* **320**, 264–282.
- MCCARTHY, T.S., BLOEM, A. & LARKIN, P.A. (1998) Observations on the hydrology and geohydrology of the Okavango Delta. *S. Afr. J. Geol.* **101**, 101–117.
- MCCARTHY, T.S. & ELLERY, W.N. (1994) The effect of vegetation on soil and ground water chemistry and hydrology of islands in the seasonal swamps of the Okavango Fan, Botswana. *J. Hydrol.* **154**, 169–193.
- MCCARTHY, T. & ELLERY, W. (1998) The Okavango Delta. *Trans. R. Soc. S. Afr.* **53**, 157–182.
- MCCARTHY, J., GUMBRICHT, T. & MCCARTHY, T.S. (2005) Ecoregion classification in the Okavango Delta, Botswana from multitemporal remote sensing. *Int. J. Remote Sens.* **26**, 4339–4357.
- MCCARTHY, T.S., ELLERY, W.N., ROGERS, K.H., CAIRNCROSS, B. & ELLERY, K. (1986) The roles of sedimentation and plant growth in changing flow patterns in the Okavango Delta, Botswana. *S. Afr. J. Sci.* **82**, 579–584.
- MEINZER, F., GOLDSTEIN, G. & ANDRADE, J. (2001) Regulation of water flux through tropical forest canopy trees: do universal rules apply? *Tree Physiol.* **21**, 19–26.
- MURRAY-HUDSON, M., WOLSKI, P. & RINGROSE, S. (2006) Scenarios of the impact of local and upstream changes in climate and water use on hydro-ecology in the Okavango Delta, Botswana. *J. Hydrol. Water Resources in Regional Development: The Okavango River*. **331**, 73–84.
- Natural resources and people (2007) Okavango Delta management plan component 5 final report-wildlife Management-Human-Wildlife Conflict. Department of Wildlife and National parks, Ministry of Environment, Wildlife and Tourism, Gaborone, Botswana.
- NAUMBURG, E., MATA-GONZALEZ, R., HUNTER, R.G., MCLONDON, T. & MARTIN, D.W. (2005) Phreatophytic vegetation and groundwater fluctuations: a review of current research and application of ecosystem response modeling with an emphasis on Great Basin vegetation. *Environ. Manage.* **35**, 726–740.

- NILSSON, C. & BERGGREN, K. (2000) Alterations of riparian ecosystems caused by river regulation dam operations have caused global-scale ecological changes in riparian ecosystems. How to protect river environments and human needs of rivers remains one of the most important questions of our time. *Bioscience* **50**, 783–792.
- NISBET, T. & BRITAIN, G. (2005) Water use by trees. Forestry Commission.
- O'GRADY, A., EAMUS, D., COOK, P., LAMONTAGNE, S., KELLEY, G. & HUTLEY, L. (2002) Tree water use and sources of transpired water in riparian vegetation along the Daly River, Northern Territory. Department of the Environment, Water, Heritage and the Arts.
- O'GRADY, A.P., EAMUS, D., COOK, P.G. & LAMONTAGNE, S. (2006) Comparative water use by the riparian trees *Melaleuca argentea* and *Corymbia bella* in the wet-dry tropics of northern Australia. *Tree Physiol.* **26**, 219–228.
- ORWA, C., MUTUA, A., KINDT, R., JAMNADASS, R. & SIMONS, A. (2009) Agroforestry database: a tree reference and selection guide version 4.0. 2009. Available at: <http://www.worldagroforestry.org/af/treedb/> (Accessed on 15 February 2011).
- POBLETE-ECHEVERRÍA, C., ORTEGA-FARIAS, S., ZUÑIGA, M. & FUENTES, S. (2012) Evaluation of compensated heat-pulse velocity method to determine vine transpiration using combined measurements of eddy covariance system and microlysimeters. *Agric. Water Manag.* **109**, 11–19.
- RINGROSE, S. (2003) Characterisation of riparian woodlands and their potential water loss in the distal Okavango Delta, Botswana. *Appl. Geogr.* **32**, 281–302.
- ROOD, S.B. & MAHONEY, J.M. (1990) Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. *Environ. Manage.* **14**, 451–464.
- SCOTT, M.L., SHAFROTH, P.B. & AUBLE, G.T. (1999) Responses of riparian cottonwoods to alluvial water table declines. *Environ. Manage.* **23**, 347–358.
- SCOTT, R.L., CABLE, W.L., HUXMAN, T.E., NAGLER, P.L., HERNANDEZ, M. & GOODRICH, D.C. (2008) Multiyear riparian evapotranspiration and groundwater use for a semiarid watershed. *J. Arid Environ.* **72**, 1232–1246.
- SHUTTLEWORTH, W.J. (1988) Evaporation from Amazonian rainforest. *Proc. R. Soc. Lond. B Biol. Sci.*, **233**, 321–346.
- SMITH, D.M. & JARVIS, P.G. (1998) Physiological and environmental control of transpiration by trees in windbreaks. *For. Ecol. Manage.* **105**, 159–173.
- Snowy Mountains Engineering Corporation (1987) *Study of Open Water Evaporation in Botswana*. Ministry of Mineral Resources and Water Affairs, Department of Water Affairs, Gaborone, Botswana.
- STROMBERG, J., TILLER, R. & RICHTER, B. (1996) Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. *Ecol. Appl.* **6**, 113–131.
- SWANSON, R. & WHITFIELD, D. (1981) A numerical analysis of heat pulse velocity theory and practice. *J. Exp. Bot.* **32**, 221–239.
- TSHEBOENG, G. & MURRAY-HUDSON, M. (2013) Spatial variation of population size structure of selected riparian tree species in the Okavango Delta, Botswana. *Biodivers. Ecol.* **5**, 341–350.
- TSHEBOENG, G., MURRAY-HUDSON, M. & KASHE, K. (2016) A baseline classification of riparian woodland plant communities in the Okavango Delta, Botswana. *South For.* **28**, 1–8.
- WOODS, B., LACEY, I.B., BROCKWAY, C.A. & JOHNSTONE, C.P. (2005) Hosts of mediterranean fruit fly *Ceratitidis capitata* (Wiedemann) (Diptera: Tephritidae) from Broome and the Broome Peninsula, Western Australia. *Aust. J. Entomol.* **44**, 437–441.
- WULLSCHLEGER, S.D., WILSON, K.B. & HANSON, P.J. (2000) Environmental control of whole-plant transpiration, canopy conductance and estimates of the decoupling coefficient for large red maple trees. *Agric. For. Meteorol.* **104**, 157–168.

(Manuscript accepted 23 November 2016)

doi: 10.1111/aje.12401